Approximating the periodic solutions of the Lotka–Volterra system

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Abstract

The two dimensional Poincaré–Lindstedt method is used to obtain approximate solutions to the periodic solutions of the Lotka–Volterra predator-prey system near the non-trivial critical point. These approximations are then used to analyze the behaviour of these solutions and provide a convenient way to describe general solution properties not available from numerical computations.

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1 Introduction

The general Lotka–Volterra equations [2, 3, 6, e.g.] constitute the simplest differential equation system for modelling the results of a two species interaction in which one species is preyed upon by the other. While these equations are too idealized to accurately model real-world communities, they do display some features that make them worthy of continued study. In particular, these equations display periodic solutions (albeit *structurally unstable* ones, in the sense that small logistic perturbations destroy the periodicity). While this system is simple, it is not possible in general to obtain closed form exact solutions (although an implicit solution may be found—see below), and numerical solutions must be used.

This system has one non-trivial critical point (equilibrium), with the periodic solutions forming closed orbits encircling this point in the phase plane. Close to the critical point, orbits are approximately ellipses, with distortion increasing with distance from that point. This prompts analysis close to this point by perturbation methods. While this has been done by Murty, Rao and Willson [4, 9], the results are unnecessarily complicated and hard to visualize. In a different approach, Rothe and Waldvogel [5, 7, 8] directed effort toward calculation of the orbital period. Section 2 applies the Poincaré–Lindstedt method [1] to obtain approximate expressions for the solutions to this system near to the critical point. Their phase plane representation may then be compared with the exact first integral (4). An important by-product of the method is an approximation to the period.

The general Lotka–Volterra system is

$$\frac{dX(T)}{dT} = X(T)\,(a - bY(T))\,, \quad \frac{dY(T)}{dT} = Y(T)\,(cX(T) - d) \tag{1}$$

where a, b, c and d are positive constants. We nondimensionalise the system by defining the following variables [3]

$$x(t) = \frac{cX(T)}{d}\,, \quad y(t) = \frac{bY(T)}{a}\,, \quad t = aT, \quad \alpha = \frac{d}{a}\,. \tag{2}$$

Then the nondimensional Lotka–Volterra system becomes

$$\frac{dx(t)}{dt} = x(t) - x(t)y(t)\,, \quad \frac{dy(t)}{dt} = -\alpha y(t) + \alpha x(t)y(t)\,. \tag{3}$$

The system (3) may be solved to give a family of implicit solutions linking x and y of the form

$$\ln y - \alpha \ln x + \alpha x - y = \text{constant}\,; \tag{4}$$

but this reveals little of the separate behaviour of x and y as functions of t.

The nonzero critical point of this system occurs at $x(t) = y(t) = 1$. In order to analyze the behaviour of the system in the close neighbourhood of this critical point $(1,1)$ we perturb the system near $(1,1)$, that is, we put

$$x(t) = 1 + \varepsilon\xi(t)\,, \quad y(t) = 1 + \varepsilon\eta(t)\,, \tag{5}$$

where ε is small. Thus (5) becomes,

$$\frac{d\xi(t)}{dt} = -\eta(t) - \varepsilon\xi(t)\eta(t)\,, \quad \frac{d\eta(t)}{dt} = \alpha\xi(t) + \varepsilon\alpha\xi(t)\eta(t)\,. \tag{6}$$

We can see from (6) that if we ignore the non-linear terms (or put $\varepsilon = 0$) the system has a solution which has a period of $2\pi/\sqrt{\alpha}$ and a frequency of $\sqrt{\alpha}$.

