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Forced Prey-Predator Oscillations*

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Abstract. In this paper existence and stability of subharmonic solutions of the Volterra-Verhulst equations with a periodic coefficient are analyzed by the method of Urabe. The study supports the view that the observed 4- and 10-yr cycles of prey-predator systems are due to seasonal fluctuations.

Key words: Volterra-Verhulst equations — Periodically forced systems — Subharmonic solutions

1. Introduction

In ecology there are many examples of populations having a prey-predator relation for which the densities fluctuate with a more or less fixed period. The example of the snowshoe hare and Canadian lynx with its 10-yr cycle is classical. For other examples, such as the 4-yr cycle of the coloured fox, we refer to Bulmer [3]. For the analysis of density fluctuations use is made of mathematical models such as systems of differential equations describing the dynamics of interacting populations. The Volterra-Lotka equations are known as the simplest model of a prey-predator system with periodic solutions. Let x and y denote, respectively, the prey- and predator density. Then the system of Volterra-Lotka equations reads

$$\frac{dx}{dt} = ax - bxy, \tag{1.1a}$$

$$\frac{dy}{dt} = -cy + dxy, \tag{1.1b}$$

where a, b, c and d denote the parameters of the system. Equations (1.1) have a one parameter family of periodic solutions depending on the initial values of the system. At this point we touch upon one of the shortcomings of this model: the amplitude and period of a solution depend upon the initial values, which is unnatural in view of the ecological background of the problem. Furthermore, the solutions turn out to be neutrally stable. As a result of this the system will not return into its cycle after some perturbation. It is clear that this model cannot explain the observed well

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defined period of prey-predator oscillations. A third objection against the model concerns its structural instability. Structural stability is a mathematical concept that can be understood by extending the model (1.1) with a Verhulst term as follows

$$\frac{dx}{dt} = ax - bxy - ex^2, \tag{1.2a}$$

$$\frac{dy}{dt} = -cy + dxy. \tag{1.2b}$$

Then for $e \neq 0$, the solution behaves qualitatively different and, therefore, the system is called structurally unstable for $e = 0$.

The objective of this paper is to formulate a model for prey-predator oscillations that comes as close as possible to the Volterra-Lotka equations and that meets the above objections. Bulmer [3] gives conditions for the system

$$\frac{dx}{dt} = xf(x, y), \tag{1.3a}$$

$$\frac{dy}{dt} = yg(x, y) \tag{1.3b}$$

in order to satisfy a set of ecological constraints with relation to prey-predator interaction. These conditions are violated by (1.1); the Volterra-Verhulst system (1.2) with positive parameter values meets all requirements. However, oscillating solutions of (1.2) tend to damp out, so that the model in this form is unsuitable for our study.

It is suggested that the answer to this problem may lie in the existence of a cycle due to the interaction of the prey with its food, e.g. a plant-herbivore relation, see [3]. However, this argument means a shift of the problem to a lower level, since such a system has the same interaction mechanism as a prey-predator system. After analyzing a series of alternatives for (1.2), Roughgarden [9, p. 449] concludes: "So the issue of exactly what mix of mechanisms causes the lynx oscillations is still open, ...". In this paper we will continue the mathematical investigations on the system (1.2) and consider the case where one of the parameters is periodic in time. Our aim is to prove the existence of asymptotically stable periodic solutions with a period being a multiple of the period of the driving term. A biological motivation for choosing periodically varying parameters is found in the influence of seasonal conditions. Let us assume that the growth rate of the prey is periodic with period 1. Since we are mainly interested in qualitative features of the system we take

$$a = a_0 + a_1 \cos 2\pi t, \tag{1.4}$$

instead of constructing a periodic function fitting data of observations. Thus, we consider the system (1.2) with the parameter a given by (1.4), that is we have a system driven by an external periodic force.

It has been proved, that in general systems of periodically forced differential equations have a periodic solution with a period equal to the driving period. It is, however, not commonly known that such systems may have stable subharmonic solutions with a period being a multiple of the driving period. In certain cases stable subharmonics with a different period may be found for the same set of parameter values. By taking such a parameter set and a specific initial point and by integrating the system numerically one will find a solution which over a large time interval will tend to a stable oscillatory state. From this approach it is not clear, however, that for other initial values the solution will tend to the same or a different oscillatory state. In order to eliminate such arbitrariness and to trace more subharmonics at the same time, we will handle the problem more systematically and integrate the equations for a sufficiently large set of initial points in the positive quadrant of the phase-plane. However, numerical integration of the system for each initial point over a large time interval is practically impossible, and, as we will see, also not necessary. Integration of the system over one period of the driving force relates an initial point to an end point. This mapping of the phase plane into itself, the so-called Poincaré mapping, will be studied in the next section. There, we construct an approximation of this mapping by which we are able to find, in an efficient numerical way, approximations to various subharmonics.

