THE PERIOD OF A LOTKA-VOLTERRA SYSTEM^{1*}

Shagi-Di Shih

Abstract. A classical Lotka-Volterra system of two first-order nonlinear differential equations modeling predator prey competition in population biology has been known to have an algebraic relation between two dependent variables for its periodic behavior in the phase plane since pioneering works by Lotka [12] on chemical reaction, Lotka [13] on parasitology, and Volterra [24] on fishing activity in the upper Adriatic Sea. The techniques of Volterra [24], Hsu [10], Waldvogel [25, 26], Rothe [19], and Shih [22] in obtaining an integral representation of the period of Lotka-Volterra system are surveyed. These integrals are then shown to be equivalent.

1. Introduction

The problem of investigating periodic solutions is very old. It first became prominent in the study of celestial mechanics and there is a well-known discussion of its importance by the French mathematician Poincaré [18]. In later years, when other physical phenomena have been analyzed mathematically by using nonlinear ordinary differential equations, periodic solutions have often played an important role in radio circuits, control theory, and, most recently, chemical and biological oscillations. In this work, an attention is paid to a predator prey problem in mathematical biology.

For two competing species model, Lotka [13, pp. 88-94] and Volterra [24] studied independently the predator prey model

Received March 1, 1997.

Communicated by S.-B. Hsu.

1991 Mathematics Subject Classification: 34-02, 34A34, 34C25, 92D25.

Key words and phrases: Lotka-Volterra predator prey system, periodic solution, period.

¹Teaching a graduate course on mathematical biology at the University of Wyoming during spring 1996 motivates the author to investigate this problem. Thus an earlier draft of this work was delivered in a series of lectures there.

^{*} Presented at the International Mathematics Conference '96, National Changhua University of Education, December 13–16, 1996. The Conference was sponsored by the National Science Council and the Math. Soc. of the R.O.C.

$$(1.1) u'(t) = u(t)\{a - bv(t)\}, v'(t) = v(t)\{cu(t) - d\},$$

where u(t) is the prey population, v(t) that of the predator at time t, and a, b, c, d are positive constants, see also Rubinow [20] and Murray [15]. Lotka [12] derives this system for the chemical reaction which exhibits periodic behavior in the chemical concentrations, see also Murray [14]. The system (1.1) is a classical but nontrivial problem. Periodic solutions of some Lotka-Volterra systems are further investigated by Davis [5], Grasman and Veling [9], Frame [7], Lauwerier [11], Dutt [6], Hsu [10], Rothe [19], and Waldvogel [25, 26]. Nonperiodic solutions of some Lotka-Volterra systems are studied by Abdelkader [1], Varma [23], Willson [27], Burnside [3], Murty and Rao [16], and Olek [17]. Several asymptotic solutions of the Lotka-Volterra equations with oscillatory behavior are reviewed in detail by Grasman [8].

The system (1.1) has only one critical point (singular point, or equilibrium point) (d/c, a/b) in the first quadrant of the uv-plane, which is the center for the linearized system of (1.1)

(1.2)
$$u'(t) = -\frac{bd}{c} \left\{ v(t) - \frac{a}{b} \right\}, \qquad v'(t) = \frac{ac}{b} \left\{ u(t) - \frac{d}{c} \right\}.$$

Moreover, the linearized problem (1.2) subject to the initial conditions $u(0) = u_0 > 0, v(0) = v_0 > 0$ has the solution

$$u(t) = \frac{d}{c} + r\sin(t\sqrt{ad} + t_*), \qquad v(t) = \frac{a}{b} + r\frac{c}{b}\sqrt{\frac{a}{d}}\cos(t\sqrt{ad} + t_*);$$

for some t_* satisfying

$$\cos(t_*) = \frac{v_0 - a/b}{r} \frac{b}{c} \sqrt{\frac{d}{a}}, \quad \sin(t_*) = \frac{u_0 - d/c}{r},$$
$$r = \sqrt{(u_0 - \frac{d}{c})^2 + (v_0 - \frac{a}{b})^2 \frac{b^2 d}{ac^2}}.$$

Hence the trajectory of the linearized problem is an ellipse with the period $2\pi/\sqrt{ad}$ in the uv-plane. The linear theory, which appears in both Lotka [12] and Volterra [24], may not predict what happens in the nonlinear system (1.1), but it is closely related to Waldvogel [25, 26] in some sense. In fact, the period for the nonlinear system (1.1) will be shown to depend on the initial data.

On the other hand, combining two equations of the system (1.1) yields

(1.3)
$$\frac{dv}{du} = \frac{v\{cu-d\}}{u\{a-bv\}},$$

which is a separable differential equation. Rewrite (1.3) as $\{a/v - b\}dv = \{c - d/u\}du$, which is integrated to give a functional relation between u and v

$$(1.4) F(u,v) = H$$

with $F(u,v) = cu+bv-d\log(u)-a\log(v)$ and some constant H. Equation (1.4) indicates that F(u,v) is a conservative quantity for all $t \geq 0$. More precisely, for given initial data $u(0) = u_0 > 0, v(0) = v_0 > 0$, we have $H = F(u_0, v_0)$. An elementary technique in calculus further shows that

$$H \ge a + d - a \log\left(\frac{a}{b}\right) - d \log\left(\frac{d}{c}\right),$$

and the minimum value takes place at u = d/c, v = a/b. In the notion of Hamiltonian systems, we write $H = a + d - a \log(a/b) - d \log(d/c) + E$ in (1.4) to obtain

$$(1.5) cu - d + bv - a - a \log\left(\frac{b}{a}v\right) - d \log\left(\frac{c}{d}u\right) = E,$$

with the energy $E \ge 0$, and E = 0 at u = d/c, v = a/b. The system (1.1) has been known to give a one parameter family of periodic solutions (1.4) or (1.5) having (d/c, a/b) as the center point since Lotka [12]. Thus many qualitative properties of the system (1.1) have been obtained from (1.4) or (1.5). For example, Lotka [12] obtains the period of the periodic orbit determined by (1.1) to be about $2\pi/\sqrt{ad}$ by linearizing the algebraic equation (1.4) at u = d/c, v = a/b.

