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# Qualitative Tools for Studying Periodic Solutions and Bifurcations as Applied to the Periodically Harvested Logistic Equation

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Diego M. Benardete, V. W. Noonburg, and B. Pollina

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## 1. INTRODUCTION.

I have especially made every effort to display those rare results... that can be established with the absolute rigor demanded by mathematicians... Here we can find in fact a solid ground that can be confidently relied on, and which will be a great advantage in all research areas, even in those not restricted to the same rigor [32, preface].

One-dimensional differential equations  $dy/dt = f(t, y)$  that are periodic in  $t$  arise in many areas of applied mathematics. The attracting and repelling periodic solutions and their bifurcations are the key qualitative features that determine the observed behavior of the system being modeled. One quickly finds that the low dimensional character of the problem conceals difficulties that in practice are resolved by numerical simulation. However, these simulations are guided by theoretical results and techniques, as suggested in a related context by Poincaré in his wonderful statement on rigor quoted above.

The authors encountered such a differential equation when studying a simplified version of the Wilson-Cowan model of two periodically stimulated coupled neurons [29]. To assemble the needed theoretical toolkit, we turned to the logistic equation with periodic harvesting, a population model that we teach in our undergraduate classes and that is featured in many introductory texts [2], [3], [4]. These tools are presented below using the logistic equation as an example, and they should be of help to students and researchers in their own simulations and theoretical studies. In addition, some suggestions for further work are given in the last section.

We also touch on the inspiring yet wavering history of science and mathematics in three places: the development of the logistic equation and its variants, the use of Poincaré's first-return map in dynamics and chaos theory, and the progress and lack of it that marks the investigation of Hilbert's still unsolved sixteenth problem. It is gratifying that, even in mathematics, humble beginnings can quickly lead to grand vistas. Though we confine ourselves to real variable techniques, we allude to results obtained with complex variables, as in the bounds on the number of periodic solutions given in a beautiful yet brief paper of Ilyashenko [17].

**2. SMALL AND LARGE PERTURBATIONS.** One way to find periodic solutions of a nonautonomous equation  $dy/dt = f(t, y)$  is to view it as a perturbation of some autonomous equation  $dy/dt = g(y)$  whose behavior is well understood. Therefore we begin with the autonomous logistic equation including some remarks on its fascinating history [13], [19].

In his famous Essay on the Principle of Population that appeared in several editions from 1798 to 1826, the Reverend Thomas Malthus argued that "population, when unchecked, goes on doubling itself every twenty five years, or increases in a geometrical ratio," while "the means of subsistence... could not possibly be made to increase

faster than in an arithmetical ratio” [25, Chapter 1]. Therefore there is an inherent tendency to physical misery and moral decay that can only be partially mitigated by wise laws and extraordinary self-restraint. Though he is conscientious in examining the available data, and though he graduated from Cambridge with honors in mathematics as ninth wrangler, *Malthus nowhere includes in his Essay an exponential function let alone a differential equation.*

Sometime about 1835, the brilliant and wide-ranging Belgian scientist and statistician Adolphe Quetelet asked the mathematician Pierre Verhulst to undertake a study of the laws of population. Verhulst, who otherwise did routine work on elliptic functions while teaching at *L'école Militaire de Belgique*, complied in a series of three articles that appeared in 1838, 1845, and 1847. Verhulst begins by referring to *le célèbre Malthus*. As might be expected of a mathematician, to clarify Malthus's hypothesis Verhulst introduces the differential equation that we write as  $dP/dt = RP$ . He then assumes that the rate of population growth declines linearly to zero as population approaches some limiting level  $L$ . He uses the term *courbe logistique* to refer to the solution of the resulting equation that we write as  $dP/dt = RP(1 - P/L)$ . Then like Malthus he compares the predictions of his model with the available data. Both authors are aware that the rate of growth can be limited by a decrease in the birth rate as well as by an increase in the death rate. However, they are cautious in discussing the first alternative because such a decrease may be the result of practices such as contraception that were even more controversial at the time than they are today.

Verhulst and his equation lapsed into oblivion until they were rediscovered in the first decades of the twentieth century. A great controversy ensued in which Raymond Pearl argued vociferously that when properly applied and modified, the logistic equation was the law of growth for animal and plant populations and individuals. Others rightly countered that it lacked predictive value and that many different models could fit the data [19]. The logistic equation with its variants prevailed as the most important single population model, perhaps because of its conceptual simplicity and the resulting ease with which it can be meaningfully adapted. Discussion of these variants is found in nearly all introductory texts on differential equations [4].

One such variant is the logistic equation with constant harvesting,

$$dP/dt = RP(1 - P/L) - H, \tag{1}$$

where  $P$  is the population,  $t$  is time,  $R$  is the intrinsic growth rate,  $L$  is the carrying capacity,  $H$  is the harvesting rate, and the parameters  $R$ ,  $L$ , and  $H$  are nonnegative.

The distinguished population biologist Mark Kot reports that around 1975 a much circulated treatment of this equation by Fred Brauer and David Sanchez “caught people's attention because of a nice example having to do with the effects of hunting pressure on sandhill crane populations” [5], [20]. As we will see, this model suggests the fragility of ecosystems by showing how a small change in harvesting can bring an otherwise sustainable population to extinction, and thus serves as a warning in managing resources such as the North Atlantic fisheries. Therefore the bifurcation value  $H^*$  of this equation has great practical significance and it is referred to in the ecology and resource management literature as the *critical harvesting rate* or as the *maximal sustainable yield* [9]. Also in those same years the study of the logistic equation with time-varying parameters began [26].

The analysis of equation (1) becomes simpler if we rescale and let  $y = P/L$  be the population expressed as a fraction of the carrying capacity. Setting  $A = H/L$ , we obtain the nonlinear autonomous differential equation

$$dy/dt = Ry(1 - y) - A. \tag{2}$$

When  $A < R/4$ , there are two equilibrium values of  $y$ , both positive, and by solving the quadratic equation  $Ry(1 - y) - A = 0$  we can explicitly obtain these equilibria in terms of  $R$  and  $A$ :

$$y = \frac{1}{2} \pm \frac{1}{2} \sqrt{1 - 4A/R}. \tag{3}$$

Plotting some solutions along with the slope field clearly shows that the larger equilibrium is a sink which attracts solutions and the smaller equilibrium is a source which repels them [Figure 1(a)]. If the rescaled harvesting rate  $A$  is increased to the bifurcation value  $R/4$ , then there is one equilibrium solution,  $y = 1/2$ . This is a node which attracts solutions starting from initial values  $y(0) > 1/2$  and repels those starting from  $y(0) < 1/2$  [Figure 1(b)]. If  $A$  becomes greater than the bifurcation value  $R/4$ , there are no equilibria and *all initial populations eventually become extinct* [Figure 1(c)]. For a more complete discussion of the autonomous case see [2] or [5].

