Princeton University Press

Chapter Title: Nonlinear Population Models: An Introduction to Qualitative Analysis Using Phase Planes

Book Title: Topics in Mathematical Modeling
Book Author(s): TUNG K. K.
Published by: Princeton University Press. (2007)
Stable URL: https://www.jstor.org/stable/j.ctt1bw1hh8.9

6

Nonlinear Population Models: An Introduction to Qualitative Analysis Using Phase Planes

Mathematics developed:
> analyzing in phase plane the solution of first-order nonlinear ordinary differential equations; concept of equilibria and their stability

6.1 Introduction

We shall consider nonlinear population models in this chapter and introduce a qualitative method for analyzing nonlinear equations.

6.2 Population Models

We consider population models of the form

$$\frac{dN}{dt} = F(N, t), \tag{6.1}$$

where $F(N, t)$ is the growth rate of a population of, say, humans or fish, of density N.

The simplest population model is given by

$$F = rN,$$

where $r = $ constant is the net growth rate per unit population. This model has been considered in a previous chapter. Its solution leads to an exponential growth in the population:

$$N(t) = N_0 e^{rt}.$$

This behavior is probably realistic only during the initial growth at low population density, when resource constraints on further growth have not yet come into play. Figure 6.1 shows the U.S. census data from
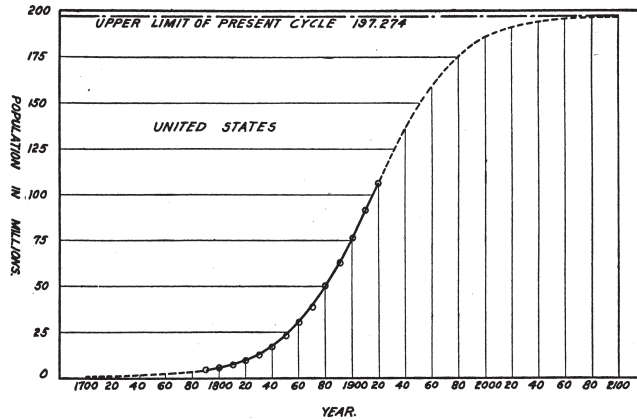
Figure 6.1. Early U.S. census data fitted to a logistic curve.
(From Pearl and Reed [1920].)

the 19th century. The growth of the population in the new continent appeared exponential for about a century after 1750.

The exponential growth stage certainly cannot continue for very long. Sooner or later the population growth taxes the support system (such as food, space, farmland, etc.) and creates overcrowding, which may lead to diseases. A more reasonable model for the growth rate F has the growth slow down as N increases. A commonly used, but controversial, model that has this behavior is the so-called *logistic growth* model, originally proposed by the 19th century Belgian mathematician Pierre François Verhulst.

$$\frac{dN}{dt} = F(N, t) = r N \left(1 - \frac{N}{K} \right), \quad K > 0. \tag{6.2}$$

The solution can be obtained by separation of variables (exercise 3) as:

$$N(t) = \frac{K}{1 + e^{a-rt}},$$

where a is a constant of integration that can be determined by the initial condition

$$N(0) = N_0 = \frac{K}{1 + e^a}.$$

For large t, the solution approaches the asymptotic value of K, i.e.,

$$\lim_{t \to \infty} N(t) = K.$$

This behavior is plotted as a dashed line in Figure 6.1.

$$\frac{dN}{dt}$$

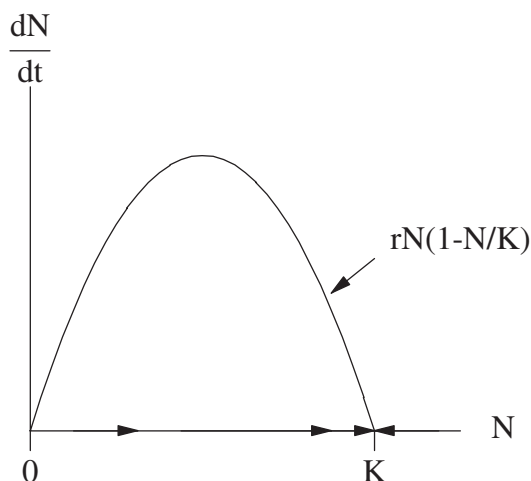rN(1-N/K)

0   K   N

Figure 6.2. F has a parabolic shape and it has two zeros, at $N^* = 0$ and $N^* = K$.