By using a diversity of techniques, there are several integral representations for the period of the periodic solution of the Lotka-Volterra system (1.1) in the literature. In what follows, a survey is given to methods employed by Volterra [24], Hsu [10], Waldvogel [25, 26], Rothe [19], and Shih [22]. Moreover, these integrals are shown to be equivalent.

2. Volterra's Method

Volterra [24] uses dimensionless variables $u = cN_1/d, v = bN_2/a$ to reduce the system

$$N_1'(t) = N_1\{a - b N_2\}, \qquad N_2'(t) = N_2\{c N_1 - d\}$$

to the system

$$(2.1) u'(t) = au\{1 - v\}, v'(t) = dv\{u - 1\},$$

which gives

$$\{u \exp(-u)\}^d = C\{v \exp(-v)\}^{-a},$$

for some positive constant C. Volterra states that if, using (2.2), we express v as a function of u, or u as a function of v, and substitute them into the equations

$$dt = \frac{du}{au\{1-v\}}, \qquad dt = \frac{dv}{dv\{u-1\}};$$

obtained from (2.1), the variables are separated and the integration is reduced to a quadrature. Instead, Volterra defines the auxiliary variable x by

(2.3)
$$x = \{u \exp(-u)\}^d = C\{v \exp(-v)\}^{-a},$$

and obtains the general behavior of the curves $x = \{u \exp(-u)\}^d$ in the ux-plane and $x = C\{v \exp(-v)\}^{-a}$ in the vx-plane, which, in turn, are used to construct the periodic orbit of (2.2) in the uv-plane.

It follows from (2.3) that $\log(x) = d\{\log(u) - u\}$, which, after differentiating with respect to t and using (2.1), gives

$$\frac{1}{x}x'(t) = ad\{1 - u\}\{1 - v\} \quad \text{or} \quad dt = \frac{dx}{adx\{1 - u\}\{1 - v\}}.$$

Volterra then concludes the following result.

Theorem 2.1. The period of fluctuation for the closed orbit determined by (2.2) is the sum of four integrals

$$(2.4) T = \int_{\widehat{SE}} \frac{dx}{adx\{1-u\}\{1-v\}} + \int_{\widehat{EN}} \frac{dx}{adx\{1-u\}\{1-v\}} + \int_{\widehat{NW}} \frac{dx}{adx\{1-u\}\{1-v\}} + \int_{\widehat{WS}} \frac{dx}{adx\{1-u\}\{1-v\}},$$

over the four segments $\widehat{SE}, \widehat{EN}, \widehat{NW}, \widehat{WS}$ of the closed orbit determined by (2.2), where points N, S have the coordinates $(1, v_2), (1, v_1)$, respectively, with v_1, v_2 satisfying $\exp(-d) = C\{v \exp(-v)\}^{-a}$ and $0 < v_1 < 1 < v_2$; and points E, W have the coordinates $(u_2, 1), (u_1, 1)$, respectively, with u_1, u_2 satisfying $C \exp(a) = \{u \exp(-u)\}^d$ and $0 < u_1 < 1 < u_2$.

Volterra also observes that the integrand of each integral in (2.4) becomes infinite at the four vertices S, E, N, W, but the integrals are absolutely convergent. Furthermore, constructing some approximate solutions to 1-u and

1-v, Volterra integrates (2.4) over four segments \widehat{SE} , \widehat{EN} , \widehat{NW} , \widehat{WS} to obtain the period of the system (2.1) to be $2\pi/\sqrt{ad}$ when fluctuations are small enough.

3. Hsu's Method

Hsu [10] chooses appropriate nondimensional variables

$$u(t) = \frac{\delta}{\gamma} N_1(\tau), \quad v(t) = \frac{\beta}{\gamma} N_2(\tau); \qquad t = \gamma \tau, \quad a = \frac{\alpha}{\gamma},$$

to reduce the Lotka-Volterra system

$$N_1'(\tau) = N_1(\tau) \{ \alpha - \beta N_2(\tau) \}, \qquad N_2'(\tau) = N_2(\tau) \{ \delta N_1(\tau) - \gamma \},$$

to the system

$$(3.1) u'(t) = u(t)\{a - v(t)\}, v'(t) = v(t)\{u(t) - 1\},$$

which, along with the initial conditions

$$(3.2) u(0) = u_0 > 0, v(0) = v_0 > 0,$$

gives

$$\int_{1}^{u} \frac{\xi - 1}{\xi} d\xi + \int_{a}^{v} \frac{\eta - a}{\eta} d\eta = C_{0}$$

or

(3.3)
$$u - 1 - \log(u) + v - a - a \log\left(\frac{v}{a}\right) = C_0,$$

with

$$C_0 = u_0 - 1 - \log(u_0) + v_0 - a - a \log\left(\frac{v_0}{a}\right).$$

Hsu employs an auxiliary system (3.6) of differential equations to obtain an integral formula for the period of the closed orbit determined by (3.3).

A manipulation of differentiating the first equation of (3.1) with respect to t and then eliminating both v'(t) [by using the second equation of (3.1)] and v(t) [by using the first equation of (3.1)] yields the nonlinear second-order differential equation

(3.4)
$$u''(t) - \frac{[u'(t)]^2}{u(t)} - \{u'(t) - au(t)\}\{u(t) - 1\} = 0,$$

which can not be integrated in terms of elementary functions. But Hsu uses a transform

$$(3.5) u = \exp(z) \text{or} z = \log(u)$$

to simplify (3.4) into the form

$$z''(t) - \{z'(t) - a\}\{\exp(z) - 1\} = 0,$$

which gives the auxiliary system

(3.6)
$$z'(t) = w, \qquad w'(t) = \{w - a\}\{\exp(z) - 1\}.$$

It follows that

(3.7)
$$\frac{dw}{dz} = \frac{\{w-a\}\{\exp(z)-1\}}{w}$$
, or $\frac{w}{w-a}dw = \{\exp(z)-1\}dz$.

Moreover, the zw-coordinates are related to the uv-coordinates by

(3.8)
$$z = \log(u)$$
 and $w = z'(t) = \frac{u'(t)}{u(t)} = a - v(t)$.