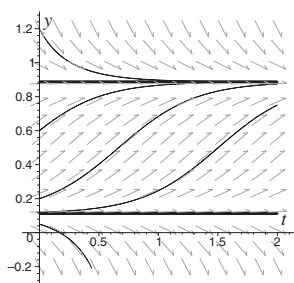


Figure 1. (a)  $A < R/4$

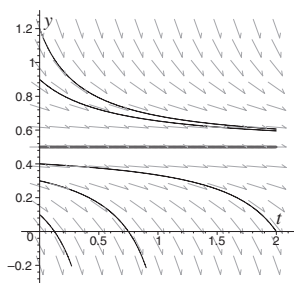


Figure 1. (b)  $A = R/4$

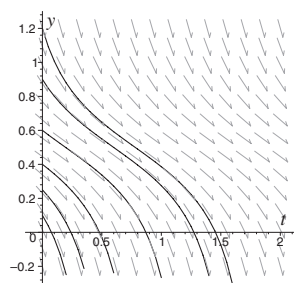


Figure 1. (c)  $A > R/4$

We now periodically perturb the autonomous logistic equation  $dy/dt = g(y) = Ry(1 - y)$  and observe the persistence of the equilibria as periodic solutions. Let the harvesting rate vary sinusoidally over one unit of time with an amplitude of  $\alpha$  about the mean harvesting rate  $A$ , thus obtaining a nonautonomous nonlinear differential equation periodically forced with period  $T = 1$ . We assume  $0 \leq \alpha \leq 1$ .

$$dy/dt = f(t, y) = Ry(1 - y) - A(1 + \alpha \sin(2\pi t)). \tag{4}$$

When the average harvesting rate  $A$  is small, the sink and source of the autonomous equation (2) are replaced respectively by an attracting and a repelling periodic cycle of period  $T = 1$  [Figure 2]. We will eventually determine the bifurcation value  $A = A^*$  for which there is precisely one periodic solution. As in the autonomous case, for  $A$  greater than the bifurcation value  $A^*$ , *all initial populations eventually become extinct* [Figure 3].

**Definition 1.** A differential equation  $dy/dt = f(t, y)$  has **period**  $T$  if for all  $t$  and  $y$ ,  $f(t + T, y) = f(t, y)$ . A solution  $y(t)$  of such a differential equation is **periodic**, or a **periodic cycle**, if for all  $t$ ,  $y(t + T) = y(t)$ .

The existence of the periodic cycles for sufficiently small perturbations  $A$  can be rigorously justified by the following theorem, which can be applied more widely to other cases where the parameters of an autonomous equation are allowed to vary periodically in time. In the language of dynamical systems, the theorem states that a

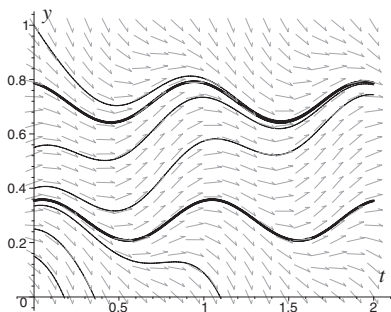


Figure 2.  $R = 5, \alpha = 0.5, A = 1$

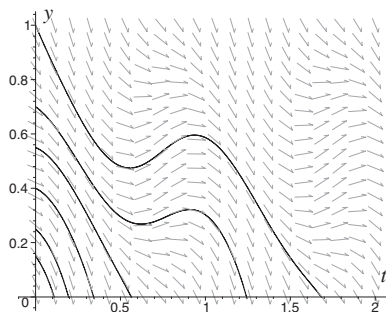


Figure 3.  $R = 5, \alpha = 0.5, A = 1.5$

hyperbolic equilibrium solution of an autonomous differential equation is *structurally stable*, that is it persists as a periodic cycle under small periodic perturbation of the parameters. Hyperbolicity and structural stability remain important themes in pure and applied treatments of more complex higher dimensional systems.

**Theorem 1.** [14]. *Let  $dy/dt = g(y)$  be an autonomous differential equation, with  $g(y_0) = 0, g'(y_0) \neq 0$ , and  $y_1(t) = y_0$  the resulting equilibrium solution. Consider  $dy/dt = f(t, y)$  where  $f(t, y)$  is periodic in  $t$  with period  $T$ . If for all  $(t, y)$ ,  $|f(t, y) - g(y)|, |f_y(t, y) - g'(y)|$ , and  $|f_t(t, y)|$  are sufficiently small, then there is a periodic solution  $y_2(t)$  of the time-dependent equation that stays arbitrarily close to the solution  $y_1(t)$  of the autonomous equation.*

We can easily demonstrate the nonexistence of periodic cycles of (4) for large values of  $A$ , and also put an upper bound on the bifurcation value  $A^*$ , by noting that  $Ry(1 - y)$  has a maximum of  $R/4$  at  $y = 1/2$ . Therefore for any solution  $y(t)$  of (4),

$$\begin{aligned} y(1) - y(0) &= \int_0^1 \frac{dy}{dt} dt \\ &= \int_0^1 [Ry(t)(1 - y(t)) - A(1 + \alpha \sin(2\pi t))] dt \\ &\leq R/4 - A. \end{aligned}$$

So if  $A > R/4$ , we see that  $y(1) < y(0)$ , implying that the solution  $y(t)$  is not periodic. Similarly, for all integers  $n$ ,

$$y(n + 1) - y(n) \leq R/4 - A < 0,$$

thus showing that  $y(t)$  diverges to  $-\infty$ .

**Proposition 1.** [7]. *For  $A > R/4$ , equation (4) has no periodic solution, and all solutions diverge to  $-\infty$ .*

**3. INVARIANT REGIONS AND GEOMETRY OF NULLCLINES.** We now estimate how small  $A$  must be to guarantee the existence of the attractor and repeller referred to in Section 2. We use a technique involving invariant regions and the *nullclines* and *generalized nullclines* of equation (4), that is, the loci of points in the  $(t, y)$  plane where, respectively,  $f(t, y) = 0$  and  $f_y(t, y) = 0$ . This technique is generally

useful in showing the existence and uniqueness of periodic orbits in a given region. Furthermore, in some cases the nullclines can be used to show the nonexistence of periodic solutions.

Let  $v_1(t) < v_2(t)$  be continuously differentiable curves of period  $T$  bounding the open region  $V$  in the  $(t, y)$  plane. We say that  $V$  is *forward invariant* if, as time increases, the slope field of  $dy/dt = f(t, y)$  points into the region along its boundary and is *backward invariant* if, as time increases, it points out of the region along its boundary. In such cases the curves  $v_1(t)$  and  $v_2(t)$  are called *fences* [16]. A fixed point argument involving the flow from the closed interval  $I = [v_1(0), v_2(0)] = [v_1(T), v_2(T)]$  to itself shows that there must be at least one periodic solution in  $V$ . This will become clearer when we introduce the Poincaré map in Section 4. Note that we can sometimes find fences that are constant functions of  $t$ .

**Theorem 2.** [14], [16]. *Consider  $dy/dt = f(t, y)$ , where  $f$  is continuous and periodic in  $t$  with period  $T$ . Any forward invariant region of the  $(t, y)$ -plane contains a periodic cycle of period  $T$ , as does any backward invariant region.*

Now let us suppose that  $f_y(t, y) < 0$  at all points  $(t, y)$  in some forward invariant region  $V$  and that  $y_1(t) < y_2(t)$  are two solutions contained in  $V$ . By the Mean Value Theorem we see that at time  $t$ ,

$$(y_2(t) - y_1(t))' = f(t, y_2(t)) - f(t, y_1(t)) = f_y(t, c)(y_2(t) - y_1(t)) < 0,$$

where  $c$  is some number between  $y_1(t)$  and  $y_2(t)$ . Therefore  $y_2(t) - y_1(t)$  is a decreasing function of  $t$ , so  $y_1(t)$  and  $y_2(t)$  cannot both be periodic, and the region  $V$  is *contracting*. A similar argument applies to a backward invariant region when  $f_y(t, y) > 0$  and shows that it is *expanding*.

