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PERIODIC SOLUTIONS OF PERIODICALLY HARVESTED LOTKA-VOLTERRA SYSTEMS*

by

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Abstract. We study a Lotka-Volterra system with periodic harvesting, find sufficient conditions for the existence of periodic solutions with the same period, and, under certain conditions, count the number of such periodic solutions.

§1. Introduction. In this paper we study the Lotka-Volterra system with periodic harvesting

$$\begin{aligned} x' &= a^{*}x - bxy - h^{**}(t)x \\ y' &= c^{*}y + dxy - k^{**}(t)y \end{aligned} \tag{1.1}$$

where ' denotes d/dt, a^{*}, b, c^{*}, d are positive real numbers, $h^{**}(t)$, $k^{**}(t) \geq 0$ are twice differentiable, and $h^{**}(t+p) = h^{**}(t)$, $k^{**}(t+p) = k^{**}(t)$ for some $p > 0$. In this model x represents the biomass of the prey species, y the biomass of the predator species, a^{*} is the "natural" rate of increase

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of the predators in the absence of the prey. d and b are constants which govern the flow of biomass from prey to predators due to predation and $h^{**}(t)$ and $k^{**}(t)$ present the harvesting effort applied to the prey and predator species respectively. $h^{**}(t), k^{**}(t) \geqslant 0$ indicates harvesting whereas $h^{**}(t)$ or $k^{**}(t) < 0$ would mean a release of new individuals into the population, an occurrence which is not physically reasonable, although it can be handled easily mathematically. The periodicity of h^{**} and k^{**} might reflect, for example, the fact that hunting seasons frequently take place on an annual basis with more or less the same number of permits issued each year. The requirement that h^{**} and k^{**} be twice differentiable is a mathematical requirement rather than a biological one.

In order to study (1.1) we make several changes of variable. If f is continuous and p-periodic, define

$$[f] = \int_0^p f(t)\,dt/p \tag{1.2}$$

With this notation, let

$$\begin{aligned} a &= a^* - [h^{**}], \quad c = c^* + [k^{**}], \\ h^*(t) &= h^{**}(t) - [h^{**}], \quad \text{and} \quad k^*(t) = k^{**}(t) - [k^{**}]. \end{aligned} \tag{1.3}$$

We require a > 0, that is that the hunting pressure on the prey species does not on the average exceed its natural growth rate. Then (1.1) becomes

$$\begin{aligned} x' &= ax - bxy - h^*(t)x \\ y' &= -cy + dxy - k^*(t)y. \end{aligned} \tag{1.4}$$

Now let

$$\begin{aligned} x &= (a/d)w, \quad y = (a/b)z, \\ t &= s/a, \quad \text{and} \quad m = c/a. \end{aligned} \tag{1.5}$$

Then we obtain

$$\dot{w} = w - wz - [h^*(s/a)/a]w$$
$$\dot{z} = -mz + wz - [k^*(s/a)/a]z \qquad (1.6)$$

where $\cdot$ denotes d/ds. We shall require later the result that the period of the periodic solutions of

$$\dot{w} = w - wz$$
$$\dot{z} = -mz + wz \qquad (1.7)$$

is a monotone function of amplitude increasing to infinity, see [2]. Finally, repace s by t and let

$$w = m e^x \ , \quad z = e^{my} \qquad (1.8)$$

which restricts attention to the first quadrant in the (w,z) plane, to obtain

$$x' = 1 - e^{my} - h(t) \qquad (1.9)$$
$$y' = -1 + e^x - k(t)$$

where

$$h(t) = h^*(t/a)/a \qquad (1.10)$$
$$k(t) = k^*(t/a)/am.$$

Note that because of the change of variables (1.8), all solutions of (1.9) correspond to positive, and hence physically realistic, solutions of (1.1). We observe that h(t) and k(t) are twice differentiable and T-periodic with T = ap. The origin is a center of

$$x' = 1 - e^{my}$$
$$y' = -1 + e^x, \qquad (1.11)$$

the family of periodic solutions enclosing the origin fills R^2, and, by the previous remark, the period of those periodic solutions is a monotone function of amplitude increasing to infinity so that the periods of the nontrivial periodic solutions lie in an interval of the form $(2\pi/\sqrt{m},\infty)$. We require that the forcing period be the same as the period of one of the periodic solutions of (1.11) and hence we shall assume that $T > 2\pi/\sqrt{m}$. Since some multiple of ap will always be greater than $2\pi/\sqrt{m}$, we can take T to be one of those multiples if necessary. Finally we note that (1.11) has a first integral

$$V(x,y) = e^{my}/m - y + e^{x} - x \quad (1.12)$$

§2. Construction of periodic solutions. In this section, we study the periodic solutions of

$$\begin{aligned} x' &= 1 - e^{my} - h(t) \\ y' &= -1 + e^{x} - k(t). \end{aligned} \quad (1.9)$$