The periodic orbit of (3.1), (3.2), which is determined by (3.3), has the left extreme point (u_*, a) and the right extreme point (u^*, a) , where u_* , u^* are two roots of $u - 1 - \log(u) = C_0$ with $u_* < u^*$. The lower branch of periodic orbit corresponds to $v \in (0, a)$ or $w \in (0, a)$ in the zw-coordinates. To compute the time T_1 traveling along the lower branch of the closed curve (3.3) from (u_*, a) to (u^*, a) , suppose that $u = u_*, v = a$ for t = 0. Then, from (3.8), we have $z = \log(u_*), w = 0$ for t = 0. It follows from z'(t) = w that

$$T_1 = \int_{\log(u_*)}^{\log(u^*)} \frac{dz}{w}.$$

To determine a formula for w in terms of z, we integrate (3.7) to get

$$\int_0^w \frac{\xi}{\xi - a} \, d\xi = \int_{\log(u_*)}^z \{ \exp(\eta) - 1 \} \, d\eta \quad \text{or} \quad F(w) = G(z),$$

with $F(w) = w + a \log(1 - w/a)$ and $G(z) = \exp(z) - z + \log(u_*) - u_* = \exp(z) - z - 1 - C_0$. From the fact that F'(w) = -w/(a-w) < 0 for $w \in (0, a)$, we have the existence of the inverse function of F(w) for $w \in (0, a)$, and thus $w = F_1^{-1}(G(z))$, where $F_1(w)$ is the restriction of F(w) on (0, a), and

(3.9)
$$T_1 = \int_{\log(u_*)}^{\log(u^*)} \frac{dz}{F_1^{-1}(G(z))}.$$

Similarly, the time T_2 traveling along the upper branch of the periodic orbit (v > a or w < 0) from (u^*, a) to (u_*, a) is

(3.10)
$$T_2 = \int_{\log(u^*)}^{\log(u_*)} \frac{dz}{F_2^{-1}(G(z))},$$

where $F_2(w)$ is the restriction of F(w) on $(-\infty, 0)$.

Hsu observes that each of two integrals in (3.9), (3.10) is an improper integral with a singularity of the square root type at both $\log(u^*)$ and $\log(u_*)$ by virtue of the fact that $G(\log(u^*)) = G(\log(u_*)) = 0$, F(0) = F'(0) = 0, and $F''(0) \neq 0$. Thus, combining (3.9), (3.10) yields the following theorem.

Theorem 3.1. The period of the periodic solution for the system (3.1) subject to the initial data (3.2) is represented as

(3.11)
$$T = \int_{\log(u_*)}^{\log(u^*)} \left\{ \frac{1}{F_1^{-1}(G(z))} - \frac{1}{F_2^{-1}(G(z))} \right\} dz,$$

where u_*, u^* are two roots of $u - 1 - \log(u) = C_0$ satisfying $u_* < u^*, C_0 = u_0 - 1 - \log(u_0) + v_0 - a - a \log(v_0/a)$, $G(z) = \exp(z) - z - 1 - C_0$, and $F_2(w), F_1(w)$ are the restrictions of $F(w) = w + a \log(1 - w/a)$ on $(-\infty, 0]$, [0, a), respectively.

4. Waldvogel's Method

Using a change of dependent variables

$$(4.1) x = \log(u), y = \log(v)$$

[or $u = \exp(x)$, $v = \exp(y)$], Waldvogel [25, 26] reduces the system having two positive constants a, d

(4.2)
$$u'(t) = au\{v-1\}, \qquad v'(t) = dv\{1-u\};$$

to

(4.3)
$$x'(t) = a\{\exp(y) - 1\}, \qquad y'(t) = d\{1 - \exp(x)\};$$

which is considered as a Hamiltonian system $x'(t) = \partial H/\partial y, y'(t) = -\partial H/\partial x$. It then follows from the theory of Hamiltonian systems that the equation

$$(4.4) H(x,y) = h > 0$$

with $H(x,y)=a\{\exp(y)-y-1\}+d\{\exp(x)-x-1\}$, defines a periodic solution. Next, Waldvogel defines increasing functions $G_1(x),G_2(y)$ such that

$$(4.5) [G_1(x)]^2 = 2d\{\exp(x) - x - 1\}, [G_2(y)]^2 = 2a\{\exp(y) - y - 1\};$$

and introduces new coordinates ξ, η by

(4.6)
$$\xi = G_1(x) \quad \eta = G_2(y), \quad \text{or} \quad x = g_1(\xi) \quad y = g_2(\eta),$$

where g_j is the inverse function of G_j . Thus, in the $\xi\eta$ -coordinates, the system (4.3) becomes

(4.7)
$$\xi'(t) = \frac{\eta}{g_1'(\xi)g_2'(\eta)}, \quad \eta'(t) = \frac{-\xi}{g_1'(\xi)g_2'(\eta)};$$

and, moreover, (4.4) is converted into an equation of the circle

$$\xi^2 + \eta^2 = 2h.$$

Finally, integrating the first equation in (4.7) gives the period of the periodic solution of (4.3)

$$T = \oint g_1'(\xi)g_2'(\eta)\frac{d\xi}{\eta},$$

where the integral is taken clockwise over the circle (4.8). With the parameterization

(4.9)
$$\xi = \sqrt{2h} \cos(s), \quad \eta = \sqrt{2h} \sin(s);$$

Waldvogel obtains the following result.

Theorem 4.1. The period of the closed orbit determined by (4.4) is given by

(4.10)
$$T = \int_0^{2\pi} g_1'(\sqrt{2h} \cos(s)) g_2'(\sqrt{2h} \sin(s)) ds,$$

where g_1 and g_2 are functions described above.

Waldvogel [25] further states that the period is written as the integral over a full period of a *continuously differentiable* periodic function, and integrals of this type can be evaluated efficiently by the means of the trapezoidal rule [25, 26]. Waldvogel seems not to be aware of the fact that the integrand has a singularity of the square root type at several places.

