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DELAY DIFFERENTIAL EQUATIONS

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All processes take time to complete. While physical processes such as acceleration and deceleration take little time compared to the times needed to travel most distances, the times involved in biological processes such as gestation and maturation can be substantial when compared to the data-collection times in most population studies. Therefore, it is often imperative to explicitly incorporate these process times into mathematical models of population dynamics. These process times are often called delay times, and the models that incorporate such delay times are referred as delay differential equation (DDE) models.

CONCEPTS AND NOTATION

Recent theoretical and computational advancements in delay differential equations reveal that DDEs are capable of generating rich and plausible dynamics with realistic parameter values. Naturally occurring complex dynamics are often naturally generated by well-formulated DDE models. This is simply due to the fact that a DDE operates on an infinite-dimensional space consisting of continuous functions that accommodate high-dimensional dynamics. For example, the Lotka–Volterra predator–prey model with crowding effect does not produce sustainable oscillatory solutions that describe population

cycles, yet the Nicholson's blowflies model can generate rich and complex dynamics.

DDEs are differential equations in which the derivatives of some unknown functions at present time are dependent on the values of the functions at previous times. Mathematically, a general delay differential equation for $x(t) \in R^n$ takes the form

$$\frac{dx(t)}{dt} = f(t, x_t),$$

where $x_t(\theta) = x(t + \theta)$ and $-\tau \leq \theta \leq 0$. Observe that $x_t(\theta)$ with $-\tau \leq \theta \leq 0$ represents a portion of the solution trajectory in a recent past. Here, f is a functional operator that takes a time input and a continuous function $x_t(\theta)$ with $-\tau \leq \theta \leq 0$ and generates a real number $(dx(t)/dt)$ as its output. A well-known example of a delay differential equation is the Hutchinson equation, or the discrete delay logistic equation, $x' = rx(1 - x(t - \tau)/K)$. Some DDEs can be conveniently solved in a stepwise fashion. In fact, the Hutchinson equation can be rewritten as $(\ln x)' = r(1 - x(t - \tau)/K)$, which can be used to solve for x for $0 \leq t \leq \tau$. Some DDEs, such as $x'(t) = rx(t)[1 - a\int_{-\infty}^{0} e^{as} x(t + s)ds/K]$, $a > 0$, are in fact a system of ordinary diffential equations (ODEs) in disguise. This can be seen by letting $y(t) = a\int_{-\infty}^{0} e^{as} x(t + s)ds$ and noticing that $y' = a(x(t) - y(t))$, which yields a system of ODEs $x'(t) = rx(t)(1 - y(t)/K)$; $y' = a(x(t) - y(t))$. Indeed, an integro-differential equation of the form $x'(t) = f(t, x(t)) + \int_{-\infty}^{0} k(s)g(x(t + s))ds$ with initial condition $x_t(\theta)$ where $-\infty < \theta \leq 0$ is equivalent to a system of ODEs with initial condition if k is a linear combination of functions $e^{at}, te^{at}, t^2 e^{at}, \ldots, t^m e^{at}$, where a is a real number and m is a positive integer. The method of reducing such a delay differential equation into a system of ODEs is called the linear chain trick.

Numerically solving most delay differential equations or systems is almost as simple as solving ODEs. The popular MATLAB-based dde23 solver developed by Shampine and Thompson for delay differential equations is well tested and user-friendly. Interested readers can find many familiar and informative examples at the website http://www.radford.edu/thompson/webddes/ddetutwhite.html, and more sophisticated users can find additional information at http://www.radford.edu/thompson/webddes/.

As with linear ODEs, stability properties of linear DDEs can be characterized and analyzed by studying their characteristic equations. For example, the characteristic equation for $x'(t) = ax(t) + bx(t - \tau)$ is $\lambda - a - be^{-\lambda\tau} = 0$. The roots λ of the characteristic equation are called characteristic roots. Notice that the root appears in the exponent of the last term in the characteristic equation, causing the characteristic equation to possess an infinite number of roots. However, there are only a finite number of roots located to the right of any vertical line in the complex plane.

SOME CHARACTERISTICS OF DDEs

In most applications of delay differential equations in the sciences, the need for incorporating time delays is often due to the presence of process times or the existence of some stage structures. In engineering applications, such time delays are often modeled via high-dimensional compartment models. In life-science applications, compartmental models can present the additional challenges of estimating some of the involved parameter values. In such cases, low-dimensional delay differential models with fewer parameters can be sensible alternatives.

Since the through-stage survival rate is often a function of such time delays, it is easy to see that these models may involve some delay-dependent parameters. The ubiquitous presence of such parameters often greatly complicates the task of a systematic study of such models. In some special cases, the stability of a given steady state can be determined by the graphs of some functions of time delay that can be expressed explicitly and thus can be depicted. The common scenario is that as time delay increases, stability changes from stable to unstable to stable, implying that a large delay can be stabilizing. This scenario often contradicts the one provided by similar models with only delay-independent parameters.