**Theorem 3.** [14], [16]. *Consider  $dy/dt = f(t, y)$ , where  $f$  is continuously differentiable in  $t$  and  $y$ , and is periodic in  $t$  with period  $T$ .*

- (a) *If for all  $(t, y)$  in a forward invariant region  $V$ ,  $f_y(t, y) < 0$ , then  $V$  is contracting and contains a unique periodic solution, and this cycle is an attractor.*
- (b) *If for all  $(t, y)$  in a backward invariant region  $V$ ,  $f_y(t, y) > 0$ , then  $V$  is expanding and contains a unique periodic solution, and this cycle is a repeller.*

The nullclines and generalized nullclines are used to understand the global geometry of the flow, to locate invariant regions, and to determine if such regions are contracting or expanding. This is easily done for equation (4).

When  $A < R/[4(1 + \alpha)]$ , we can use the quadratic formula to see that for all  $t$ , there are two values of  $y$  for which  $f(t, y) = 0$ . In fact, the nullclines of (4) consist of two continuously differentiable curves  $z_1$  and  $z_2$  for which  $0 < z_1(t) < 1/2 < z_2(t) < 1$ , and  $y = 1/2$  is the generalized nullcline [Figure 4]. Note:

$$\begin{aligned} f(t, y) < 0 & \text{ if } y < z_1(t) \text{ or } y > z_2(t), \\ f(t, y) > 0 & \text{ if } z_1(t) < y < z_2(t), \\ f_y(t, y) < 0 & \text{ if } y > 1/2, \\ f_y(t, y) > 0 & \text{ if } y < 1/2. \end{aligned}$$

It follows that  $y = 0$  and  $y = 1/2$  are constant fences bounding an expanding backward invariant region  $V_1$ , and  $y = 1/2$  and  $y = 1$  are constant fences bounding a con-

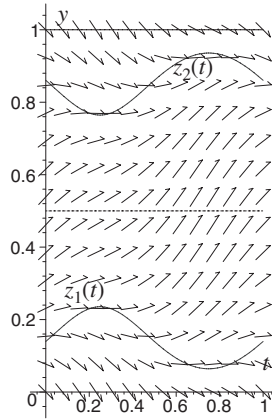


Figure 4. Nullclines,  $A < \frac{R}{4(1+\alpha)}$

tracting forward invariant region  $V_2$ . Thus we are led to the following proposition adapted from Campbell and Kaplan [7].

**Proposition 2.** *In equation (4), when  $A < R/[4(1 + \alpha)]$ , there exist precisely two periodic cycles, a repeller  $y_1(t)$  and an attractor  $y_2(t)$ , satisfying for all  $t$ ,  $0 < y_1(t) < 1/2 < y_2(t) < 1$ .*

When the nullclines of  $dy/dt = f(t, y)$  pinch together and are no longer defined in some interval of time, they can be used to show the nonexistence of periodic solutions for the equation  $dy/dt = cf(t, y)$  so long as  $c$  is sufficiently large.

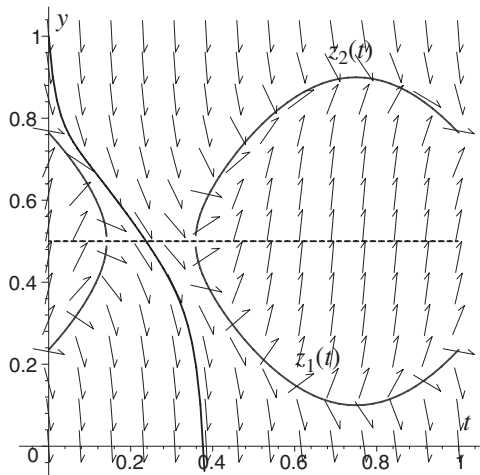


Figure 5. Pinched nullclines,  $\frac{R}{4(1+\alpha)} < A < \frac{R}{4}$

In equation (4), if  $1/[4(1 + \alpha)] < A/R \leq 1/4$ , then the nullcline curves  $z_1$  and  $z_2$  pinch together and are no longer defined on an interval centered at  $t = 1/4$ . For all  $t$  in this interval,  $f(t, y) < 0$  [Figure 5]. If we rewrite equation (4) as

$$dy/dt = f(t, y) = R[y(1 - y) - (A/R)(1 + \alpha \sin(2\pi t))]$$

we see that for a fixed value of  $A/R$ , an increase in  $R$  leaves the nullclines unchanged but makes more negative the slopes  $f(t, y)$  for  $t$  values in the interval for which the nullclines are undefined. Therefore, for large enough  $R$ , the solution  $y(t)$  with  $y(0) = 1$  becomes less than zero and thus remains negative for as long as it is defined. The same will hold for  $y(0) < 1$ , because uniqueness implies noncrossing of solutions. There can be no periodic solution with  $y(0) > 1$ , since for all  $y > 1$ ,  $f(t, y) < 0$ .

**Proposition 3.** *For any fixed value of  $A/R$  satisfying  $1/[4(1 + \alpha)] < A/R \leq 1/4$ , equation (4) has no periodic cycles for all sufficiently large  $R$ .*

**4. POINCARÉ MAP.** The Poincaré map is an important tool used in studying differential equations. The consideration of periodically forced one-dimensional problems affords a gentle approach both to its conceptual underpinnings and to its power. Its historical development is well told in [1].

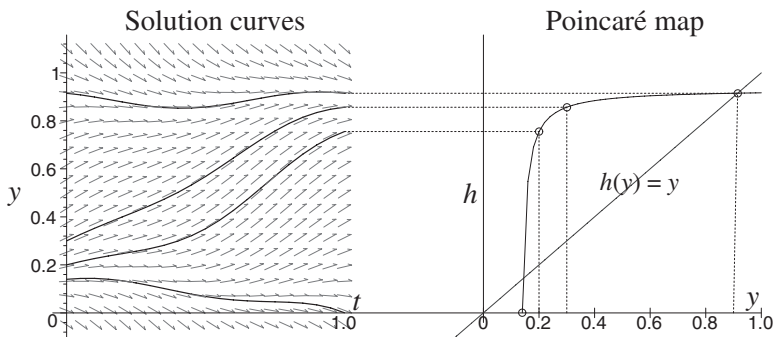
In a series of articles published in the years 1880 through 1886, Henri Poincaré initiated the qualitative theory of differential equations. This qualitative approach was intended to both guide and show the limits of numerical methods such as the series solutions much used at the time. He even offered a partial analysis of periodically forced polynomial differential equations similar to those we consider here [31, p. 80]. The techniques he developed were used in his groundbreaking studies of celestial mechanics, including his 1890 paper on the three-body problem, which won a prize offered by King Oscar of Sweden with Mittag-Leffler, Hermite, and Weierstrass on the award committee. One such technique is the first-return map on a cross-section to an orbit. The map is defined by taking a point on a cross-section and following its image under the flow of the differential equation until it returns to the same cross-section. The continuous flow of a differential equation on a space can thus be more easily studied by looking at the iterates of a discrete map on a space of one lower dimension.