5. Rothe's Method

Introducing the new coordinates (x, y) defined by $u = \exp(x), v = \exp(y)$, Rothe [19] transforms the system having positive constants a, d

(5.1)
$$u'(t) = au\{1 - v\} \quad v'(t) = dv\{u - 1\}$$

to the Hamiltonian system

(5.2)
$$x'(t) = -\frac{\partial H}{\partial y} \qquad y'(t) = \frac{\partial H}{\partial x}$$

with the Hamiltonian

(5.3)
$$H(x,y) = d\{\exp(x) - x - 1\} + a\{\exp(y) - y - 1\}.$$

Based on thermodynamics, the state sum of the Hamiltonian system (5.2), (5.3) is

$$Z(\beta) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp[-\beta H(x, y)] dx dy$$

for the inverse absolute temperature $\beta \in (0, \infty)$. It follows that $Z(\beta) = z(\beta a) z(\beta d)$ where we have with a substitution $s = \exp(x)$

$$z(\gamma) = \int_{-\infty}^{\infty} \exp[-\gamma \{\exp(x) - x - 1\}] dx$$
$$= \exp(\gamma) \int_{0}^{\infty} \exp(-\gamma s) s^{\gamma - 1} ds = \exp(\gamma) \gamma^{-\gamma} \Gamma(\gamma),$$

with the Gamma function Γ defined by Euler's integral of the second kind

$$\Gamma(\gamma) = \int_0^\infty \exp(-\sigma) \, \sigma^{\gamma - 1} \, d\sigma, \quad \gamma > 0.$$

On the other hand, the state sum is related to the energy-period function T(E) via

$$Z(\beta) = \int_0^\infty T(E) \exp(-\beta E) dE := \mathcal{L}[T](E).$$

In other words, the Laplace transform of the energy-period function is the canonical state sum. It follows from the inverse Laplace transform that

$$T(E) = \mathcal{L}^{-1}[Z](\beta) = \mathcal{L}^{-1}[z](\beta a) * \mathcal{L}^{-1}[z](\beta d).$$

To determine the function z is a Laplace transform, consider the function h from $(-\infty, \infty)$ to $[0, \infty)$ defined by $h(x) = \exp(x) - x - 1$. Let $x_- \in (-\infty, 0)$

and $x_+ \in (0, \infty)$ be two solutions of h(x) = E for $E \in (0, \infty)$. Define the functions $\tau_{\pm} : (0, \infty) \to (0, \infty)$, and $\tau : (0, \infty) \to (0, \infty)$ by

$$\tau_{+}(E) = \frac{1}{|h'(x_{+})|} = \frac{1}{\exp(x_{+}) - 1} = \frac{1}{E + x_{+}},$$
$$\tau_{-}(E) = \frac{1}{|h'(x_{-})|} = \frac{1}{1 - \exp(x_{-})} = \frac{1}{|x_{-}| - E},$$

and $\tau(E) = \tau_{+}(E) + \tau_{-}(E)$, respectively. Then $\mathcal{L}[\tau](E) = z(\beta)$. Moreover, we have

$$z(\beta a) = \mathcal{L}\left[\frac{1}{a}\tau\left(\frac{E}{a}\right)\right] \qquad z(\beta d) = \mathcal{L}\left[\frac{1}{d}\tau\left(\frac{E}{d}\right)\right].$$

The period is formulated as a convolution integral via the Laplace transform. Thus Rothe obtains the following result.

Theorem 5.1. The period of oscillations of the system (5.1) is given by

(5.4)
$$T(E) = \frac{1}{ad} \int_0^E \tau\left(\frac{s}{d}\right) \tau\left(\frac{E-s}{a}\right) ds,$$

where τ is the function described above.

6. Shih's Method

It seems in the literature that the algebraic equation (1.4) or (1.5) can not be solved explicitly for either variable in terms of the other; see, for example, Boyce and DiPrima [2, p. 475] among others. In Shih [22], we solve (1.5) explicitly for one variable in terms of the other, from which two integral representations of the period are obtained. The basic notations we employ are two inverse functions W(0,x), W(-1,x) of $x \exp(x)$ restricted to the intervals $[-1,0), (-\infty,-1]$, respectively. Our method can be considered to be elementary but elegant.

First of all, the function $x \exp(x)$ has the positive derivative $(x+1) \exp(x)$ if x > -1. Define the inverse function of $x \exp(x)$ restricted on the interval $[-1, \infty)$ to be W(0, x). Similarly, we define the inverse function of $x \exp(x)$ restricted on the interval $(-\infty, -1]$ to be W(-1, x). For the nature of this study, both W(0, x) and W(-1, x) will be employed only for $x \in [-\exp(-1), 0)$.

In 1779, Euler obtained a series expansion for the solution of the trinomial equation $x^{\alpha} - x^{\beta} = (\alpha - \beta)vx^{\alpha+\beta}$ in the limiting case as $\alpha \to \beta$, which was proposed in 1758 by Lambert. In this case, the equation becomes $\log(x) = vx^{\beta}$, which has the solution $x = \exp(-W(0, -\beta v)/\beta)$. Shih [21] uses W(0, x)

for x > 0 to describe a slowly moving shock of Burgers' equation in the quarter plane. Functions W(-k,x) are denoted as LambertW(-k,x) in the computer algebra system Maple V release 4b (available since August 1996), and ProductLog [-k,x] in Mathematica version 3 (released in November 996), respectively. Both of them are found to have some bugs in asymptotic behavior of W(-1,x) with $x = -\exp(-1)$. A good reference of these functions is Corless, Gonnet, Hare, Jeffrey, and Knuth [4].