Verhulst called this solution the "logistic curve." The French term "logistique" was used to signify the art of calculation. Later, in 1920, this curve was reintroduced by American scientists Raymond Pearl and Lowell J. Reed and promoted as a natural "law" for the growth of any population. Never mind that their fit of U.S. population data in Figure 6.1 covered less than one third of the logistic curve, giving no hint of the eventual saturation limit. Many other models of population growth probably would fit the data just as well.

We shall for convenience use the logistic model as one of the examples of nonlinear population models of the form of Eq. (6.1) to illustrate the use of qualitative methods for their analysis.

For a derivation of this model, see the exercises.

6.3 Qualitative Analysis

Since F is also $\frac{dN}{dt}$, a positive F indicates that N is increasing with time. We indicate this in a plot of $\frac{dN}{dt}$ vs. N, called the phase diagram (Figure 6.2), by an arrow pointing towards larger N, for those N's that make $F(N, t)$ positive. At the zeros of $F(N)$, we have $\frac{d}{dt} N = 0$. These are *equilibria* of Eq. (6.2). These equilibria are either *stable* or *unstable*, depending on whether a small perturbation from the equilibrium solution will lead it back to or move it away from the equilibrium solution, respectively. We see from Figure 6.2 that $N^* = K$ is a *stable* equilibrium because increasing N from N^* will create a negative $\frac{dN}{dt}$, and decreasing N from N^* will create a positive $\frac{dN}{dt}$. These then tend to move N back to $N^* = K$

(see Figure 6.2). K is called the *carrying capacity* of the population. It can be inferred observationally from the "equilibrium" population, in the absence of external inference. The quantity r can be measured by the net growth rate of a small population, as

$$r \cong \frac{1}{N}\frac{d}{dt}N \quad \text{for } N/K \ll 1.$$

6.4 Harvesting Models

As an exercise involving nonlinear population models we now consider the harvesting of fish. A good reference is the book by Wan (1989). The logistic model of fish growth is used as one of the examples. We assume that the carrying capacity K is the natural population of the fish in a particular fishery in the absence of harvesting. The object of the study is to determine the optimal amount of fish one can harvest from a fishery in a sustainable manner.

Let H be the harvest rate. We consider, then,

$$\frac{d}{dt}N = rN\left(1 - \frac{N}{K}\right) - H. \tag{6.3}$$

The harvest rate in an unregulated fishery should be proportional to N: the higher the fish population, the higher the catch. The proportionality constant should be dependent on E, the level of effort spent to fish. Typically

$$H = qEN, \tag{6.4}$$

with q being a proportionality constant. qE is known as the "fishing mortality"; it has the same dimension as r.

The new equation, now incorporating logistic growth and harvesting,

$$\frac{d}{dt}N = rN\left(1 - \frac{N}{K}\right) - qEN, \tag{6.5}$$

has two equilibria. These can be found by setting $\frac{d}{dt}N = 0$ in Eq. (6.5). They are