Poincaré showed that under certain simplifying assumptions the three-body problem can be understood by considering a differential equation on a three dimensional space with a two dimensional cross-section. He observed the transverse intersection of the manifold of points leading to a fixed point of the first-return map with the manifold of points leading away from it and was astonished by the complexity of the resulting dynamics: "... these intersections form a type of trellis, tissue, or grid with infinitely fine mesh. . . . The complexity of this figure is striking, and I shall not even try to draw it. Nothing is more suitable for providing us with an idea of the complex nature of the three body problem. . . ." [32, Volume 3, Section 397]. He is thus considered to be one of the discoverers of what is now called mathematical chaos and his trellis is referred to as a *homoclinic tangle* [35]. In other cases, the first-return map determined an area-preserving map on an annulus that twisted its boundaries in opposite directions. He conjectured that such a map must have at least two fixed points. As his life ebbed away, he relaxed his usual standards and published partial results in 1912, leaving the rest of the work to posterity.

From the first appearance of what is now called the Poincaré map, it took about thirty years before it became standard equipment for research in differential equations. In 1913 the American mathematician George Birkhoff created a sensation with an elegant proof of Poincaré's twist map conjecture. Both Birkhoff and Hadamard used the Poincaré map in their investigations of geodesic flows on surfaces. Somewhat later, second order periodically forced nonlinear oscillators  $y'' = f(t, y, y')$  were studied by considering the Poincaré map on the  $(y, y')$ -phase space. Around 1965, Stephen Smale developed his horseshoe map as a geometric model of the phenomena that Mary Cartwright and John Littlewood had encountered with such an oscillator in their work

on radar during World War II, and that Norman Levinson had analyzed in an important 1949 paper [22], [27], [23]. The horseshoe has become the paradigm case of a structurally stable chaotic strange attractor.

For any one-dimensional differential equation  $dy/dt = f(t, y)$  with period  $T$  in  $t$ , the *Poincaré map*  $h$  is defined as follows. Let  $y(t)$  be the solution of the initial-value problem  $dy/dt = f(t, y)$ ,  $y(0) = y_0$ . Then  $h(y_0) = y(T)$ . To illustrate the concept, we show a set of solutions of equation (4) together with the induced Poincaré map in Figure 6. The periodicity of  $f(t, y)$  allows the identification of the line of points  $(0, y)$  with the line of points  $(T, y)$  to make the definition conform with the usual notion of first-return to the same cross-section. We summarize some important properties and formulas, and then apply them to the logistic equation with periodic harvesting (4).



**Figure 6.** Poincaré Map for  $y' = 5y(1 - y) - 0.5(1 + 0.5 \sin(2\pi t))$

If  $f(t, y)$  is continuously differentiable in  $t$  and  $y$ , the domain of the Poincaré map is either empty or an open interval in  $y$ . An initial condition  $y(0) = y_0$  corresponds to a periodic solution of period  $T$  if and only if  $y(T) = y(0)$ ; that is, if  $h(y_0) = y_0$ . In other words, periodic solutions of the differential equation correspond to fixed points of the Poincaré map. Applying the Mean Value Theorem to  $h$  in a small neighborhood of a fixed point  $y_0$ , we see that a periodic solution is attracting if  $h'(y_0) < 1$  and repelling if  $h'(y_0) > 1$ . The uniqueness theorem for  $y' = f(t, y)$  tells us that solutions cannot cross in the  $(t, y)$  plane. This implies that if  $\phi$  and  $\psi$  are two solutions and  $\phi(0) < \psi(0)$  then  $\phi(T) < \psi(T)$ ; that is,  $h(\phi(0)) < h(\psi(0))$ . In other words, the Poincaré map is a strictly increasing function on its domain [14].

If the partial derivative  $\partial^n f / \partial y^n$  exists and is continuous for all  $(t, y)$ , then in the domain of  $h$ , the derivative  $h^{(n)}$  exists and is continuous. Let  $y(t)$  be the solution with initial value  $y_0$ . The following formulas express  $h$  and its derivatives at  $y_0$  in terms of integrals along  $y(t)$ . Formulas (7) and (8) are less familiar [11].

Let  $\phi(t, y_0)$  be the particular solution  $y(t)$  satisfying  $y(0) = y_0$ . Since  $dy/dt = f(t, y)$ , from the fundamental theorem of calculus we obtain the integral representation

$$\phi(t, y_0) = y_0 + \int_0^t f(s, \phi(s, y_0)) ds.$$

Formula (5) below follows by observing that  $h(y_0) = \phi(T, y_0)$ .

Differentiating the above formula under the integral sign with respect to  $y_0$ , using the chain rule, and letting  $z(t) = \frac{\partial}{\partial y_0} \phi(t, y_0)$ , we obtain

$$z(t) = 1 + \int_0^t f_y(s, \phi(s, y_0)) z(s) ds.$$

Taking the derivative with respect to  $t$  yields the separable differential equation  $z'(t) = f_y(t, \phi(t, y_0))z(t)$ , which has the solution  $z(t) = \exp(\int_0^t f_y(s, \phi(s, y_0)) ds)$  since  $z(0) = 1$ . Formula (6) below follows because by definition  $z(T) = h'(y_0)$ .

The second derivative is found by differentiating under the integral sign formula (6) with respect to  $y_0$ , using the chain rule, and recalling that by definition  $y(t) = \phi(t, y_0)$ . We obtain

$$\begin{aligned} h''(y_0) &= \exp\left(\int_0^T f_y(t, y(t))dt\right) \left[\frac{\partial}{\partial y_0} \left(\int_0^T f_y(t, \phi(t, y_0)) dt\right)\right] \\ &= h'(y_0) \int_0^T f_{yy}(t, \phi(t, y_0)) \frac{\partial}{\partial y_0} \phi(t, y_0) dt = h'(y_0) \int_0^T f_{yy}(t, \phi(t, y_0))z(t) dt. \end{aligned}$$

Formula (7) follows from the exponential expression for  $z(t)$  in the previous paragraph. A similar differentiation of formula (7) yields formula (8).

$$h(y_0) = y_0 + \int_0^T f(t, y(t))dt \tag{5}$$

$$h'(y_0) = \exp\left(\int_0^T f_y(t, y(t))dt\right) \tag{6}$$

$$h''(y_0) = h'(y_0) \left(\int_0^T f_{yy}(t, y(t)) \left[\exp\left(\int_0^t f_y(s, y(s)) ds\right)\right] dt\right) \tag{7}$$

$$\begin{aligned} h'''(y_0) &= h'(y_0) \left( (3/2)(h''(y_0)/h'(y_0))^2 \right. \\ &\quad \left. + \int_0^T f_{yyy}(t, y(t)) \left[\exp\left(2 \int_0^t f_y(s, y(s)) ds\right)\right] dt \right) \tag{8} \end{aligned}$$

Like any powerful conceptual tool, the Poincaré map illuminates the ideas and proofs behind a multitude of otherwise disparate results, as seen in a reconsideration of the previously cited Theorems 1, 2, and 3.

Let  $h_1$  be the Poincaré map of the autonomous differential equation  $dy/dt = g(y) = g(t, y)$  trivially considered as nonautonomous. The conditions that  $g(y_0) = 0$  and  $g'(y_0) \neq 0$  together with formulas (5) and (6) imply  $h_1(y_0) = y_0$  and  $h_1'(y_0) \neq 1$ ; i.e.,  $y_0$  is a hyperbolic fixed point of the map  $h_1$ . Let  $h_2$  be the Poincaré map of the small  $C^1$  perturbation  $f(t, y)$  in the hypotheses of Theorem 1. Formulas (5) and (6) suggest that  $h_1$  and  $h_2$  are also  $C^1$  close. A standard result in one-dimensional dynamics that is obtained using the implicit function theorem then implies that  $h_2$  has a hyperbolic fixed point near  $y_0$  [10]. This hyperbolic fixed point of  $h_2$  corresponds to the periodic solution of  $dy/dt = f(t, y)$  referred to in the conclusion of Theorem 1.