Rewrite (1.5) as

$$-\frac{b}{a}v\exp\left(-\frac{b}{a}v\right) = -\left(\frac{c}{d}u\right)^{-d/a}\exp\left(\frac{c}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right),$$

which lies in the interval $[-\exp(-1), 0)$ for positive v. Solving this equation for v gives

$$(6.1) v = g_k(u) g_k(u) = -\frac{a}{b} W\left(-k, -\left(\frac{c}{d}u\right)^{-d/a} \exp\left(\frac{c}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right)\right),$$

for k = 0, 1. Next, we determine the range of u. From

$$-\left(\frac{c}{d}u\right)^{-d/a}\exp\left(\frac{c}{a}u-1-\frac{d}{a}-\frac{E}{a}\right)\in[-\exp(-1),0),$$

we get the inequality

$$-\frac{c}{d}u\exp\left(-\frac{c}{d}u\right) \le -\exp\left(-1 - \frac{E}{d}\right),\,$$

which is solved to give

(6.2)
$$u \in [u_{\min}, u_{\max}], \quad u_{\min} = -\frac{d}{c}W\left(0, -\exp\left(-1 - \frac{E}{d}\right)\right),$$
$$u_{\max} = -\frac{d}{c}W\left(-1, -\exp\left(-1 - \frac{E}{d}\right)\right).$$

Finally, substituting (6.1) into the first equation of (1.1) gives

$$dt = \frac{du}{u\{a - b \, q_k(u)\}}$$

for k=0,1. Then traveling along the lower branch described by $v=g_0(u)$ from the point $(u_{\min},a/b)$, with $t=t|_{P_w}$, to the point $(u_{\max},a/b)$, with $t=t|_{P_e}$, in the counterclockwise direction yields

(6.3)
$$t|_{P_e} - t|_{P_w} = \int_{u_{\min}}^{u_{\max}} \frac{du}{u\{a - b \, q_0(u)\}};$$

while traveling along the upper branch described by $v = g_1(u)$ from the point $(u_{\text{max}}, a/b)$, with $t = t|_{P_e}$, to the point $(u_{\text{min}}, a/b)$, with $t = t|_{P_w}$, in the counterclockwise direction yields

(6.4)
$$t|_{P_w} - t|_{P_e} = \int_{u_{\text{max}}}^{u_{\text{min}}} \frac{du}{u\{a - b \, q_1(u)\}}.$$

Thus an integral representation of the period is obtained.

Theorem 6.1. The closed trajectory determined by (1.5) has the period

(6.5)
$$T(E) = \int_{u_{\min}}^{u_{\max}} \left\{ \frac{1}{u\{a - b g_0(u)\}} + \frac{-1}{u\{a - b g_1(u)\}} \right\} du,$$

where the functions $g_0(u)$, $g_1(u)$ are given by (6.1); and two endpoints u_{\min} , u_{\max} of the integral are defined by (6.2).

It is easy to see from $g_k(u) = a/b$ at $u = u_{\text{max}}$ and $u = u_{\text{min}}$ for k = 0, 1 that each integrand in (6.3), (6.4) is singular at each endpoint of the integration. In particular, it is a weak singularity of the square-root type. The phenomenon of having a weak singularity in the integral for the period takes place even in the linear problems.

The period depends on the energy E, and thus on initial data u_0 , v_0 . This is different from the linearized problem.

With a splitting of the integration interval and a simple substitution, one can reduce the integral of the period (6.5) to be of the convolution type.

Theorem 6.2. The period of the closed trajectory determined by (1.5) can be expressed as

(6.6)
$$T(E) = \frac{1}{ad} \int_0^E \Phi\left(\frac{s}{d}\right) \Phi\left(\frac{E-s}{a}\right) ds,$$

where

(6.7)
$$\Phi(s) = \{1 + W(0, -\exp(-1-s))\}^{-1} -\{1 + W(-1, -\exp(-1-s))\}^{-1}.$$

Proof. A splitting of the integration interval in (6.5) yields

$$\begin{split} T = & \int_{u_{\min}}^{d/c} \left\{ \frac{1}{u\{a - b\,g_0(u)\}} + \frac{-1}{u\{a - b\,g_1(u)\}} \right\} \, du + \\ & \int_{d/c}^{u_{\max}} \left\{ \frac{1}{u\{a - b\,g_0(u)\}} + \frac{-1}{u\{a - b\,g_1(u)\}} \right\} \, du. \end{split}$$

By using properties of the functions W(-k,x) with k=0,1, the substitution

(6.8)
$$u(s) = -\frac{d}{c}W\left(0, -\exp\left(-1 - \frac{s}{d}\right)\right)$$

gives

$$\int_{u_{\min}}^{d/c} \frac{1}{u\{a - b g_0(u)\}} du = \frac{1}{ad} \int_0^E \phi_3(s) ds,$$
$$\int_{u_{\min}}^{d/c} \frac{-1}{u\{a - b g_1(u)\}} du = \frac{1}{ad} \int_0^E \phi_2(s) ds;$$

and the substitution

(6.9)
$$u(s) = -\frac{d}{c}W\left(-1, -\exp\left(-1 - \frac{s}{d}\right)\right)$$

gives

$$\int_{d/c}^{u_{\text{max}}} \frac{1}{u\{a - b g_0(u)\}} du = \frac{1}{ad} \int_0^E \phi_4(s) ds,$$
$$\int_{d/c}^{u_{\text{max}}} \frac{-1}{u\{a - b g_1(u)\}} du = \frac{1}{ad} \int_0^E \phi_1(s) ds,$$

where $\phi_1(s), \phi_2(s), \phi_3(s), \phi_4(s)$ are defined by

$$\phi_1(\sigma) = \left\{ 1 + W\left(-1, -\exp\left(-1 - \frac{\sigma}{d}\right)\right) \right\}^{-1} \left\{ 1 + W\left(-1, -\exp\left(\frac{\sigma}{a} - 1 - \frac{E}{a}\right)\right) \right\}^{-1},$$

$$\phi_2(\sigma) = -\left\{ 1 + W\left(0, -\exp\left(-1 - \frac{\sigma}{d}\right)\right) \right\}^{-1} \left\{ 1 + W\left(-1, -\exp\left(\frac{\sigma}{a} - 1 - \frac{E}{a}\right)\right) \right\}^{-1},$$

$$\phi_3(\sigma) = \left\{ 1 + W\left(0, -\exp\left(-1 - \frac{\sigma}{d}\right)\right) \right\}^{-1} \left\{ 1 + W\left(0, -\exp\left(\frac{\sigma}{a} - 1 - \frac{E}{a}\right)\right) \right\}^{-1},$$

$$\phi_4(\sigma) = -\left\{ 1 + W\left(-1, -\exp\left(-1 - \frac{\sigma}{d}\right)\right) \right\}^{-1} \left\{ 1 + W\left(0, -\exp\left(\frac{\sigma}{a} - 1 - \frac{E}{a}\right)\right) \right\}^{-1},$$

respectively. It then follows that

$$T = \frac{1}{ad} \int_0^E \{\phi_1(s) + \phi_2(s) + \phi_3(s) + \phi_4(s)\} ds,$$

which gives (6.6).