In addition, a closer look at the cause of a time delay often suggests that the time delay itself maybe dependent on some key model variables. In short, the delays are state dependent. These state-dependent delay differential equations are notoriously difficult to study mathematically. However, they may possess some surprising and more plausible dynamics.

SOME SIMPLE DELAY DIFFERENTIAL EQUATION MODELS

Many consumer species go through two or more life stages as they proceed from birth to death. In order to capture the oscillatory behavior often observed in nature, various models are proposed. They include many difference models and delay differential models. The Hutchinson equation,

$$x' = rx(1 - x(t - \tau)/K), \tag{1}$$

and its variations are among the ones that are most frequently employed in theoretical ecology models. In Equation 1, r is the growth rate, K is the carrying capacity, and τ is a time delay that may have no real biological meaning. Like logistic equations, these models are ad hoc and hence can be misleading. Indeed, they produces artificially complex dynamics such as excessive volatility and huge peak-to-valley ratios (Fig. 1).

On the other hand, if we assume the adults have a constant birth rate of r, the newborns mature in τ units of time, and the mortality rate is proportional to the adult population density, then the following model may be a reasonable model for the adult population:

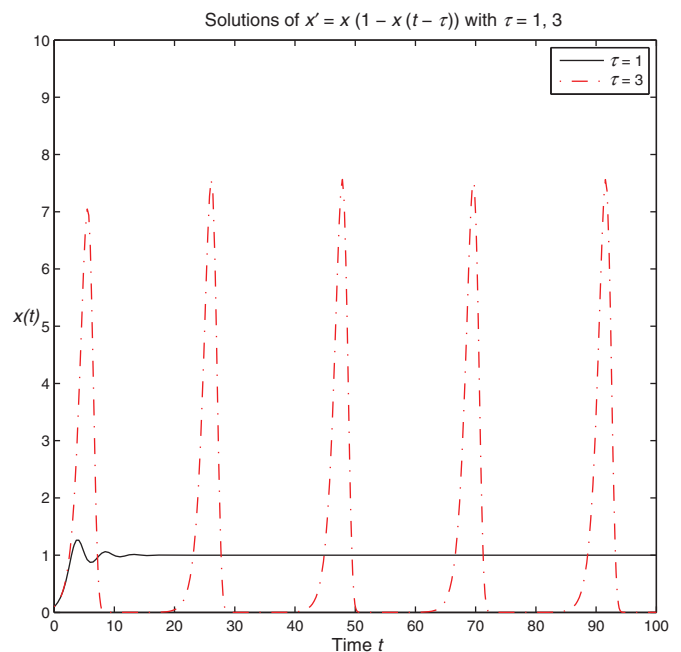$$x' = rx(t - \tau)e^{-m\tau} - rx^2/K. \tag{2}$$

FIGURE 1 Solutions of the Hutchinson equation with delay values of 1 and 3. Note that the peak-to-valley ratio is well over 2000 when the delay is 3.

However, the positive steady state of model 2 is always (globally) stable, similar to the case when the delay is zero. On the other hand, the well-known Nicholson blowflies model,

$$x' = px(t - \tau)e^{-ax(t-\tau)} - mx, \qquad (3)$$

exhibits plausible and rich dynamics. In other words, the dynamics of delay differential equations are extremely sensitive to model forms.

To further support the above statement, let us now examine some predator–prey models with age structure. We assume that the prey or the renewable resource, denoted by x, can be modeled by a logistic equation when the consumer is absent. The predators or consumers are divided into two age groups, juveniles and adults, and they are denoted by y_j and y, respectively. We also assume that only adult predators are capable of preying on the prey species and that the juvenile predators live on other resources. We then have the following two-stage predator-prey interaction model:

$$
\begin{aligned}
x' &= rx(1 - x/K) - yp(x), \\
y' &= be^{-d_j\tau} y(t - \tau)p(x(t - \tau)) - d_a y - my^2. \quad (4)
\end{aligned}
$$

With the aid of the geometric stability switch criteria that were specifically developed to deal with models with delay-dependent parameters, it can be shown that this model generates increasingly more complex dynamics,

as its characteristic equation produces more roots with positive real part when we increase the time delay from 0.25 to 25 (Fig. 2). If we assume that the maturation time delay in population dynamics is determined by the resource uptake, then we may have

$$\int_{-\tau}^{0} p(x(s))ds = M \qquad (5)$$

for some positive constant M that measures the resource requirement for a newborn to mature. With this additional reality, solutions of model 4 tend to a steady-state or a limit-cycle dynamics. In addition, the time to approach the limit cycle is much shorter than a typical model without time delay or with constant time delay, suggesting that the more realistic formulation of time delay (Eq. 5) satisfactorily describes the often-observed short duration of transition dynamics in nature (Fig. 3).