Under the conditions of Theorem 2 for a forward invariant region, the Poincaré map is a continuous function from the closed interval  $I = [v_1(0), v_2(0)] = [v_1(T), v_2(T)]$  to itself. This map has a fixed point by the Brouwer fixed point theorem, a theorem that in this one-dimensional setting is the Intermediate Value Theorem of one-dimensional calculus. The fixed point corresponds to a periodic solution of the differential equation. The result for a backward invariant region is obtained by applying the same argument to the time reversal of the original equation. Furthermore, under the condition  $f_y(t, y) < 0$  of the hypothesis of Theorem 3(a), formula (6) implies that the Poincaré map has on the interval  $I$  a derivative satisfying  $0 < h'(y) < 1$ . By the Mean Value

Theorem,  $h$  is a contracting map on  $I$ , and so by the contracting mapping theorem for complete metric spaces,  $h$  has a unique fixed point on  $I$ . This corresponds to the unique periodic cycle referred to in the conclusion of Theorem 3(a).

We now return to equation (4), the logistic equation with periodic harvesting.

For equation (4),  $f_{yy} = -2R < 0$  and  $f_{yyy} = 0$ . Formula (7) implies that  $h'' < 0$  and  $h$  is therefore concave down over its domain. It follows that  $h(y) = y$  for at most two values of  $y$ , allowing us to conclude that equation (4) has 0, 1, or 2 periodic solutions. For a similar analysis see [21]. Formula (8) reduces to a differential equation in  $y_0$ :

$$h'''(y_0) = h'(y_0)[(3/2)(h''(y_0)/h'(y_0))^2]. \quad (9)$$

As an exercise this equation can be integrated by hand, or instead the honor can be left to a computer algebra system such as MAPLE. Whenever the domain of  $h$  is nonempty, we obtain the following formulas for  $h$ :

$$h(y) = ay + b \quad \text{or} \quad h(y) = \frac{a}{y + b} + c. \quad (10)$$

A differential equation  $dy/dt = f(t, y)$  which is quadratic in  $y$  and periodic in  $t$  is called a *periodic Riccati equation*. Since  $f_{yyy} = 0$  for such an equation, its Poincaré map likewise satisfies formula (10). Setting  $h(y) = y$  yields a quadratic equation, which shows that for any periodic Riccati equation either all the solutions that are defined for at least one period are periodic or there are no more than two periodic solutions. For an alternative more algebraic proof involving cross ratios of solutions see [30] or [33]. For an elegant proof due to Smale that uses complex analysis to show that  $h$  must be a fractional linear transformation see [28]. An example with infinitely many periodic solutions is  $y' = \sin(t)y^2$ , for which  $y = 0$  and  $y = \frac{1}{C + \cos(t)}$  are the solutions and the Poincaré map has domain  $(-\infty, \frac{1}{2})$  [33].

The combination of derivatives appearing in (9) is suggestive. In fact, for any function  $g(x)$ , its *Schwarz derivative*  $(Sg)(x)$  is  $g'''(x)/g'(x) - \frac{3}{2}(g''(x)/g'(x))^2$ . So equation (9) states that the Schwarz derivative of  $h$  vanishes. This derivative is much used in the theory of the dynamics of a one-dimensional real or complex function  $g(x)$ , where it is well known that the vanishing of  $S(g)$  implies that  $g(x)$  has the form  $\frac{ax+b}{cx+d}$ ; that is,  $g$  is a fractional linear transformation [10].

Formula (10) for  $h$  allows rigorous theory to assist computation rather in the manner suggested by Poincaré in the epigraph to this paper. Numerically solving equation (4) for three initial conditions yields  $h(y)$  for three distinct values of  $y$  which can be substituted into equation (10). The resulting system of three simultaneous equations can then be numerically solved for the constants  $a$ ,  $b$ , and  $c$ . Doing this we obtained the graph of the Poincaré map shown in Figure 6. Observe that a periodic differential equation which is not quadratic in  $y$  usually needs to be numerically solved for many more than three initial conditions in order to reasonably approximate the graph of its Poincaré map.

If we explicitly note in equation (4) the dependence of  $f(t, y)$  on the parameter  $A$ , we see that  $\partial f/\partial A < 0$  except when  $\alpha = 1$  and  $t = 3/4$ . So if we differentiate formula (5) with respect to  $A$ , we obtain  $\partial h/\partial A < 0$ ; that is, for a fixed value of  $y$ , the value  $h(y)$  of the Poincaré map decreases continuously with increasing  $A$ . Since the Poincaré map is concave down, this implies there is at most one value  $A = A^*$  for which  $h$  has a unique fixed point and consequently for which equation (4) has a unique periodic cycle.

**5. SYMMETRY.** As elsewhere in mathematics, exploiting available symmetries is a powerful tool that can be used to obtain simpler and more precise results. We first summarize the main results of the previous sections in the following theorem which applies to equation (4):  $dy/dt = f(t, y) = Ry(1 - y) - A(1 + \alpha \sin(2\pi t))$ .

**Theorem 4.** *For all  $R$  there exists a value  $A^*(R)$ , satisfying  $R/[4(1 + \alpha)] \leq A^*(R) \leq R/4$ , such that*

- (a) *if  $A > A^*$  then (4) has no periodic solutions;*
- (b) *if  $A = A^*$  then (4) has precisely one periodic solution;*
- (c) *if  $A < A^*$  then (4) has two periodic solutions.*

It remains to estimate the *bifurcation value*  $A^*$ . It is well known that a first order equation  $dy/dt = f(t, y)$  for which the slope field is symmetric about the origin, that is  $f(t, y) = f(-t, -y)$ , has the property that  $y = Q(t)$  is a solution if and only if  $y = -Q(-t)$  is a solution [16]. In the following, this result is generalized to the case where the slope field is symmetric about an arbitrary point  $(c, d)$  in the  $(t, y)$  plane and is also periodic in  $t$ .

Consider the reflection  $S$  from  $\mathbf{R}^2$  to  $\mathbf{R}^2$  about the point  $(c, d)$ ; that is, for all real numbers  $a$  and  $b$ ,  $S(c + a, d + b) = (c - a, d - b)$ .  $S$  maps the graph of any function  $\sigma(t)$ , defined on some domain in  $\mathbf{R}$ , to the graph of another function which we denote by  $S^*\sigma$ . Explicitly,  $S(t, \sigma(t)) = S(c + (t - c), d + (\sigma(t) - d)) = (c - (t - c), d - (\sigma(t) - d)) = (2c - t, 2d - \sigma(t)) = (s, 2d - \sigma(2c - s)) = (s, (S^*\sigma)(s))$ , where  $s$  is set equal to  $2c - t$ . Thus we obtain the formula

$$(S^*\sigma)(s) = 2d - \sigma(2c - s). \tag{11}$$

Note that the function  $\sigma$  has period  $T$  if and only if  $S^*\sigma$  has period  $T$ .