7. Equivalence of the Integrals

As a unified treatment to the period of the periodic solution of the Lotka-Volterra system (1.1), its integral representations known in the literature are shown to be equivalent to ours.

Theorem 7.1. Volterra's integral formula (2.4) is reduced to the form (6.5) having a = b, c = d, and $C = \exp(-a - d - E)$.

Proof. There are two steps in the proof. Step I: Express (2.4) in terms of Lambert W functions. In terms of Lambert W functions, we obtain

$$v_1 = -W\left(0, -C^{1/a} \exp\left(\frac{d}{a}\right)\right), \quad v_2 = -W\left(-1, -C^{1/a} \exp\left(\frac{d}{a}\right)\right);$$
$$u_1 = -W\left(0, -C^{1/d} \exp\left(\frac{a}{d}\right)\right), \quad u_2 = -W\left(-1, -C^{1/d} \exp\left(\frac{a}{d}\right)\right).$$

Furthermore, the segment $\stackrel{\frown}{SE}$ of the closed orbit determined by (2.2) can be represented by $u=-W(-1,-x^{1/d}), v=-W(0,-(C/x)^{1/a})$ in the counterclockwise direction as x moves from $\exp(-d)$ to $C\exp(a)$; the segment $\stackrel{\frown}{EN}$ of the closed orbit determined by (2.2) can be represented by $u=-W(-1,-x^{1/d}), v=-W(-1,-(C/x)^{1/a})$ in the counterclockwise direction as x moves from $C\exp(a)$ to $\exp(-d)$; the segment $\stackrel{\frown}{NW}$ of the closed orbit determined by (2.2) can be represented by $u=-W(0,-x^{1/d}), v=-W(-1,-(C/x)^{1/a})$ in the counterclockwise direction as x moves from $\exp(-d)$ to $C\exp(a)$; the segment $\stackrel{\frown}{WS}$ of the closed orbit determined by (2.2) can be represented by $u=-W(0,-x^{1/d}), v=-W(0,-(C/x)^{1/a})$ in the counterclockwise direction as x moves from $C\exp(a)$ to $\exp(-d)$. It follows that the period (2.4) is of the form

$$(7.1) T = T_{se} + T_{en} + T_{nw} + T_{ws},$$

where

$$T_{se} = \frac{1}{ad} \int_{\exp(-d)}^{C \exp(a)} \frac{dx}{x\{1 + W(-1, -x^{1/d})\}\{1 + W(0, -(C/x)^{1/a})\}},$$

$$T_{en} = \frac{1}{ad} \int_{C \exp(a)}^{\exp(-d)} \frac{dx}{x\{1 + W(-1, -x^{1/d})\}\{1 + W(-1, -(C/x)^{1/a})\}},$$

$$T_{nw} = \frac{1}{ad} \int_{\exp(-d)}^{C \exp(a)} \frac{dx}{x\{1 + W(0, -x^{1/d})\}\{1 + W(-1, -(C/x)^{1/a})\}},$$

$$T_{ws} = \frac{1}{ad} \int_{C \exp(a)}^{\exp(-d)} \frac{dx}{x\{1 + W(0, -x^{1/d})\}\{1 + W(0, -(C/x)^{1/a})\}}.$$

Step II: Apply a change of variable to each integral in (7.1) along with the conversion between C and E. It follows from (1.5), (2.2), and the conditions a = b, c = d that $C = \exp(-a - d - E)$. A substitution

(7.2)
$$u = -W(-1, -x^{1/d}) \quad \text{or} \quad x = \{u \exp(-u)\}^d$$
having $\frac{dx}{(1-u)x} = \frac{d}{u}du$ gives

$$T_{se} = \frac{1}{a} \int_{1}^{-W(-1, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W\left(0, -u^{-d/a}\right) + \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right) \right\}^{-1} du,$$

and

$$T_{en} = \frac{-1}{a} \int_{1}^{-W(-1, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W\left(-1, -u^{-d/a}\right) + \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right) \right\}^{-1} du;$$

while a substitution

(7.3)
$$u=-W(0,-x^{1/d}) \quad \text{ or } \quad x=\{u \exp(-u)\}^d$$
 having $\frac{dx}{(1-u)x}=\frac{d}{u}du$ yields

$$T_{nw} = \frac{1}{a} \int_{1}^{-W(0, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W\left(-1, -u^{-d/a} \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right)\right) \right\}^{-1} du,$$

and

$$T_{ws} = \frac{-1}{a} \int_{1}^{-W(0, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W\left(0, -u^{-d/a} \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right)\right) \right\}^{-1} du.$$

Thus, we have

$$T_{en} + T_{nw} = \frac{-1}{a} \int_{-W(0, -\exp(-1-E/d))}^{-W(0, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W \left(-1, -u^{-d/a} \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right) \right) \right\}^{-1} du,$$

$$T_{ws} + T_{se} = \frac{1}{a} \int_{-W(0, -\exp(-1-E/d))}^{-W(-1, -\exp(-1-E/d))} u^{-1} \left\{ 1 + W \left(0, -u^{-d/a} \exp\left(\frac{d}{a}u - 1 - \frac{d}{a} - \frac{E}{a}\right) \right) \right\}^{-1} du.$$

This completes the proof.

It is interesting to note that the definition (2.3) used by Volterra is related to the substitutions (7.2), (7.3) in the proof.

Theorem 7.2. Hsu's integral formula (3.11) is reduced to (6.5) with $E = C_0$, b = 1, c = 1, d = 1.