In section 3 the existence of periodic solutions near such approximations will be investigated by making use of a theorem of Urabe [10]. This theorem yields a practical method of proving the existence of isolated periodic solutions in the neighbourhood of periodic functions satisfying the differential system with a sufficient accuracy. The theorem provides us with error bounds for these approximations and gives also a decisive answer on the stability of the periodic solutions. In section 4 the method is worked out for two specific examples.

In section 5 we discuss possible implications of these results in the modelling of periodic phenomena in population dynamics. Besides the prey-predator oscillations mentioned above we refer to the observed cycles in the densities of rodent populations and the periodic outbursts of epidemic diseases.

2. The Poincaré Mapping

By an appropriate scaling of the dependent variables the system (1.2), (1.4) is transformed into

$$\frac{dx_1}{dt} = \alpha x_1(1 + \gamma \cos 2\pi t - x_2 - \eta x_1), \tag{2.1a}$$

$$\frac{dx_2}{dt} = \beta x_2(-1 + x_1). \tag{2.1b}$$

In order to trace periodic solutions of this system for a specific choice of the parameters we consider the Poincaré mapping

$$P\colon x(0) \to x(1). \tag{2.2}$$

Furthermore, we introduce the sequence of functionals

$$V_n(x) = \|P^n x - x\|, \qquad n = 1, 2, \ldots, \tag{2.3}$$

where $\|\cdot\|$ denotes the Euclidean norm of a vector. Apparently V_n is positive semi-definite and vanishes at a fixed point of P^n, which corresponds to a periodic solution of period k with k such that n/k is a positive integer. Comparing the occurrence of zeroes of V_n for different values of n one may conclude about the period of a solution at such a point. For the approximation of V_n in a certain domain of the phase plane we adapted the following strategy. Let $A_1 \subset \mathbb{R}_2$ be a compact domain and define

$$B_i = \{y \mid y = Px, x \in A_i\}. \tag{2.4}$$

If we let $A_{i+1} = A_i \cap B_i$, then for a given domain A_1, we compute $V_n(x)$ for $x \in A_n$ from a numerical approximation of P on A_1. This approximation of P is based on a numerical integration of the system over the interval (0, 1] for a set of initial points x_0 on a lattice $\mathscr{L}$ covering A_1. Since for $n > 1$ $P^i x$, $i = 1, 2, \ldots, n-1$ is not a point of the lattice $\mathscr{L}$ we interpolate P over the points of the lattice nearest to $P^i x$ to find $P^{i+1}x$. Thus the construction of $P^{i+1}x$ from $P^i x$ for $i > 0$ is completely based on interpolation, so that expensive numerical integration of the system is avoided. Once we have a global picture of V_n from its values on the lattice $\mathscr{L}$, we approximate the fixed points of P^n more accurately as follows. Near a minimum of V_n on the lattice we step locally along the path of steepest descent to trace the possible zero of V_n. In this process the stepsize is taken sufficiently small and the numerical integration sufficiently accurate in order to attain the accuracy required for a successful application of Urabe's method. The value of V_n in the last point is a measure for the accuracy in approximating the initial point of the corresponding periodic solution.

3. Existence and Stability of Subharmonic Solutions

For the proof of existence of a periodic solution in the neighbourhood of an approximate solution we use a method developed by Urabe [10]. Let us sketch how we apply this method to the class of problems (2.1). We consider the periodic nonlinear system of differential equations

$$\frac{dx}{dt} = f(x, t), \qquad f(x, t) = f(x, t + 2\pi), \tag{3.1}$$

and assume that $f(x, t)$ and its partial derivatives with respect to x and t are continuously differentiable in a region $D \times L$, where D is a bounded closed set in the state space and L the t-axis. The following theorem (Proposition 3 of [10]) enables us to investigate, in a numerical way, the existence of a 2π-periodic solution. For that purpose we determine a 2π-periodic approximate solution of (3.1) being a 2π-periodic vector function that satisfies (3.1) with a given accuracy. The conditions under which the theorem applies are such that one and only one periodic solution will lie in a neighbourhood of the approximate solution, so the theorem only deals with isolated periodic solutions.

Theorem 3.1. *Let $x = \bar{x}(t)$, lying within D, be a 2π-periodic approximate solution of (3.1). Let $A(t)$ be some continuous 2π-periodic matrix such that the multipliers of $y' = A(t)y$ are all different from one. Let $\Phi(t)$ be its fundamental matrix satisfying $\Phi(0) = E$, E the unit matrix, and define $H(t, s)$ as the piecewise continuous matrix*

$$H(t, s) = \Phi(t)[E - \Phi(2\pi)]^{-1}\Phi^{-1}(s) \qquad \text{for} \quad 0 \leqslant s \leqslant t \leqslant 2\pi, \tag{3.2a}$$

$$H(t, s) = \Phi(t)[E - \Phi(2\pi)]^{-1}\Phi(2\pi)\Phi^{-1}(s) \qquad \text{for} \quad 0 \leqslant t < s \leqslant 2\pi. \tag{3.2b}$$