(1.9) can be written as

$$z' = f(z) + F(t,z,e) \quad (2.1)$$

where $z = \binom{x}{y}$, $f:\mathbb{R}^2 \to \mathbb{R}$ is twice differentiable and is given by $f(z) = \binom{1 - e^{my}}{-1 + e^{x}}$, and $e = (h(t),k(t))$, is a parameter in the Banach space $B = C(T)\times C(T)$ where $C(T) = \{h:\mathbb{R} \to \mathbb{R} \mid h$ is continuous and T-periodic$\}$. The equation

$$z' = f(z) \quad (2.2)$$

possesses a T-periodic solution which we shall denote by $u = \binom{u_1}{u_2}$. $F:\mathbb{R}\times\mathbb{R}^2\times B \to \mathbb{R}^2$ is T-periodic in its first variable and is given by $F(t,z,e) = \binom{-h(t)}{-k(t)} = -e$. F is twice differentiable on its domain.

Finally, u is seen to be non-degenerate. That is, u is a member of a one parameter family of periodic solutions of (2.2) and the only T-periodic solutions of the linear variational equation

$$w' = f_z(u(t))w \quad (2.3)$$

are multiples of $u'(t)$. This can be proved based on the properties of the period as a function of amplitude.

Equation (2.1), under less restrictive hypotheses than those mentioned above, has been studied in [1]. In order to state the result which we require in this article, some terminology is necessary. For $h \in C(T)$, let $|h|_T$ denote the sup norm

$$|h|_T = \sup_{0<t<T} |h(t)| \tag{2.4}$$

and let

$$\|e\| = \|(h,k)\| = |h|_T + |k|_T .$$

Let $v = (h^o,k^o) = e/\|e\|$ and define

$$\begin{aligned} g(s) = L(v)(s) &= \int_0^T \{[e^{u_1(t+s)} - 1]h^o(t) + [e^{mu_2(t+s)} - 1]k^o(t)\}dt \\ &= \int_0^T [u_2'(t+s)h^o(t) - u_1'(t+s)k^o(t)]\,dt. \end{aligned} \tag{2.5}$$

The simple roots of g indicate the existence of T-periodic solutions of (1.9), and hence of (1.1). More precisely, the following theorem is a summary of two results proved in [1].

THEOREM 2.1. *Let* $v_o = (h^o,k^o)$ *and* s_o *be such that*

$$L(v_o)(s_o) = 0 \quad \text{and} \quad L(v_o)'(s_o) \neq 0. \tag{2.6}$$

Then there exist $\varepsilon_1, \varepsilon_2 > 0$, *a continuously differentiable function* $s^*:\{v \mid \|v-v_o\| < \varepsilon_1\} \to [0,T]$ *such that* $s^*(0) = s_o$, *and functions* $z:\mathbb{R}\times\{v \mid \|v-v_o\| < \varepsilon_1\} \to \mathbb{R}^2$ *and* $r:\mathbb{R}\times\{v \mid \|v-v_o\| < \varepsilon_1\}\times(-\varepsilon_2,\varepsilon_2) \to \mathbb{R}^2$ *with the following properties:*

1) *z is continuously differentiable in its first argument and continuous in its second argument;*

2) $\lim_{\beta\to 0} |r(t,v,\beta)|/\beta = 0$, *uniformly in* t;

3) $z(t+T,v) = z(t,v)$ *and* $r(t+T,v,\beta) = r(t,v,\beta)$; *and*

4) *if* $0 < |e| < \varepsilon_2$ *and* $\|e/\|e\| - v_0\| < \varepsilon_1$, *then*

$$x(t,e) = u(t+s^*(e/\|e\|)) + \|e\| z(t,e/\|e\|) + r(t,e\|e\|,\|e\|) \qquad (2.7)$$

is a T-periodic solution of (1.9).

Hence, it is necessary to analyze g(s) in order to obtain information about T-periodic solutions of (1.9).

§3. Analysis of g and the number of periodic solutions.