Proof. The proof is similar to that for Volterra's integral formula. First of all, we have $C_0 = E$ by using (1.5), (3.3), and the conditions b = 1, c = 1, d = 1. Next, in terms of Lambert W functions, we have

$$u_* = -W(0, -\exp(-1 - E)), \quad u^* = -W(-1, -\exp(-1 - E));$$

$$F_1^{-1}(z) = a + aW\left(0, -\exp\left(-1 + \frac{z}{a}\right)\right), \quad F_2^{-1}(z) = a + aW\left(-1, -\exp\left(-1 + \frac{z}{a}\right)\right);$$
and (3.11) becomes

$$T = \int_{\log(-W(0, -\exp(-1-E)))}^{\log(-W(-1, -\exp(-1-E)))} \left\{ \left\{ a + a W \left(0, -\exp\left(\frac{\exp(z)}{a} - \frac{z}{a} - 1 - \frac{1}{a} - \frac{E}{a} \right) \right) \right\}^{-1} - \left\{ a + a W \left(-1, -\exp\left(\frac{\exp(z)}{a} - \frac{z}{a} - 1 - \frac{1}{a} - \frac{E}{a} \right) \right) \right\}^{-1} \right\} dz,$$

which, after using the substitution

(7.4)
$$z = \log(u)$$
 or $u = \exp(z)$, gives

$$T = \int_{-W(0, -\exp(-1-E))}^{-W(-1, -\exp(-1-E))} u^{-1} \left\{ \left\{ a + aW \left(0, -u^{-1/a} \exp \left(\frac{u}{a} - 1 - \frac{1}{a} - \frac{E}{a} \right) \right) \right\}^{-1} - \left\{ a + aW \left(-1, -u^{-1/a} \exp \left(\frac{u}{a} - 1 - \frac{1}{a} - \frac{E}{a} \right) \right) \right\}^{-1} \right\} du.$$

This completes the proof.

We make a remark here that the change of variable (3.5) used by Hsu is related to the substitution (7.4) in the proof.

Theorem 7.3. Waldvogel's integral formula (4.10) is reduced to the form (6.6) having E = h, a = b, and c = d.

Proof. Note that h = E by virtue of (1.5), (4.4), and the assumed conditions a = b, c = d. The definitions of $G_1(x)$ and $G_2(y)$ give

$$G_1(x) = \begin{cases} \sqrt{2d\{\exp(x) - x - 1\}}, & x \ge 0; \\ -\sqrt{2d\{\exp(x) - x - 1\}}, & x \le 0; \end{cases}$$

$$G_2(y) = \begin{cases} \sqrt{2a\{\exp(y) - y - 1\}}, & y \ge 0; \\ -\sqrt{2a\{\exp(y) - y - 1\}}, & y \le 0. \end{cases}$$

In terms of Lambert W functions, $g_1(\xi)$ and $g_2(\eta)$ become

$$g_1(\xi) = \begin{cases} \log(-W(-1, -\exp(-1 - \frac{\xi^2}{2d}))), & \xi \ge 0; \\ \log(-W(0, -\exp(-1 - \frac{\xi^2}{2d}))), & \le 0; \end{cases}$$

$$g_2(\eta) = \begin{cases} \log(-W(-1, -\exp(-1 - \frac{\eta^2}{2a}))), & \eta \ge 0; \\ \log(-W(0, -\exp(-1 - \frac{\eta^2}{2a}))), & \eta \le 0; \end{cases}$$

along with their first derivatives

$$g_1'(\xi) = \begin{cases} \frac{-\xi}{d\{1 + W(-1, -\exp(-1 - \xi^2/(2d)))\}}, & \xi > 0; \\ \frac{-\xi}{d\{1 + W(0, -\exp(-1 - \xi^2/(2d)))\}}, & \xi < 0; \end{cases}$$

$$g_2'(\eta) = \begin{cases} \frac{-\eta}{a\{1 + W(-1, -\exp(-1 - \eta^2/(2a)))\}}, & \eta > 0; \\ \frac{-\eta}{a\{1 + W(0, -\exp(-1 - \eta^2/(2a)))\}}, & \eta < 0. \end{cases}$$

According to the positive and negative signs of $\cos(s)$ and $\sin(s)$, the integral (4.10) is split into four parts as follows:

$$\begin{split} T &= \frac{2h}{ad} \int_0^{\pi/2} \frac{\cos(s)}{1 + W(-1, -\exp(-1 - (h/d)\cos^2(s)))} \frac{\sin(s)}{1 + W(-1, -\exp(-1 - (h/a)\sin^2(s)))} \, ds \\ &+ \frac{2h}{ad} \int_{\pi/2}^{\pi} \frac{\cos(s)}{1 + W(0, -\exp(-1 - (h/d)\cos^2(s)))} \frac{\sin(s)}{1 + W(-1, -\exp(-1 - (h/a)\sin^2(s)))} \, ds \\ &+ \frac{2h}{ad} \int_{\pi}^{3\pi/2} \frac{\cos(s)}{1 + W(0, -\exp(-1 - (h/d)\cos^2(s)))} \frac{\sin(s)}{1 + W(0, -\exp(-1 - (h/a)\sin^2(s)))} \, ds \\ &+ \frac{2h}{ad} \int_{3\pi/2}^{2\pi} \frac{\cos(s)}{1 + W(-1, -\exp(-1 - (h/d)\cos^2(s)))} \frac{\sin(s)}{1 + W(0, -\exp(-1 - (h/a)\sin^2(s)))} \, ds \end{split}$$

which, after a substitution

$$(7.5) \rho = h\cos^2(s)$$

in each integral, becomes

$$\begin{split} T = & \frac{-1}{ad} \int_{h}^{0} \frac{1}{1 + W(-1, -\exp(-1 - \rho/d))} \frac{1}{1 + W(-1, -\exp(-1 - (h - \rho)/a))} \, d\rho \\ & + \frac{-1}{ad} \int_{0}^{h} \frac{1}{1 + W(0, -\exp(-1 - \rho/d))} \frac{1}{1 + W(-1, -\exp(-1 - (h - \rho)/a))} \, d\rho \\ & + \frac{-1}{ad} \int_{h}^{0} \frac{1}{1 + W(0, -\exp(-1 - \rho/d))} \frac{1}{1 + W(0, -\exp(-1 - (h - \rho)/a))} \, d\rho \\ & + \frac{-1}{ad} \int_{0}^{h} \frac{1}{1 + W(-1, -\exp(-1 - \rho/d))} \frac{1}{1 + W(0, -\exp(-1 - (h - \rho)/a))} \, d\rho. \end{split}$$

In other words, we obtain

(7.6)
$$T = \frac{1}{ad} \int_0^h \Phi(\frac{\rho}{d}) \Phi(\frac{h-\rho}{a}) d\rho,$$

with $\Phi(\rho)$ defined by (6.7). This completes the proof.