Let $\|\cdot\|$ *denote the Euclidean norm, and further, let* M *and* r *be positive constants such that*

$$\max_{0\leqslant t\leqslant 2\pi} \int_0^{2\pi} \sum_{p,q} H_{p,q}^2(t,s)\,ds \leqslant \frac{M^2}{2\pi}, \tag{3.3}$$

$$\max_{0\leqslant t\leqslant 2\pi} \|\bar{x}'(t) - f(\bar{x}(t),t)\| \leqslant r, \tag{3.4}$$

where $H_{p,q}$ *are the elements of the matrix* H. *Finally, let* $\Psi(x,t) = f_x(x,t)$. *Now, if there exist constants* $\delta > 0$ *and* $0 < \kappa < 1$ *such that*

$$D_\delta = \{x \mid \|x - \bar{x}(t)\| \leqslant \delta \text{ for all } t \in L\} \subset D, \tag{3.5a}$$

$$\|\Psi(x,t) - A(t)\| \leqslant \kappa/M \qquad \text{for} \quad t \in L \quad \text{and all} \quad x \in D_\delta, \tag{3.5b}$$

$$Mr/(1-\kappa) \leqslant \delta, \tag{3.5c}$$

then (3.1) *has a unique* 2π*-periodic solution* $x = \hat{x}(t)$ *in* D_δ *and this solution is isolated. Further, we have*

$$\max_{0\leqslant t\leqslant 2\pi} \|\bar{x}(t) - \hat{x}(t)\| \leqslant Mr/(1-\kappa). \qquad \square \tag{3.6}$$

It is noted that this theorem yields an error bound for the approximation $\bar{x}(t)$. Because of the fact that the theorem requires a 2π-periodic system we transform our prey-predator equations (2.1) to

$$\frac{dx_1}{dt} = \frac{\alpha T}{2\pi} x_1(1 + \gamma\cos(Tt) - \eta x_1 - x_2), \tag{3.7a}$$

$$\frac{dx_2}{dt} = \frac{\beta T}{2\pi} x_2(-1 + x_1), \tag{3.7b}$$

where $T \in I\!N^+$. Obviously this system of differential equations is 2π-periodic in t and if it has a 2π-periodic solution $x = \hat{x}(t)$ then $x = \hat{x}(2\pi t/T)$ is a periodic solution of (2.1) with period T, that is, a subharmonic of order T.

The conditions (3.5) are verified for the system (3.7) as follows. Let the matrix $A(t)$ be given by

$$A(t) = \Psi(\bar{x}_1(t), \bar{x}_2(t), t) \tag{3.8}$$

with Ψ being the Jacobian matrix of (3.7). An elementary calculation yields

$$\begin{aligned} &\|\Psi(x_1,x_2,t) - \Psi(\bar{x}_1(t),\bar{x}_2(t),t)\|^2 \\ &\quad = (4\pi^2)^{-1}T^2\{\alpha^2(2\eta(x_1 - \bar{x}_1(t)) + x_2 - \bar{x}_2(t))^2 \\ &\qquad + (\alpha^2 + \beta^2)(x_1 - \bar{x}_1(t))^2 + \beta^2(x_2 - \bar{x}_2(t))^2\} \\ &\quad \leqslant (4\pi^2)^{-1}T^2 \max(2\alpha^2 + \beta^2, \alpha^2 + \beta^2 + 8\eta^2\alpha^2) \\ &\qquad \times \{(x_1 - \bar{x}_1(t))^2 + (x_2 - \bar{x}_2(t))^2\}. \end{aligned}$$

Consequently, for any (x_1, x_2) lying in

$$D_\delta = \{(x_1,x_2) \mid (x_1 - \bar{x}_1(t))^2 + (x_2 - \bar{x}_2(t))^2 \leqslant \delta^2\}, \qquad \delta > 0$$

we have

$$\|\Psi(x,t) - \Psi(\bar{x}(t),t)\| \leqslant (2\pi)^{-1}\,\delta T\sqrt{q}, \quad q = \max(2\alpha^2 + \beta^2, \alpha^2 + \beta^2 + 8\eta^2\alpha^2).$$

If we succeed in finding a $\delta > 0$ and a κ, $0 < \kappa < 1$, such that

$$(2\pi)^{-1}\,\delta T\sqrt{q} \leqslant \kappa/M \qquad \text{and} \qquad Mr/(1-\kappa) \leqslant \delta, \tag{3.9a, b}$$

then we have completed the proof of existence of a unique isolated subharmonic solution of (2.1), provided the condition on the multipliers is satisfied. For convenience we set

$$\delta = Mr/(1-\kappa). \tag{3.10}$$

Then condition (3.9a) reads

$$(2\pi)^{-1} rTM^2\sqrt{q} \leqslant \kappa(1-\kappa). \tag{3.11}$$

Hence, this condition is satisfied if

$$\xi = (2\pi)^{-1} rTM^2\sqrt{q} < \tfrac{1}{4}. \tag{3.12}$$

It is observed that for a given set of parameters the magnitude of rM^2 is of crucial importance. Since the accuracy of the approximation $\bar{x}(t)$ determines the magnitude of the residual constant r, a successful application of Urabe's theorem can only be realized if the approximation is sufficiently accurate.