It is helpful in following the subsequent argument to observe that for any  $T > 0$ , we have  $S(t + nT, y) = S(t, y) + (-nT, 0)$ , which implies that  $S$  induces a function  $S^\#$  on the mapping cylinder obtained by identifying, for all integers  $n$ , the point  $(t, y)$  with the point  $(t + nT, y)$ . If this cylinder is embedded as a right circular cylinder in  $\mathbf{R}^3$ , and  $P$  and  $Q$  are the points on this embedding corresponding respectively to  $(c, d)$  and  $(c + T/2, d)$ , then the function  $S^\#$  is simply rotation by 180 degrees about the axis passing through  $P$  and  $Q$ .

The following theorem shows that if a periodic differential equation has a symmetry  $S$  about a point  $(c, d)$ , then restrictions are placed on the locations of its periodic orbits. We then apply this result to symmetric differential equations which are quadratic in  $y$ , such as equation (4) which has a symmetry  $S$  about the point  $(c, d) = (1/4, 1/2)$  [Figure 7].

**Theorem 5.** *Suppose the differential equation  $dy/dt = f(t, y)$  has period  $T$  in  $t$  and for all  $(t, y)$ ,  $f(S(t, y)) = f(t, y)$ , where  $S$  is a reflection about the point  $(c, d)$ . Let  $\sigma$  be a function of  $t$ .*

- (a)  *$\sigma$  is a solution if and only if  $S^*\sigma$  is a solution.*
- (b)  *$\sigma$  is a periodic solution if and only if  $S^*\sigma$  is a periodic solution.*
- (c) *Let  $\sigma$  be a solution. Then the graph of  $\sigma$  passes through the point  $(c, d)$  if and only if  $S^*\sigma = \sigma$ .*
- (d) *Let  $\sigma$  be the solution with graph passing through the point  $(c, d)$ . Then  $\sigma$  is periodic if and only if the graph of  $\sigma$  also passes through the point  $(c + T/2, d)$ .*

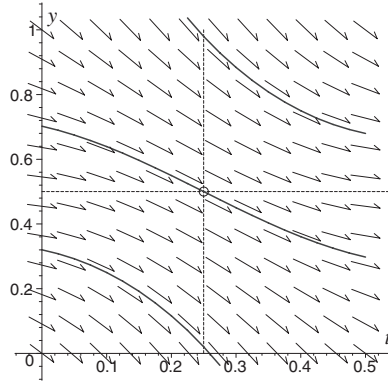


Figure 7. Symmetry of  $f(t, y)$  about  $(\frac{1}{4}, \frac{1}{2})$

- (e) If the number of periodic solutions is finite, then the number is odd if and only if there exists a solution with graph that passes through both  $(c, d)$  and  $(c + T/2, d)$ .

*Proof.* (a) Suppose  $\sigma$  is a solution. Using formula (11), we show  $S^*\sigma$  is a solution.

$$\begin{aligned} (S^*\sigma)'(s) &= -\sigma'(2c - s)(-1) = \sigma'(2c - s) = f(2c - s, \sigma(2c - s)) \\ &= f(S(2c - s, \sigma(2c - s))) = f(s, 2d - \sigma(2c - s)) = f(s, (S^*\sigma)(s)). \end{aligned}$$

The converse follows since  $S^*S^*\sigma = \sigma$ .

- (b) The statement follows directly from formula (11).  
 (c) Note that  $(c, d)$  is a fixed point of  $S$ . Therefore if the graph of  $\sigma$  passes through  $(c, d)$ , so too does the graph of  $S^*\sigma$ . By uniqueness of solutions,  $S^*\sigma = \sigma$ . Conversely suppose  $S^*\sigma = \sigma$ . Then  $(S^*\sigma)(c) = \sigma(c)$ . By definition of  $S^*\sigma$ ,  $S(c, \sigma(c)) = (c, (S^*\sigma)(c)) = (c, \sigma(c))$ . Since  $(c, d)$  is the unique fixed point of  $S$ ,  $\sigma(c) = d$ ; that is, the graph of  $\sigma$  passes through  $(c, d)$ .  
 (d) Let  $\sigma$  be the solution with graph passing through the point  $(c, d)$ . By (c) above,  $S^*\sigma = \sigma$ . Using formula (11) it follows that:

$$\begin{aligned} \sigma &\text{ is periodic of period } T \\ &\text{if and only if } \sigma(c + T/2) = \sigma(c - T/2) \\ &\text{if and only if } \sigma(c + T/2) = (S^*\sigma)(c - T/2) \\ &\text{if and only if } \sigma(c + T/2) = 2d - \sigma(c + T/2) \\ &\text{if and only if } \sigma(c + T/2) = d; \end{aligned}$$

that is, the graph of  $\sigma$  passes through the point  $(c + T/2, d)$ .

- (e) Suppose that the number of periodic solutions is finite. By (b), there can be an odd number of periodic solutions if and only if there is a periodic solution  $\sigma$  for which  $S^*\sigma = \sigma$ . By (c) and (d) above, there can be such a periodic solution  $\sigma$  if and only if the graph of  $\sigma$  passes through the points  $(c, d)$  and  $(c + T/2, d)$ . ■

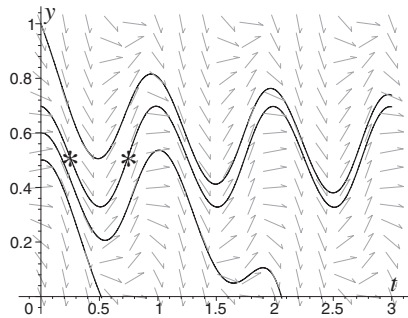
**Theorem 6.** Consider the differential equation  $y' = f(t, y) = a(t)y^2 + b(t)y + c(t)$ , where  $a(t)$ ,  $b(t)$ , and  $c(t)$  are continuous functions symmetric about  $t = u$  and sharing

a common period  $T$ ,  $b(t) = ka(t)$  for some constant  $k$ , and  $a(t)$  is not uniformly zero. Then there is a solution passing through both of the points  $(u, -k/2)$  and  $(u + T/2, -k/2)$  if and only if either all of the continuously many solutions defined for time  $T$  are periodic, or there is precisely one periodic solution.

*Proof.* Under the given hypotheses on the coefficient functions,  $f(S(t, y)) = f(t, y)$  where  $S$  is a reflection about the point  $(u, -k/2)$ . We observed in Section 4 that for any periodic Riccati equation either there are no more than two periodic solutions or all of the continuously many solutions defined for at least time  $T$  are periodic. In the former case, the result follows by part (e) of Theorem 5. In the latter case, consider the set  $J$  of values  $y$  such that the solution through  $(u, y)$  is periodic.  $J$  is an open interval corresponding to the open interval that is the domain of the Poincaré map. As shown by formula (11) and part (b) of Theorem 5, the symmetry implies that  $J$  is symmetric about, and therefore contains, the value  $y = -k/2$ ; that is, the solution through  $(u, -k/2)$  is periodic, and the result follows by part (d) of Theorem 5. ■

The equation  $y' = \sin(t)y^2$  satisfies the conditions of Theorem 6 with  $T = 2\pi$ ,  $u = \pi/2$ , and  $k = 0$ , and the solution  $y = 0$  passes through both of the points referred to in the theorem. As noted in Section 4, for this example, all solutions defined for at least time  $T$  are periodic.

We return to equation (4),  $dy/dt = f(t, y) = Ry(1 - y) - A(1 + \alpha \sin(2\pi t))$ , which has a symmetry  $S$  about the point  $(t, y) = (1/4, 1/2)$ . By Theorem 5(b), when there are two periodic solutions, if  $\sigma$  is the repeller, then  $S^*\sigma$  must be the attractor. We can observe this symmetry in Figure 2.