Delay differential equation models can be more effective and accurate compared to ordinary differential equation–based models when it is necessary to capture oscillatory dynamics with specific periods and amplitudes. This characteristic has been successfully employed to explain why lemmings often have a 4-year cycle whereas snowshoe hares have a 10-year cycle, and why the putative cycles of the moose–wolf interactions on Isle Royale, Michigan, is 38 years long. In addition, some simple and plausible models with two time delays can generate the
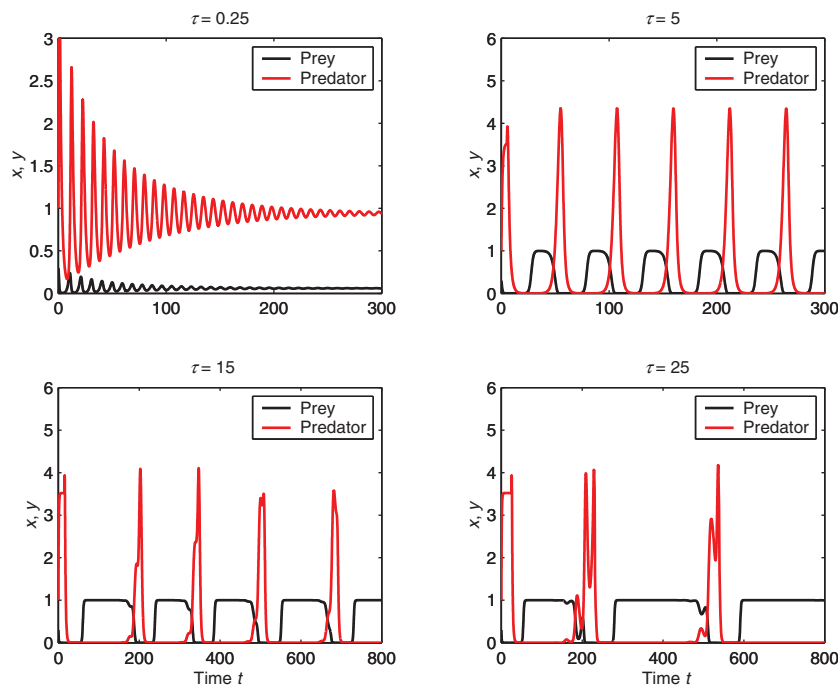

FIGURE 2 A solution of model 4 with $p(x) = px$, where $r = K = 1$, $p = 1$, $b = 10$, $d_j = 0$, $d_a = 0.5$, $m = 0.1$, and τ varies from 0.25 to 25.
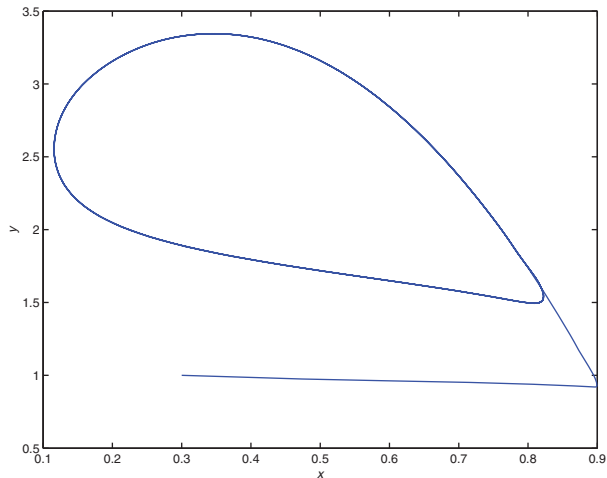
FIGURE 3 Maturation time delay may not generate complex dynamics other than periodic solution. In addition, maturation time delay may significantly cut the transition time from an initial point to an attracting limit cycle.

ubiquitous ultradian insulin secretory oscillations in the human glucose–insulin regulatory system.

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FURTHER READING

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DEMOGRAPHIC STOCHASTICITY

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DEMOGRAPHY

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Demography is the study of vital rates, such as mortality and fecundity rates, and their effects on population dynamics. Studies usually focus on how vital rates depend on traits such as age; in ecology, vital rates may include individual growth or shrinkage rates (the latter being most relevant for plants), and the traits on which they depend may include size, developmental stage, or any other state through which individuals transition, including spatial location and environmental state. Commonly investigated population consequences of the vital rates include the population growth rate and the population trait structure (the proportion of individuals in each age, size, stage, or other state class). The predominant tool for the ecological study of demography is the population projection matrix, a discrete-trait approach that is amenable to parameterization using empirical data and which allows analyses of factors such as environmental variation.

OVERVIEW

In almost any population, the rates describing individual activities depend on individual traits, and the activities most likely to have population consequences are the rates at which individuals reproduce, die, and change with respect to rate-determining traits. For example, in an animal population, juveniles may be more likely to die and less likely to reproduce than adults, so differentiating the two developmental stages and understanding the rates at which individuals pass through them is important for understanding overall population death and birth rates. In addition, older or larger animals may survive or reproduce better or worse than younger or smaller ones; better habitat quality in some places or at some times may similarly influence vital rates. Figure 1 illustrates the potential effects of two such traits and hypothetical transitions between trait states. Demography encompasses these and similar processes. Without context, the term is usually taken generally to mean the population dynamics of humans, whose vital rates depend on age and may also depend on socioeconomic status, nationality, or behaviors such as cigarette smoking, for instance. Demography departments in a university or other such organizational units are therefore often interdisciplinary social science units, most often including economists and sociologists.