2 Analysis using the Poincaré–Lindstedt method

Since we expect our solutions of (6) to have a period of approximately $2\pi/\sqrt{\alpha}$ and a frequency of approximately $\sqrt{\alpha}$, we introduce a new time scale

$$\tau = \omega t\,, \tag{7}$$

where ω depends on ε; that is, $\omega = \omega(\varepsilon)$ and $\omega(0) = \sqrt{\alpha}$. Thus, the transformed solutions are 2π periodic in τ, since $0 \le t \le 2\pi/\sqrt{\alpha}$ corresponds to $0 \le \tau \le 2\pi$. With this new time scale the non-linear system (6) becomes

$$\omega\frac{d\xi(\tau)}{d\tau} = -\eta(\tau) - \varepsilon\xi(\tau)\eta(\tau)\,, \quad \omega\frac{d\eta(\tau)}{d\tau} = \alpha\xi(\tau) + \varepsilon\alpha\xi(\tau)\eta(\tau)\,. \tag{8}$$

Thus we seek solutions of the form

$$\begin{aligned} \xi(\tau) &= \xi_0 + \varepsilon\xi_1 + \varepsilon^2\xi_2 + \cdots\,, \\ \eta(\tau) &= \eta_0 + \varepsilon\eta_1 + \varepsilon^2\eta_2 + \cdots\,, \\ \omega &= \sqrt{\alpha} + \varepsilon\omega_1 + \varepsilon^2\omega_2 + \cdots\,, \end{aligned} \tag{9}$$

where $\xi_i = \xi_i(\tau)$ and $\eta_i = \eta_i(\tau)$ are 2π periodic in τ. Now substituting these expansions into (8) and collecting like powers of ε we obtain a sequence of differential equations. From the leading $O(1)$ terms we get

$$\sqrt{\alpha}\frac{d\xi_0}{d\tau} = -\eta_0\,, \quad \sqrt{\alpha}\frac{d\eta_0}{d\tau} = \alpha\xi_0\,; \tag{10}$$

from the $O(\varepsilon)$ terms,

$$\omega_1\frac{d\xi_0}{d\tau} + \sqrt{\alpha}\frac{d\xi_1}{d\tau} = -\eta_1 - \xi_0\eta_0\,, \quad \omega_1\frac{d\eta_0}{d\tau} + \sqrt{\alpha}\frac{d\eta_1}{d\tau} = \alpha\xi_1 + \alpha\xi_0\eta_0\,; \tag{11}$$

and from the $O(\varepsilon^2)$ terms,

$$\omega_2\frac{d\xi_0}{d\tau} + \omega_1\frac{d\xi_1}{d\tau} + \sqrt{\alpha}\frac{d\xi_2}{d\tau} = -\eta_2 - \xi_0\eta_1 - \xi_1\eta_0\,,$$

$$\omega_2\frac{d\eta_0}{d\tau}+\omega_1\frac{d\eta_1}{d\tau}+\sqrt{\alpha}\frac{d\eta_2}{d\tau}=\alpha\xi_2+\alpha\xi_0\eta_1+\alpha\xi_1\eta_0\,. \qquad (12)$$

The two dimensional linear system (10) has solutions

$$\xi_0=A\cos(\tau+\phi)\,,\quad \eta_0=A\sqrt{\alpha}\sin(\tau+\phi) \qquad (13)$$

where A and ϕ are arbitrary constants, which are found by the initial conditions. On substituting the solutions (13) into (11) we obtain the following differential equations

$$\begin{aligned}\sqrt{\alpha}\frac{d\xi_1}{d\tau}+\eta_1&=\omega_1A\sin(\tau+\phi)-\frac{A^2\sqrt{\alpha}}{2}\sin 2(\tau+\phi)\,,\\ \sqrt{\alpha}\frac{d\eta_1}{d\tau}-\alpha\xi_1&=-\omega_1A\sqrt{\alpha}\cos(\tau+\phi)+\frac{A^2\alpha\sqrt{\alpha}}{2}\sin 2(\tau+\phi)\,. \qquad (14)\end{aligned}$$

At this point, we introduce the following simple result.