To conclude this section we now discuss some computational aspects of Urabe's theorem. For a 2π-periodic approximation of the 2π-periodic solution of (3.7) we use the trigonometric vector polynomial

$$\bar{x}(t;m) = a_0 + \sum_{n=1}^{m} a_{2n-1}\sin nt + a_{2n}\cos nt. \tag{3.13}$$

By application of quadrature rules (see [12]) its Fourier coefficients are determined from the numerical solution that starts in the fixed point of the iterated Poincaré mapping (see foregoing section). Substitution of (3.13) into (3.1) gives us, in principle, the possibility of computing the Fourier coefficients with the method of Galerkin, see [11, p. 108]. However, for the corresponding system of nonlinear algebraic equations the roots related with the subharmonic solutions are hard to find if one has no good initial estimate. In order to obtain an estimate for M, the initial value problem

$$\Phi' = \Psi(\bar{x}(t;m),t)\Phi, \qquad \Phi(0) = E, \qquad 0 \leqslant t \leqslant 2\pi \tag{3.14a, b}$$

is solved numerically and the integration of (3.3) is carried out. As proposed by Urabe and Reiter, the standard 4th-order Runge-Kutta method and the quadrature rule of Simpson are used. The bound r is estimated from the maximum of the residual function over a sufficiently large number of points. Since in general the maximum will lie somewhere in between, we choose a safe, larger value for r. Since (3.14) approximates the first variational equation of the exact solution, we can investigate the asymptotic stability of a periodic solution from this equation. The eigenvalues of the matrix $\Phi(2\pi)$ are the multipliers of the linear system (3.14), see Hale [6, p. 117].

4. Numerical Solutions

In this section we restrict ourselves to the class of systems (2.1) with a small Verhulst term ($0 < \eta \ll 1$). For an autonomous system ($\gamma = 0$) this would lead to oscillatory solutions damping out very slowly. Near the equilibrium $(x_1, x_2) = (1, 1 - \eta)$ these oscillations will have a frequency of $(2\pi)^{-1}\sqrt{\alpha\beta}$ which will increase with the amplitude of the oscillatory state. By introduction of a sufficiently large forcing term there will appear asymptotically stable periodic solutions of period