**Figure 8.** Unique periodic solution passing through  $(\frac{1}{4}, \frac{1}{2})$  and  $(\frac{3}{4}, \frac{1}{2})$  when  $A = A^*$

Let  $\phi(t)$  be the solution of differential equation (4) satisfying  $\phi(\frac{1}{4}) = \frac{1}{2}$ . By the standard result on continuation of solutions for such equations, the solution  $\phi$  either extends to  $t = \frac{3}{4}$  or diverges to  $\pm\infty$  as  $t$  approaches some value  $t_1 \leq \frac{3}{4}$ . However, for this problem, for all  $y > 1$ , we have  $f(t, y) < 0$ , so divergence to  $+\infty$  is not possible. The following theorem states that the number of periodic cycles depends only on the value of  $\phi(\frac{3}{4})$ . That is, numerical simulation of only one particular solution suffices to determine the number of periodic cycles. In particular, as shown in Figure 8, at the bifurcation value of  $A$ , the unique periodic cycle passes through the points  $(\frac{1}{4}, \frac{1}{2})$  and  $(\frac{3}{4}, \frac{1}{2})$ . Again we see an instance of the theme first raised in the introduction; theoretical results anchor numerical approximation.

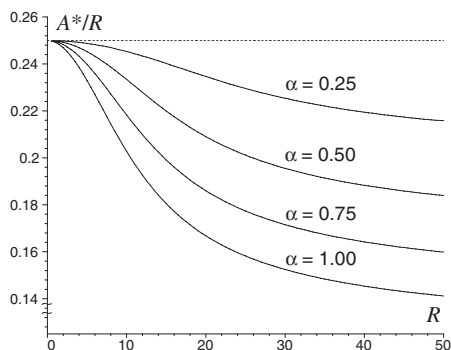
**Theorem 7.** Let  $\phi(t)$  be the solution of (4) satisfying  $\phi(\frac{1}{4}) = \frac{1}{2}$ .

- (a) If  $\phi(\frac{3}{4}) = \frac{1}{2}$  then there is precisely one periodic solution.
- (b) If  $\phi(\frac{3}{4}) < \frac{1}{2}$  or  $\phi(\frac{3}{4})$  is undefined then there are no periodic solutions.
- (c) If  $\phi(\frac{3}{4}) > \frac{1}{2}$  then there are precisely two periodic solutions.

*Proof.* By trichotomy it suffices to prove the converse statements.

Equation (4) satisfies the hypotheses of Theorem 6, where the coefficient functions  $a(t) = -R$ ,  $b(t) = R$ , and  $c(t) = -A(1 + \alpha \sin(2\pi t))$  are symmetric about  $t = u = \frac{1}{4}$  and share a common period  $T = 1$ . Also  $b(t) = ka(t)$ , for  $k = -1$ . Furthermore, this equation can have no more than two periodic solutions [Theorem 4]. Therefore part (a) and its converse follow directly from Theorem 6.

By Theorem 4, if there are no periodic solutions, then  $A > A^*$ . However, if  $A = A^*$ , there is precisely one periodic solution, and, as noted above,  $\phi(3/4) = 1/2$ . Since  $\phi$  is a solution of (4),  $\phi(3/4) = \phi(1/4) + \int_{1/4}^{3/4} f(t, \phi(t))dt$ . But  $\partial f/\partial A = -(1 + \alpha \sin(2\pi t))$ ; that is, the partial derivative of the slope field with respect to the parameter  $A$  is always negative except when  $t = 3/4$  and  $\alpha = 1$ . Therefore as  $A$  increases and becomes greater than  $A^*$ ,  $\phi(3/4)$  decreases and becomes less than  $1/2$  or is eventually no longer defined. By a similar argument, if there are two periodic solutions, then  $A < A^*$ , and  $\phi(3/4) > 1/2$ . ■



**Figure 9.** Values of  $A^*/R$  plotted against  $R$ , for  $\alpha = 0.25, 0.5, 0.75, 1.0$

We can also answer a question of Campbell and Kaplan in [7] and determine the limiting behavior of  $A^*(R)$  as  $R$  goes to infinity. The indicated convergence is shown in Figure 9. The values of  $A^*$  were determined by using a bisection algorithm to approximately find  $A$  for which  $\phi(\frac{3}{4}) = \frac{1}{2}$ .

**Theorem 8.** As  $R$  approaches infinity, the ratio  $A^*/R$  converges to  $1/[4(1 + \alpha)]$ .

*Proof.* Proposition 3 can be restated as follows. For all  $\epsilon > 0$ , if  $A/R$  is fixed equal to  $1/[4(1 + \alpha)] + \epsilon$  then there exists an  $R_0$  such that for all  $R > R_0$ , there are no periodic solutions. But by Proposition 2, if  $A/R < 1/[4(1 + \alpha)]$ , there are two periodic solutions. Therefore, for all  $\epsilon > 0$ , there is an  $R_0$ , such that for all  $R > R_0$ , we have  $1/[4(1 + \alpha)] \leq A^*(R)/R < 1/[4(1 + \alpha)] + \epsilon$ . This establishes the theorem by the definition of convergence. ■

**6. PAST AND PRESENT.** At the International Congress of Mathematicians held in Paris in 1900, David Hilbert delivered his famous address in which he posed to the

coming century a list of 23 problems that gave direction to much of the research that followed. An engaging popular account of these developments can be found in [12]. Considering the esoteric character of much current research, it is heartening that the still unsolved sixteenth problem leads to open questions about first order polynomial-type equations of the sort considered in this paper. However, we are chastened by the astonishing way that an important error regarding such a significant problem went undetected for over half a century. For surveys see [8] or [18].

A *limit cycle* is an attracting or repelling periodic solution of either an autonomous differential equation in the  $(x, y)$ -plane,  $x' = f(x, y)$ ,  $y' = g(x, y)$ , or of a differential equation  $y' = f(t, y)$  that is periodic in  $t$ . The second part of the sixteenth Hilbert problem can be restated as follows. Consider the system  $x' = P(x, y)$ ,  $y' = Q(x, y)$ , where  $P$  and  $Q$  are polynomials in  $x$  and  $y$ . For a fixed degree of  $P$  and  $Q$ , determine an upper bound on the number of limit cycles. A simpler version is to determine such a bound in the case that there is a single equilibrium about which the orbits circle [11], [24]. Changing to polar coordinates and letting  $\theta$  represent time, we obtain a problem that is sometimes named after Charles Pugh: Let  $y' = f(t, y)$  be periodic in  $t$  and polynomial in  $y$ . For a fixed degree of this polynomial, determine an upper bound on the number of limit cycles.

We have seen that equation (4) has no more than two periodic cycles. We present results on periodic cycles and limit cycles of related differential equations and also indicate the present status of both the Pugh and Hilbert problems.

The *periodic Riccati* differential equation has the form  $y' = f(t, y)$  where  $f$  is periodic in  $t$  and quadratic in  $y$ ; that is,  $y' = a(t)y^2 + b(t)y + c(t)$ , where  $a(t)$ ,  $b(t)$ , and  $c(t)$  are continuous functions sharing a common period  $T$ , with  $a(t)$  not uniformly zero. We observed in Section 4 that such an equation has at most two periodic cycles unless all the solutions defined for at least one period are periodic cycles.