In this section, we study the function

$$g(s) = \int_0^T [u_2'(t+s)h(t) - u_1'(t+s)k(t)]dt \qquad (3.1)$$

where $|h|_T + |k|_T = 1$. We have immediately

PROPOSITION 3.1. $g(s) = 0$ *always possesses at least two roots.*

Proof. By direct calculation, $\int_0^T g(s)ds = 0$. Hence g cannot have only one sign. But since $g(0) = g(T)$, it must have at least two roots. ▲

Let n be a real number. It can be shown that g satisfies the second order differential equation

$$g''(s) + n^2 g(s) = P(s;n) \qquad (3.2)$$

where

$$P(s;n) = \int_0^T \{u_2'(t+s)[h''(t) + n^2 h(t)] - u_1'(t+s)[k''(t) + n^2 k(t)]\}dt. \qquad (3.3)$$

If P were zero, g(s) would take the form

$$g(s) = A \cos n(s-a) \qquad (3.4)$$

where a is an appropriate phase angle and $A^2 = g(0)^2+[g'(0)/n]^2$. In this case, we would be able to count the number of solutions of $g(s) = 0$ and all roots would be simple. If P is small, $g(s) = 0$ has the same number of roots as when $P = 0$ and they are still simple. One can estimate

$$|P|_T < K_P[|h'' + nh|_T + |k'' + nK|_T] \tag{3.5}$$

where

$$K_P = T[|u_2'|_T + |u_1'|_T]. \tag{3.6}$$

By the variation of constants formula,

$$g(s) = A\cos n(s-a)+ \frac{1}{n}\int_0^T P(t;n)\sin n(s-t)\,dt$$

and (3.7)

$$g'(s) = -A\,n\sin n(s-a) + \int_0^T P(t;n)\cos n(s-t)\,dt$$

where a and A are above.

By direct calculation using (3.7),

$$[n\,g(s)]^2+ g'(s)^2 = n^2A^2 - 2An\int_0^T P(t;n)\sin n(t-a)\,dt$$
$$+ [\int_0^T P(t;n)\sin n(s-t)\,dt]^2+[\int_0^T P(t;n)\cos n(s-t)dt]^2 \tag{3.8}$$

or

$$[n\,g(s)]^2+g'(s)^2 \geq n^2A^2-2An\int_0^T P(t;n)\sin n(t-a)\,dt, \tag{3.9}$$

or, using (3.5),

$$[n\,g(s)]^2+g'(s)^2 \geq n^2A^2-2AnTK_P[|h'' + n^2h|_T+|k''+n^2k|_T]. \tag{3.10}$$

As long as $[ng(s)]^2 + g'(s)^2 > 0$, all roots of $g(s) = 0$ are simple and there are as many when $P = 0$; i.e. when $g(s) = A\cos n(s-a)$. We summarize the above discussion in

THEOREM 3.1. *Let* $nT/2\pi$ *be an integer greater than or equal to* 1 *and suppose that* $A^2 = g(0)^2 + |g'(0)/n|^2 > 0$. *If*

$$|h'' + n^2 h|_T + |k'' + n^2 k|_T < nA/2TK_P \quad (3.11)$$

then the equation $g(s) = 0$ *possesses* nT/π *solutions and, moreover, at each such solution* $g'(s) \neq 0$.

Finally, we interpret Ths. 2.1 and 3.1 as they apply to (1.9).

THEOREM 3.2. *Suppose the following hypotheses:*

1) $nT/2\pi$ *is an integer greater than or equal to 1;*
2) $A^2 = g(0)^2 + [g'(0)/n]^2 > 0$;
3) $|h'' + n^2 h|_T + |k'' + n^2 k|_T < nA/2TK_P$;
4) $|\tilde{h}|_T + |\tilde{k}|_T$ *is sufficiently small; and*
5) $(\tilde{h}, \tilde{k})/[|h|_T + |\tilde{k}|_T]$ *is sufficiently close to* (h,k).

Then (1.9) *with* (h,k) *replaced by* $(\tilde{h}, \tilde{k})$, *has* nT/π *T-periodic solutions branching from translates of* u.

Returning to (1.1), Th. 3.2 says that if the deviations of h^{**} and k^{**} from their mean values are sufficiently small and if the parts of h^{**} and k^{**} with mean value zero form an element of $C(T) \times C(T)$ sufficiently close to certain preferred directions there, then (1.1) possesses T-periodic solutions branching from translates of u and, moreover, the number of such T-periodic solutions can be obtained.

LITERATURE

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