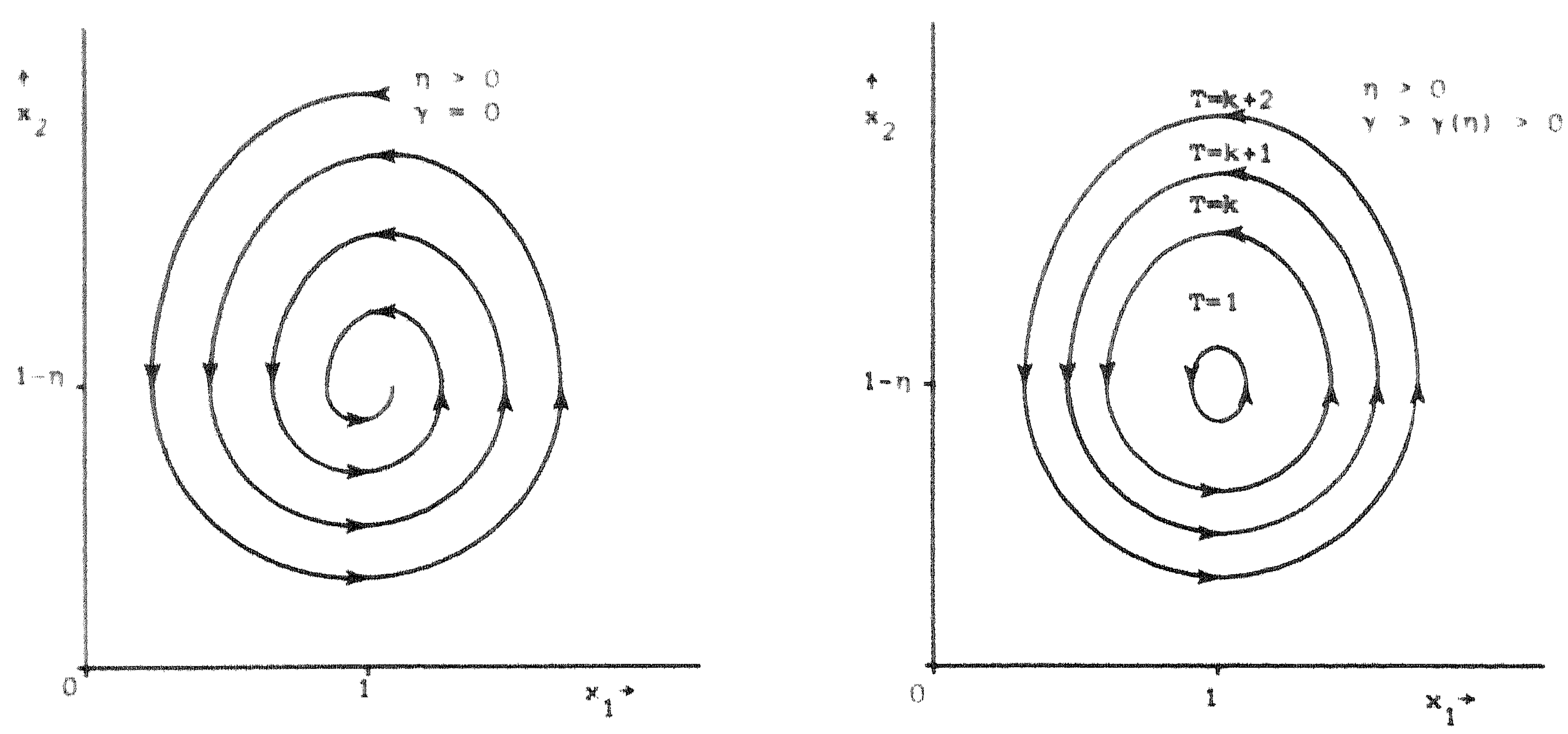

Fig. 1. (a) Damped oscillatory solution of autonomous Volterra-Verhulst system. **(b)** Stable sub-harmonic solutions of forced Volterra-Verhulst system

Table 1. The parameter values for the two examples

	α	β	γ	η	$2\pi/\sqrt{\alpha\beta}$
Example I	4.539	1.068	0.25	0.0025	2.85
Example II	3.4	0.8	0.25	0.0025	3.81

Table 2. Initial values of 4 approximate periodic solutions of Example I. In all 4 cases the existence of an exact solution has been established

T	$x_1(0)$ $x_2(0)$	Multipliers	M	r	$\xi\ (< \frac{1}{4})$
1	0.98961058 0.963138653	$-0.59 \pm 0.80i$ stable	8.5	${}^{2}10^{-9}$	${}^{1.5}10^{-7}$
3	0.407008521 1.484111304	$0.76 \pm 0.62i$ stable	67	10^{-8}	${}^{1.4}10^{-4}$
3	0.40555853 1.05763779	1.51, 0.64 unstable	54	${}^{6}10^{-9}$	${}^{1.8}10^{-5}$
4	0.095179161 0.2697495821	$-0.37 \pm 0.90i$ stable	1245	10^{-8}	${}^{1.6}10^{-2}$