The relation between the dependent variable u defined by (4.2) and the integrator ρ in (7.6) is

(7.7)
$$\rho = h\cos^2(s) = \frac{\xi^2}{2} = d\{\exp(x) - x - x\} = d\{u - \log(u) - 1\}$$

by using (7.5), (4.9), (4.6), (4.5), and (4.1). Thus, (7.7) is equivalent to substitutions (6.8), (6.9) used to convert (6.5) into (6.6).

Theorem 7.4. Rothe's integral formula (5.4) is reduced to the form (6.6) having a = b and c = d.

As shown above, Rothe's method is not as *elementary* as ours in obtaining a convolution integral for the period of the periodic solution of the Lotka-Volterra system (1.1).

References

- 1. M. A. Abdelkader, Exact solutions of Lotka-Volterra equations, *Math. Biosci.* **20** (1974), 293-297.
- 2. W. E. Boyce and R. C. DiPrima, Elementary Differential Equations and Boundary Value Problems, fifth edition, John Wiley & Sons Inc., 1992.
- 3. R. R. Burnside, A note on exact solutions of two prey-predator equations, *Bull. Math. Biol.* 44 (1982), 893-897.
- 4. R. M. Corless, G. H. Gonnet, D.E.G. Hare, D. J. Jeffrey, and D. E. Knuth, On Lambert W function, *Adv. Comput. Math.* 5 (1996), 329-359.

- H. T. Davis, Introduction to Nonlinear Differential and Integral Equations, United States Atomic Energy Commission, Washington, D.C., 1960. Reissued by Dover, New York, 1962.
- R. Dutt, Application of Hamilton-Jacobi theory to the Lotka-Volterra oscillator, Bull. Math. Biol. 38 (1976), 459-465.
- 7. J. S. Frame, Explicit solutions in two species Volterra systems, *J. Theor. Biol.* **43** (1974), 73-81.
- 8. J. Grasman, Asymptotic Methods for Relaxation Oscillations and Applications, Springer-Verlag, New York, 1987.
- 9. J. Grasman and E. Veling, An asymptotic formula for the period of a Volterra-Lotka system, *Math. Biosci.* **18** (1973), 185-189.
- S.-B. Hsu, A remark on the period of the periodic solution in the Lotka-Volterra system, J. Math. Anal. Appl. 95 (1983), 428-436.
- 11. H. A. Lauwerier, A limit case of a Volterra-Lotka system, Mathematical Centre, Amsterdam, Report TN 79, 1975.
- 12. A. J. Lotka, Undamped oscillations derived from the law of mass action. J. Amer. Chem. Soc. 42 (1920), 1595-1599.
- A. J. Lotka, Elements of Physical Biology, William and Wilkins, Baltimore, 1925. Reissued as Elements of Mathematical Biology, Dover, New York, 1956. pp. 88-90.
- J. D. Murray, Lectures on Nonlinear-Differential-Equation Models in Biology, Clarendon Press, Oxford, 1977.
- J. D. Murray, Mathematical Biology, Second, corrected edition, Springer, New York, 1993.
- 16. K. N. Murty and D.V.G. Rao, Approximate analytical solutions of general Lotka-Volterra equations, *J. Math. Anal. Appl.* **122** (1987), 582-588.
- 17. S. Olek, An accurate solution to the multispecies Lotka-Volterra equations, SIAM Rev., **36** (1994), 480-488.
- 18. J. H. Poincaré, Les Méthodes Nouvelles de la Mécanique Céleste, Volume I (1892), Volume II (1893), Volume III (1899), Gauthier-Villars, Paris. Reprinted by Dover, New York in 1958. English translation of all 3 volumes (1967) as NASA TT F-450, TT F-451, TT F-452, NASA, Washington, D.C.
- 19. F. Rothe, The periods of the Volterra-Lotka system, *J. Reine Angew. Math.* **355** (1985), 129-138.
- S. I. Rubinow, Introduction to Mathematical Biology, John Wiley & Sons, New York, 1975.
- 21. S.-D. Shih, A very slowly moving viscous shock of Burgers' equation in the quarter plane, Applicable Analysis, 56 (1/2), 1-18, 1995.

- 22. S.-D. Shih, Periodic Solution of a Lotka-Volterra System, preprint, 1996.
- 23. V. S. Varma, Exact solutions for a special prey-predator or competing species system, *Bull. Math. Biol.* **39** (1977), 619-622.
- 24. V. Volterra, Variazioni e fluttuazioni del numero d'individui in specei animali conviventi, Mem. R. Acad. Naz. dei Lincei, (ser. 6), 2 (1926), 31-113. A translation of much of this paper with title Variations and fluctuations of the number of individuals in animal species living together, by Mary E. Welk, appeared in J. Conseil Permanent International pour l'Exploitation de la Mer, 3 (1928), 1-51; and also as an appendix to R. N. Chapman, Animal Ecology, New York, McGraw Hill, 1931, 409-448. A complete translation with title Variations and fluctuations of popular size in coexisting animal species, in Applicable Mathematics of Non-physical Phenomena, F. Oliveira-Pinto and B. W. Conolly, John Wiley and Sons, 1982, 23-115.
- J. Waldvogel, The period in the Volterra-Lotka predator-prey model, SIAM J. Numer. Anal. 20 (1983), 1264-1272.
- 26. J. Waldvogel, The period in the Volterra-Lotka system is monotonic, *J. Math. Anal. Appl.* **114** (1986), 178-184.
- 27. A. J. Willson, On Varma's prey-predator problem, Bull. Math. Biol. 42 (1980), 599-600.

Department of Mathematics, University of Wyoming Laramie, WY 82071-3036, U.S.A. sdshih@uwyo.edu