The *periodic Abel* differential equation has the form  $y' = f(t, y)$  where  $f$  is periodic in  $t$  and cubic in  $y$ ; that is,  $y' = a(t)y^3 + b(t)y^2 + c(t)y + d(t)$  where the coefficients  $a(t)$ ,  $b(t)$ ,  $c(t)$ , and  $d(t)$  are continuous functions sharing a common period  $T$ , with  $a(t)$  not uniformly zero. If  $a(t)$  has a constant positive sign, then formula (8) implies that  $h'''$  has constant positive sign, and hence that  $h$  has at most three fixed points. Therefore if  $a(t)$  has constant positive sign, the periodic Abel equation has at most three periodic cycles. A slight modification, involving the consideration of the backward flow, shows that if  $a(t)$  has constant negative sign then there also are at most three periodic cycles [11]. In Section 7, we indicate some common population models involving constant sign Abel equations.

The related question about limit cycles of nonconstant sign Abel equations was settled in the negative in an important paper by Alcide Lins Neto [28], [34]. He showed that for any positive integer  $n > 3$ , there is an Abel equation that has at least  $n$  limit cycles. We have seen above that for such an example  $a(t)$  must vary in sign. Neto then observed that it follows easily by a perturbation argument that for any  $n$ , there is a differential equation having at least  $n$  limit cycles of the form  $y' = f(t, y)$  with  $f$  quartic in  $y$ , and for which the coefficient of the  $y^4$  term is equal to 1. The latest result along these lines is that of Ilyashenko, who in a brief note beautifully deploys techniques such as Jensen's inequality that are found in a first-year graduate course in complex analysis. If  $f(t, y)$  is periodic in  $t$  and of degree  $d$  in  $y$  with the  $y^d$  term having coefficient 1, he shows that there is some number  $N$ , depending only on  $d$  and the maximum  $C$  of the absolute values of the coefficients, such that  $y' = f(t, y)$  has no more than  $N$  limit cycles. This number satisfies

$$N(C, d) \leq 8 \exp \{ (3C + 2) \exp [(3/2)(2C + 3)^d] \},$$

but the right hand side of this inequality is very large and is not likely to be a sharp estimate of  $N(C, d)$  [17].

As for Hilbert's original problem involving polynomial differential equations in the  $(x, y)$ -plane, in 1923 Dulac claimed to prove that for such an equation the number of limit cycles must be finite. This result went unchallenged until in 1982 Ilyashenko noted a major flaw in the argument. About the same time, a word of warning was issued by Chicone and Tian in this journal [8]. Finally a correct proof of Dulac's claim was given independently by Ilyashenko in 1991 and Écalle in 1992. In the mid 1950s, Petrovskii and Landis claimed to show that there could be no more than three limit cycles when  $P$  and  $Q$  are both quadratic. Alas, quadratic examples with four limit cycles were exhibited in 1979 and 1980. It is still unknown in the quadratic case whether, for arbitrarily large  $n$ , there is an example with  $n$  limit cycles. However, Lins Neto showed that this problem is equivalent to determining whether there is a uniform upper bound on the number of limit cycles for the class of equations  $y' = a(t)y^3 + b(t)y^2 + cy$  where the coefficient  $a(t)$  is a homogeneous polynomial of degree 6 in  $\cos(t)$  and  $\sin(t)$ ,  $b(t)$  is a homogeneous polynomial of degree 3 in  $\cos(t)$  and  $\sin(t)$ , and  $c$  is a constant [28]. We thus return to the type of question with which we began.

**7. RELATED DIFFERENTIAL EQUATIONS.** Using the techniques presented in this paper, one can study the periodic orbits and bifurcations obtained when any or all of the coefficients  $R$ ,  $L$ , and  $H$  in equation (1) are periodically varied with common period. One can also study the kind of periodic harvesting obtained if  $H$  is replaced by a term of the form  $H(t)P$ , where  $H(t)$  is periodic. We obtain for these models a periodic Riccati equation. As shown in Section 4, if  $R(t)$  has constant sign, there can be no more than two such orbits, and the Poincaré map has the form  $h(y) = a/(y + b) + c$ , where  $a$ ,  $b$ , and  $c$  are constants that can be computed by first solving the differential equation numerically for three initial conditions, and then solving the resulting system of three simultaneous equations in the three unknowns  $a$ ,  $b$ , and  $c$ . However to use the symmetry arguments of Section 5, the conditions of Theorem 6 must be satisfied. It is curious that there are examples in which the nullclines  $z_1(t)$  and  $z_2(t)$  are defined for all  $t$ , yet there are no periodic solutions. There is a large literature for this equation. For some further results see [14]. For a discussion of other single-population models with logistic-like behavior see [6].

The logistic equation can be refined by adding a parameter  $M$ , the minimal sustainable population level in the absence of harvesting, thus obtaining [2, p. 90], [4, p. 83]

$$dP/dt = RP(1 - P/L)(P/M - 1) - H.$$

If these parameters are varied with a common period  $T$ , then we have shown in Section 6 that if  $R(t)$  has constant sign, there are at most three periodic cycles. These cycles and their bifurcations can be examined.

The parameters can be periodically varied for any nonlinear equation  $y' = f(t, y)$  which is of interest, and the resulting periodic orbits and bifurcations studied. A stimulating nonpolynomial example is the following differential equation that models a single neuron:  $y' = -y + g(\theta + cy)$ , where  $g(z) = 1/(1 + e^{-z})$  is a sigmoidal response function [15]. For constant parameters  $\theta$  and  $c$ , there are at most three equilibria, and these persist as periodical cycles under small periodic perturbation of the parameters.

If two of the single neurons described above interact, one excitatory and one inhibitory, we obtain the Wilson-Cowan system that is often used to model one or more

neural oscillators [15]. If either or both of the neurons is periodically forced by external excitations, one obtains a nonautonomous two-dimensional system that is difficult to analyze rigorously. However, under a natural simplifying assumption, this system reduces to a periodic differential equation in one variable of the form  $u' = f(t, u)$ . The periodic solutions and bifurcations of this equation have been studied using the techniques of Sections 2-4 above [29].

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**DIEGO MAIR BENARDETE** received his doctorate in mathematics from the City University of New York in 1985 and has ever since researched pure and applied aspects of dynamical systems and differential equations. At the University of Hartford, he enjoys teaching undergraduate mathematics in its range from the logarithm of precalculus to the epsilons and deltas of real analysis. He also has an amateur's interest in history, literature, philosophy, and religion that manifests itself professionally in the study and teaching of the history and philosophy of mathematics.

*Department of Mathematics, College of Arts and Sciences, University of Hartford, West Hartford, CT 06117*  
*benardete@hartford.edu*

**ANNE NOONBURG** received her Ph.D. from Cornell University in 1967, and is currently a professor of mathematics at the University of Hartford. Her major research interest is ordinary differential equations; in particular, applications to mathematical biology.

*Department of Mathematics, College of Arts and Sciences, University of Hartford, West Hartford, CT 06117*  
*noonburg@hartford.edu*

**BEN POLLINA** received his B.A. from Fordham University in 1970 and his Ph.D. from Yale University in 1975. Since then, he has spent all of his career at the University of Hartford. His current interests center on the use of technology in the teaching and learning of mathematics.

*Department of Mathematics, College of Arts and Sciences, University of Hartford, West Hartford, CT 06117*  
*pollina@hartford.edu*