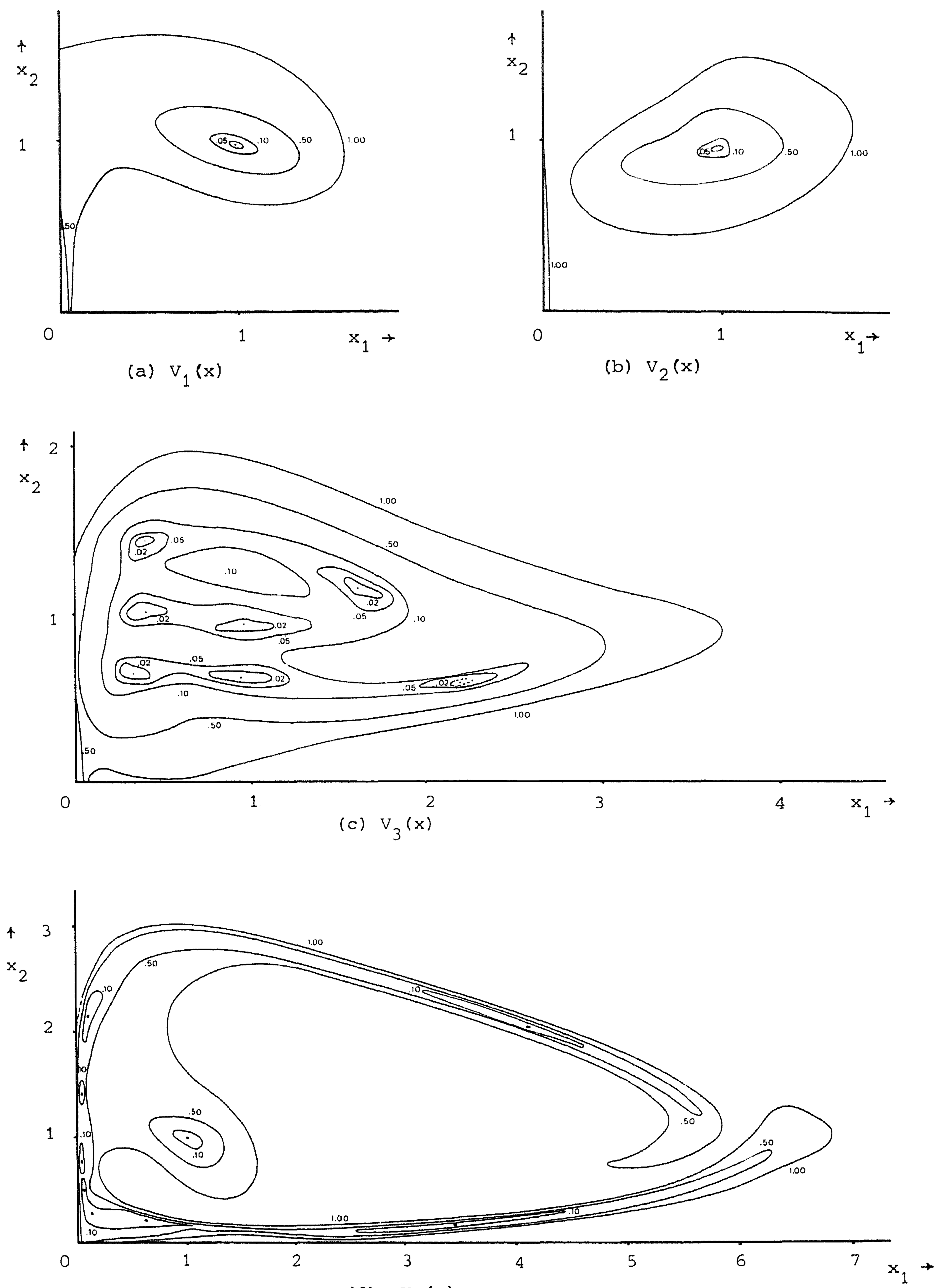

Fig. 2. Level lines of the functional V_n, $n = 1, 2, 3, 4$ for Example I

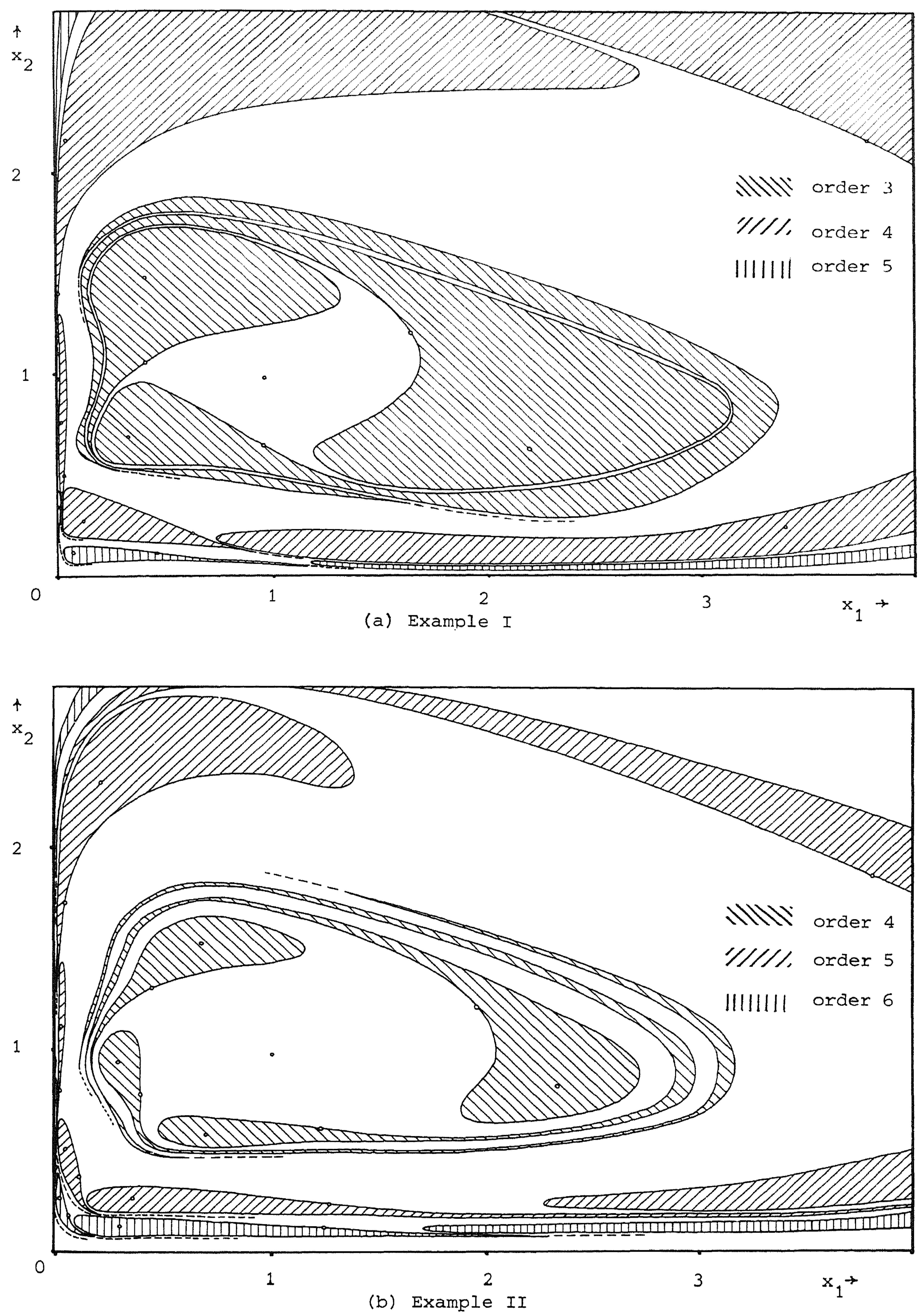

Fig. 3. Domains of attraction of the subharmonic solutions in the phase plane at time $t = 0$

$T = 1, k, k+1, k+2, \ldots$ with k depending on the value of the product $\alpha\beta$ (see Fig. 1). We computed such periodic solutions for two specific examples (see Table 1). The results are presented in Tables 2 and 3.

In Fig. 2 we depicted the functional (2.3) for Example I. By the method of Hayashi [7] we constructed the domains of attraction of the stable periodic solutions for the two examples, see Fig. 3. Asymptotically stable periodic solutions of Example II are given as a function of time in Fig. 4.