Lemma 1 *For the system*

$$\begin{aligned}\frac{dx}{dt}+y&=A\sin t+B\cos t+\textit{higher harmonics}\,,\\ \frac{dy}{dt}-x&=C\sin t+D\cos t+\textit{higher harmonics}\;,\end{aligned}$$

to have periodic solutions, it is necessary and sufficient that

$$A-D=0\quad\textit{and}\quad B+C=0\,.$$

This may be easily proved by reducing this system to an equivalent single second order equation and invoking the relationships between A, B, C, D required for a periodic solution.

Applying the lemma (suitably adapted with $x=\sqrt{\alpha}\,\xi_1\,, y=\eta_1$), we see that the system (14) will have 2π periodic solutions only if we choose $\omega_1=0$, giving

$$\xi_1=\frac{A^2\sqrt{\alpha}}{6}\sin 2(\tau+\phi)+\frac{A^2}{3}\cos 2(\tau+\phi)\,,$$

$$\eta_1 = \frac{A^2\sqrt{\alpha}}{6}\sin 2(\tau+\phi) - \frac{A^2\alpha}{3}\cos 2(\tau+\phi)\,. \tag{15}$$

Note that (15) is the *particular solution* of (14), arising from the higher harmonics on the right-hand side of that system. No complementary solution is included. Since the general solution of the original system (6) will involve two arbitrary constants, we expect our approximate solution to reflect this. The solution of (13) involves two such constants (A and ϕ), so we repress the appearance of arbitrary constants in later terms in the sequence $\xi_i(\tau)$ and $\eta_i(\tau)$.

On substituting (15) into (12) and noting $\omega_1 = 0$, we obtain

$$\begin{aligned}
\sqrt{\alpha}\frac{d\xi_2}{d\tau} + \eta_2 &= \left(\omega_2 A + \frac{A^3\sqrt{\alpha}}{12}\right)\sin(\tau+\phi) + \frac{A^3\alpha}{12}\cos(\tau+\phi) \\
&\quad + \frac{A^3\alpha}{4}\cos 3(\tau+\phi) - \frac{A^3\sqrt{\alpha}}{4}\sin 3(\tau+\phi)\,, \\
\sqrt{\alpha}\frac{d\eta_2}{d\tau} - \alpha\xi_2 &= -\frac{A^3\alpha\sqrt{\alpha}}{12}\sin(\tau+\phi) - \left(\omega_2 A\sqrt{\alpha} + \frac{A^3\alpha^2}{12}\right)\cos(\tau+\phi) \\
&\quad - \frac{A^3\alpha^2}{4}\cos 3(\tau+\phi) + \frac{A^3\alpha\sqrt{\alpha}}{4}\sin 3(\tau+\phi)\,.
\end{aligned} \tag{16}$$

Applying the Lemma to (16), we find that to ensure 2π periodic solutions we must choose

$$\omega_2 = -\frac{A^2\sqrt{\alpha}}{24} - \frac{A^2\alpha\sqrt{\alpha}}{24}\,, \tag{17}$$

and so we obtain the following particular solutions

$$\begin{aligned}
\xi_2 &= \frac{A^3\sqrt{\alpha}}{12}\sin(\tau+\phi) + \frac{A^3}{24}(\alpha-1)\cos(\tau+\phi) + \frac{A^3\sqrt{\alpha}}{8}\sin 3(\tau+\phi) \\
&\quad + \frac{A^3}{32}(3-\alpha)\cos 3(\tau+\phi)\,, \\
\eta_2 &= \frac{A^3\sqrt{\alpha}}{32}(1-3\alpha)\sin 3(\tau+\phi) - \frac{A^3\alpha}{8}\cos 3(\tau+\phi)\,.
\end{aligned} \tag{18}$$

A calculation analogous to the above but too long to include here gives $\omega_3 = 0$.

Thus three term approximations to $x = 1 + \varepsilon\xi$ and $y = 1 + \varepsilon\eta$, which have a frequency of ω are

$$\begin{aligned}
x &= 1 + a\cos(\tau+\phi) + \frac{a^2}{3}\left[\frac{\sqrt{\alpha}}{2}\sin 2(\tau+\phi) + \cos 2(\tau+\phi)\right] \\
&\quad + \frac{a^3\sqrt{\alpha}}{12}\sin(\tau+\phi) + \frac{a^3}{24}(\alpha-1)\cos(\tau+\phi) + \frac{a^3\sqrt{\alpha}}{8}\sin 3(\tau+\phi) \\
&\quad + \frac{a^3}{32}(3-\alpha)\cos 3(\tau+\phi) + O(a^3), && (19) \\
y &= 1 + a\sqrt{\alpha}\sin(\tau+\phi) + \frac{a^2\sqrt{\alpha}}{3}\left[\frac{1}{2}\sin 2(\tau+\phi) - \sqrt{\alpha}\cos 2(\tau+\phi)\right] \\
&\quad + a^3\left[\frac{\sqrt{\alpha}}{32}(1-3\alpha)\sin 3(\tau+\phi) - \frac{\alpha}{8}\cos 3(\tau+\phi) + O(a^3)\right], && (20) \\
\omega &= \sqrt{\alpha} - \frac{a^2\sqrt{\alpha}}{24}(1+\alpha) + O(a^4), && (21)
\end{aligned}$$

where $a = \varepsilon A$ may be viewed as the (small) amplitude of the variation of (x, y) from $(1, 1)$.

3 Results and discussion

Using the approximations (19), (20) and (21) we plot the approximate solutions of x and y along with the implicit solution (4) for various initial conditions. Figures 1–3 show the results for the values $\alpha = 0.2$, $\varepsilon = 0.1$ and $\phi = 0$.

Figures 1–3 show that the orbits close to the critical point are virtually elliptical, while as we move further from the critical point we find that the solutions begin to take on more of the typical Lotka–Volterra orbit shape [3]

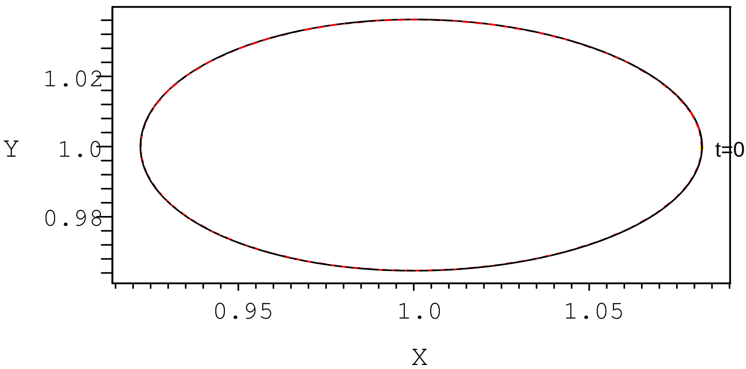

Figure 1: Plot of implicit solution (black) and approximate solution (red dash) using the initial condition $x(0) = 1.08216\,,\ y(0) = 0.99560$ (corresponding to $a = 0.08$).

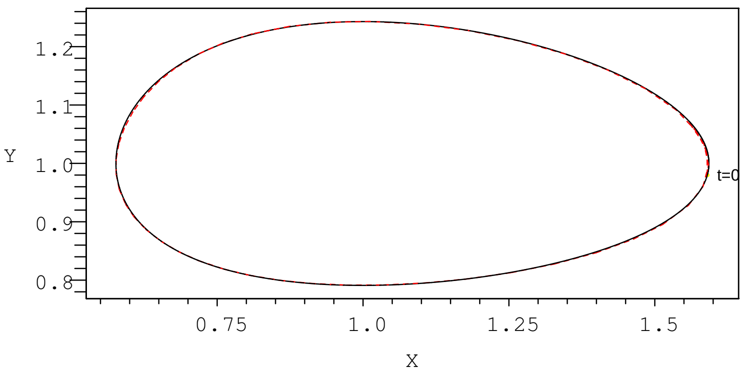

Figure 2: Plot of implicit solution (black) and approximate solution (red dash) using the initial condition $x(0) = 1.59010\,,\ y(0) = 0.98021$ (corresponding to $a = 0.5$).