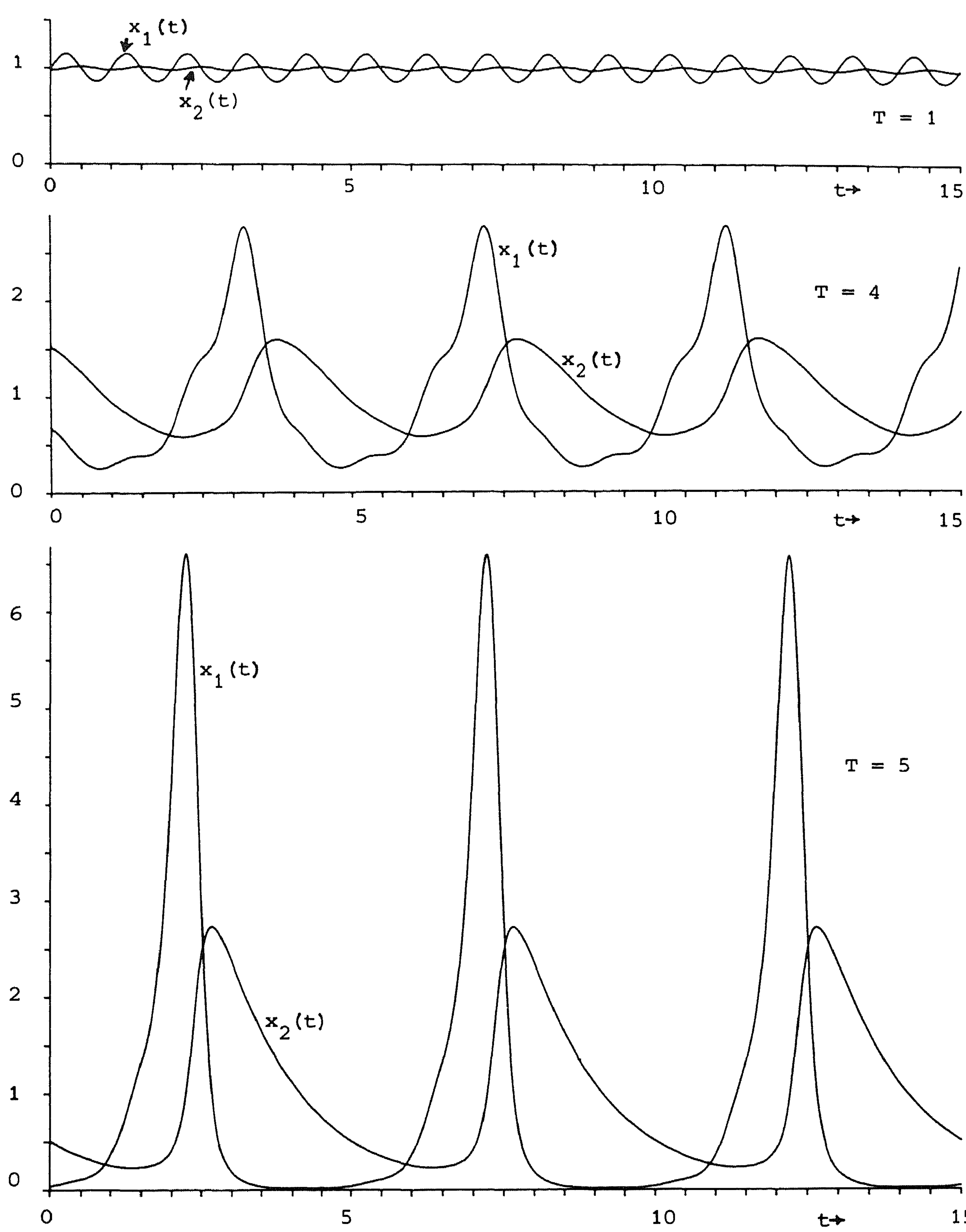

Fig. 4. Stable (sub)harmonic solutions of Example II

Table 3. Initial values of 4 approximate periodic solutions of Example II. In all 4 cases the existence of an exact solution has been established

T	$x_1(0)$ $x_2(0)$	Multipliers	M	r	$\xi\ (<\frac{1}{4})$
1	0.9948671 0.9791929	$-0.08 \pm 0.99i$ stable	10	10^{-6}	$^{7.8}10^{-5}$
4	0.682447607 1.528681362	$0.93 \pm 0.32i$ stable	145	10^{-7}	$^{6.6}10^{-3}$
4	0.447779739 1.306031262	1.32, 0.73 unstable	162	$^{2}10^{-9}$	$^{1.6}10^{-4}$
5	0.0415914697 0.5085066681	$0.20 \pm 0.96i$ stable	657	$^{5}10^{-9}$	$^{8.4}10^{-3}$

5. Periodic Phenomena in Population Dynamics

In the foregoing sections we have established the existence of asymptotically stable subharmonic solutions of the Volterra-Verhulst system (1.2) with the parameter a satisfying (1.4). This model is proposed for describing the existence of fluctuations in the densities of interacting preys and predators with a well defined period. In the model we incorporated the changing influence of the season acting upon the growth rate of the prey. The existence of asymptotically stable subharmonic solutions supports the view that the observed 4- and 10-yr cycles in prey-predator systems arise as a result of seasonal effects. Similarly, the model may explain the 5-yr cycle of the hare (a plant-herbivore interaction), see [3, p. 148]. From our mathematical investigations we conclude that for given parameter values several stable solutions with different periods are possible. This result meets Bulmer's objections against a model with a driving periodic force as it gives a possible explanation for the existence of different lynx cycles in European Russia (8-yr) and Siberia (10-yr).

We expect a similar qualitative behaviour of the system if other parameters are varied periodically as well. For example, if we let a and c of (1.2) be periodic in time, we arrive at a model studied by Dekker [4] describing the existence of rodent cycles. Dekker explains the possible lengthening of the period from a critical passage in the phase plane. Taking the parameters b and d periodic in time the model (1.2) may be of use for describing the periodic outbursts of epidemical diseases in populations. For this type of problem x and y denote, respectively, the densities of the susceptible and the infective population. The periodicity in b and d account for seasonal variations in the contagion. In this respect the 2-yr cycle in the occurrence of measles [5] and the 3-yr cycle of rabies in foxes [1, p. 91] should be mentioned.

6. Concluding Remarks

In our mathematical analysis we left several interesting aspects of the mathematical problem untouched. First of all it is worth to investigate the way in which the lower subharmonics of (2.1) disappear near the equilibrium of the autonomous system as the product $\alpha\beta$ decreases and the expression $2\pi/\sqrt{\alpha\beta}$ passes an integer value. The KBM-method [2] of analyzing almost linear systems would provide the appropriate tools for such a study. Furthermore, one may compute the conditions on γ

and η in order to have existency and stability of subharmonic solutions. Besides the periodic solutions with an integer rotation number, see Hale [6, p. 66], there may also exist solutions with a fractional rotation number. As an illustration one may consider example I of section 4 and look for solutions of period 7 consisting of one cycle of about 3 years which, instead of closing its orbit, first makes another cycle of 4 years. Such a solution may explain the existence of 3.5-yr cycles. However, since it is expected that these solutions have a small domain of attraction we should also take into consideration the influence of stochastic effects making the system switch between the 3-yr cycle and the 4-yr cycle. Such arguments also apply to the 10-yr cycle of the Canadian lynx, as its observed period actually comes closer to a 9.5-yr cycle. Kannan [8] has studied the influence of small stochastic effects upon the system (1.2) with periodic coefficients near the harmonic solution. Since solutions of such a system will leave any bounded domain with probability one in a finite time, it is also worthwhile to concentrate on global results for stochastic systems for which the corresponding deterministic system has several stable periodic solutions with different periods.

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