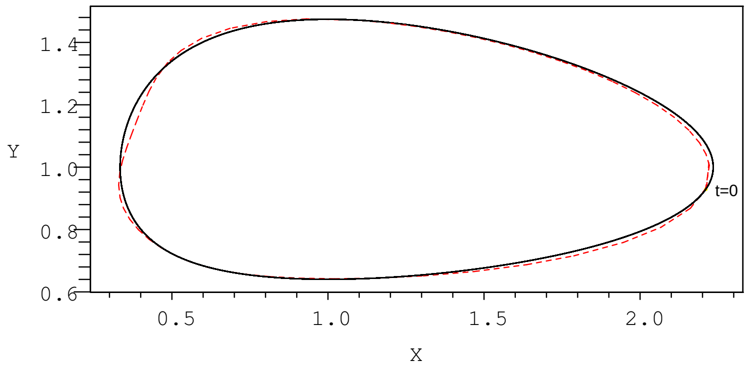

Figure 3: Plot of implicit solution (black) and approximate solution (red dash) using the initial condition $x(0) = 2.20949$, $y(0) = 0.92778$ (corresponding to $a = 0.9$).

that we expect. However, if we use an initial condition that is too far from the critical point (or an amplitude, a, that is too large) then the orbits produced by the approximation deviate from the exact solution. This is to be expected, as the approximate solutions assume that the amplitude is small, so using a large amplitude is forcing the approximation to evaluate something which is outside of its realm of validity.

The plots of Figures 1–3 have been obtained from (19) and (20) by nominating values for a and ϕ. In most cases, initial conditions are given in cartesian form, that is, values $x(0)$ and $y(0)$ are nominated. In such a case, the values for a and ϕ may be found by setting $x = x(0)$ and $y = y(0)$ in (19) and (20) and solving implicitly for a and ϕ. This is most easily done by solving using a package such as Maple and gives approximate values for a and ϕ.

Figures 4–6 compare the approximations for x and y obtained from (19) and (20) with numerical solutions of the Lotka–Volterra system for the various orbits shown in Figures 1–3. The x approximation has a larger amplitude

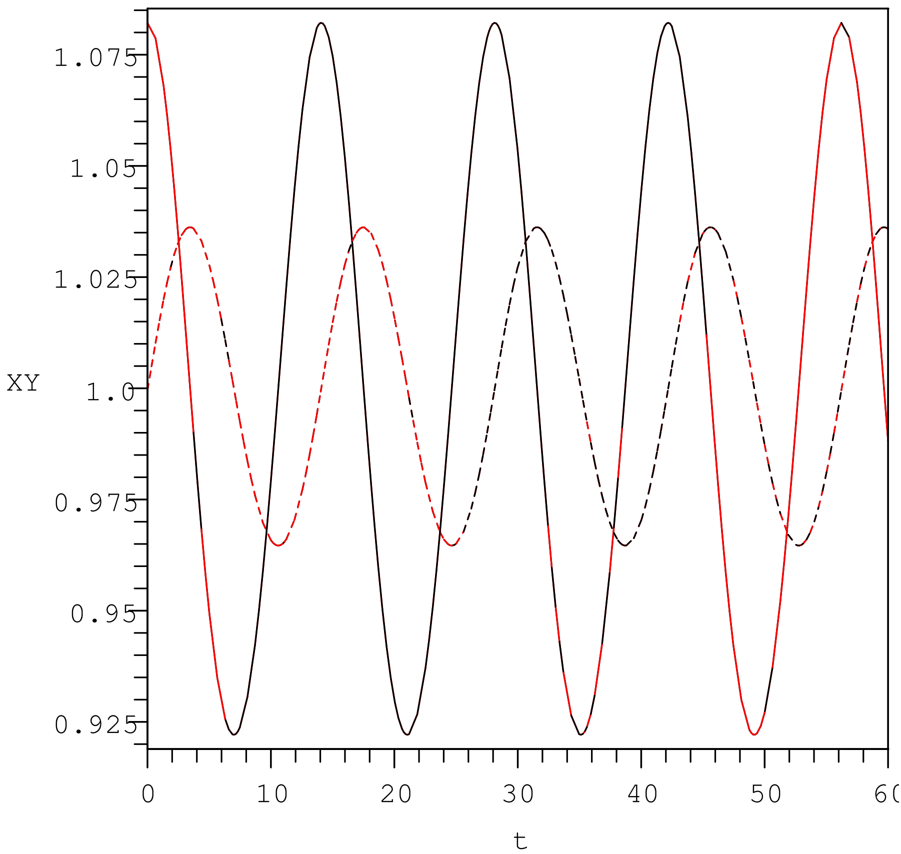

FIGURE 4: Plot of x (solid line) and y (dashed line) for both the implicit (black) and approximate (red) solutions shown in Figure 1.

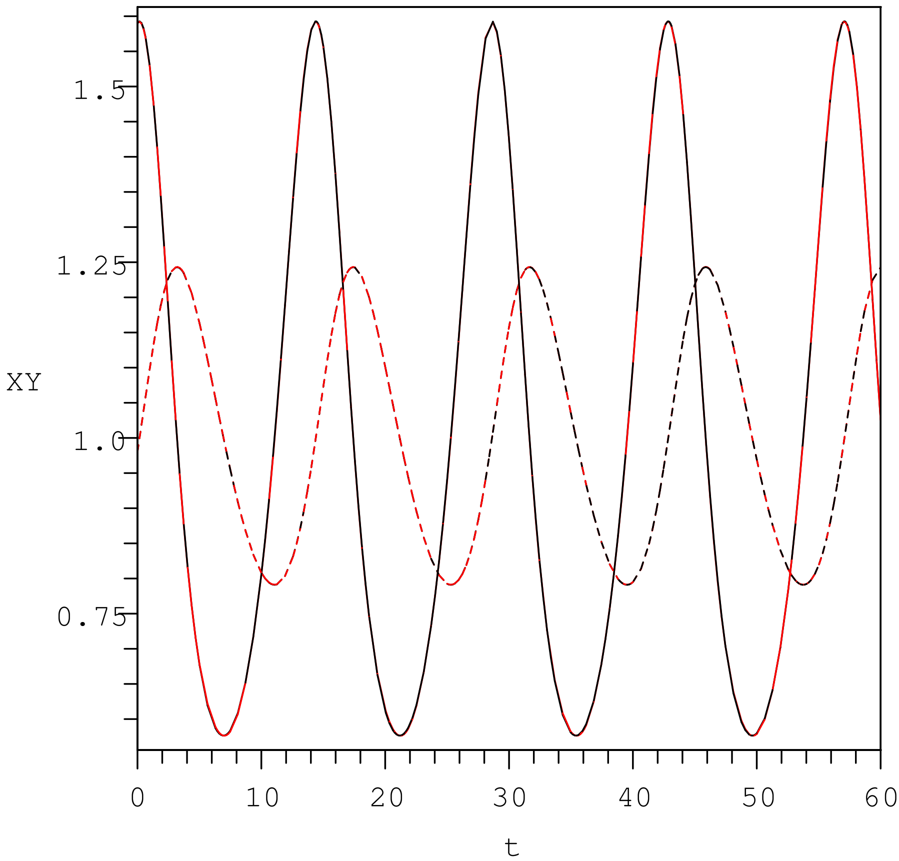

Figure 5: Plot of x (solid line) and y (dashed line) for both the implicit (black) and approximate (red) solutions shown in Figure 2.

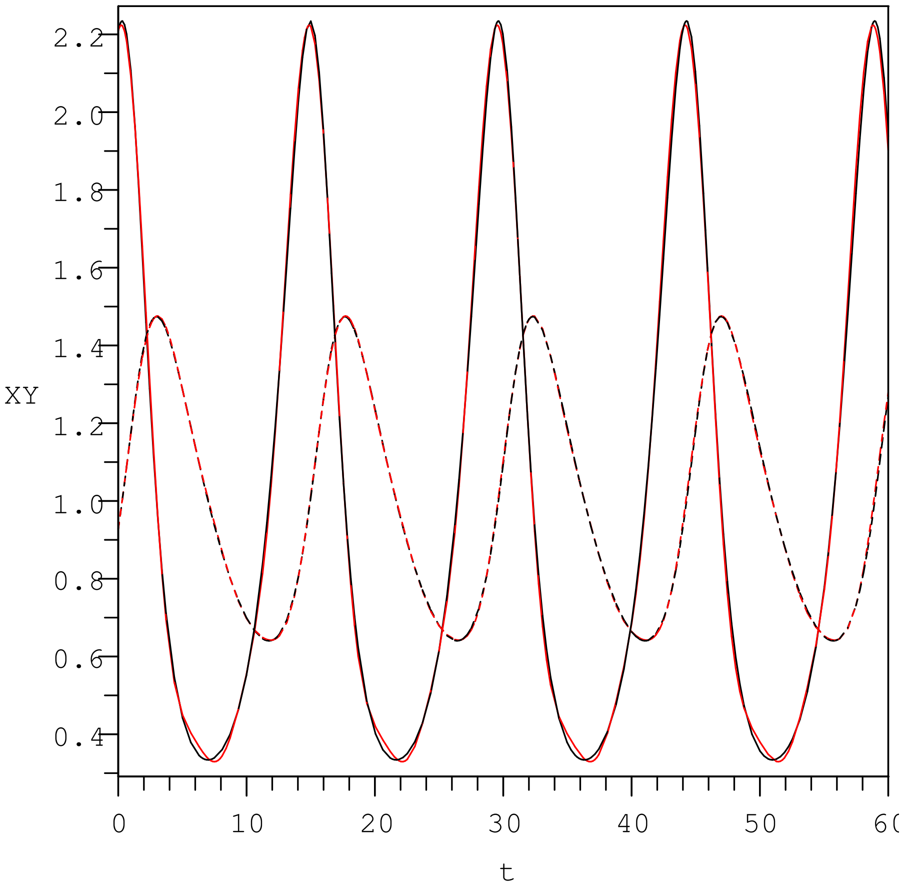

FIGURE 6: Plot of x (solid line) and y (dashed line) for both the implicit (black) and approximate (red) solutions shown in Figure 3.

than the y approximation in Figures 4–6, resulting in the elliptical orbits shown in Figures 1–3. If we consider $\alpha > 1$ then the elliptical orbits will be vertical rather than the horizontal ones we obtained for $\alpha < 1$ meaning that the y approximation will have a larger amplitude than the x; however, if $\alpha = 1$ we obtain circular orbits.

The result (21) gives an approximation to the period T of these orbits as

$$T = \frac{2\pi}{\omega} = \frac{2\pi}{\sqrt{\alpha}[1 - \frac{a^2}{24}(1+\alpha) + O(a^4)]}\,, \tag{22}$$

giving a higher–order approximation to the period for small a. This result also shows that T increases monotonically with a (for small a), in agreement with the findings of Waldvogel [8].

4 Conclusion

The two dimensional Poincaré–Lindstedt method used here has proved to be a successful tool in dealing with this nonlinear system, as it has in many other applications [1] The truncated expansions (19) and (20) provide explicit, readily applicable approximations to the solutions $x(t)$ and $y(t)$ of the Lotka–Volterra predator-prey system near the non-trivial critical point. They compare well with numerically generated solutions in particular cases. However, they are also applicable in a range of the system parameter values, giving information that is only available from numerics after numerous recalculations—and then in a limited way. In particular, the approximation to the period of the solutions (22) gives general information that is just not available from numerical calculations.

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