$$N_1^* = 0 \quad \text{and} \quad N_2^* = K(1 - qE/r). \tag{6.6}$$

The equilibrium N_2^* is stable, as can be inferred from Figure 6.3, which shows that perturbations away from N_2^* will tend back to N_2^*.
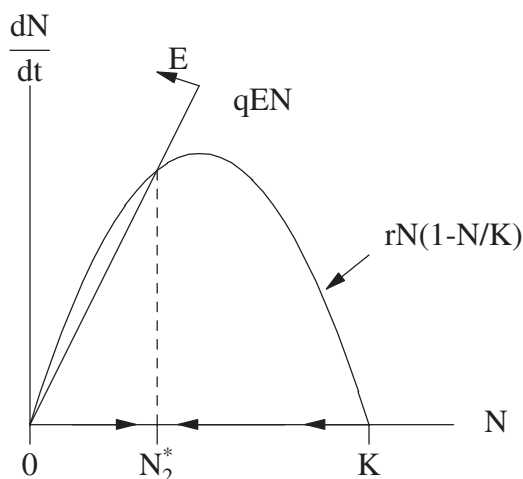
Figure 6.3. This diagram plots each of the two terms on the right-hand side of Eq. (6.5) against N. $\frac{dN}{dt}$ is the difference of the two curves plotted. $N^* = N_2^*$ is a stable equilibrium.
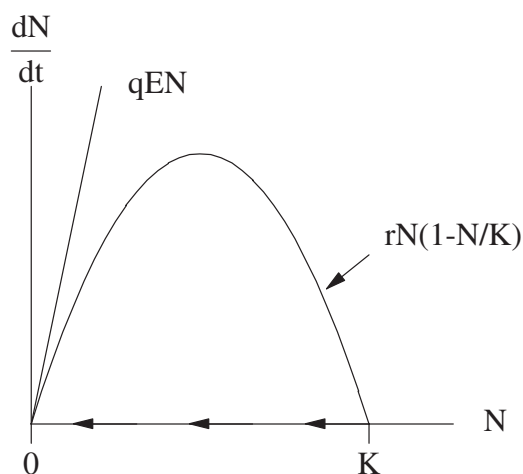

Figure 6.4. Now, $N_1^* = 0$ is stable. Extinction of the fish stock is the only stable solution.

This equilibrium population, although less than the natural carrying capacity K, is sustainable. That is, it is sustainable as long as $qE/r < 1$ in Eq. (6.6). When the fishing mortality qE is greater than the growth rate r ($qE/r > 1$), N_2^* becomes negative and we have only one equilibrium ($N^* = 0$). The stability behavior of the system also changes (see Figure 6.4).
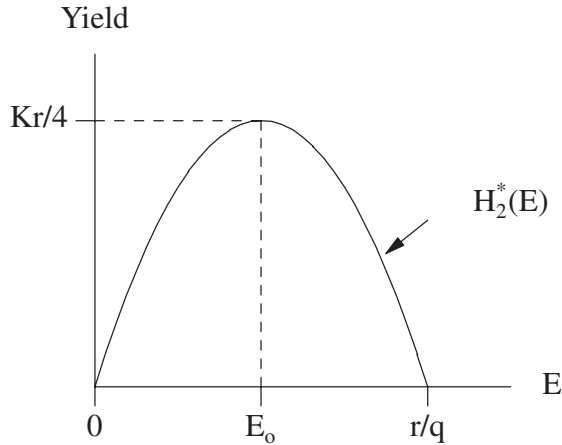
Yield

Figure 6.5. Sustained yield curve as a function of
fishing effort E. The optimal effort is given by
$E = E_0 \equiv r/2q$. The maximum yield is $H = \frac{1}{4}Kr$.

To have a sustainable harvest, one must have

$$qE/r < 1.$$

The corresponding harvest rate, called the *sustained yield*, is given by

$$H(N_2^*, E) = qE N_2^* = qEK(1 - qE/r) \equiv H_2^*.$$

The yield corresponding to the other equilibrium, $N_1^* = 0$, is obviously
zero:

$$H(N_1^*, E) = 0 \equiv H_1^*.$$

The sustained-yield curves, $H_2^*(E)$, are shown in Figure 6.5, as a function of E.

6.5 Economic Considerations

Economic considerations would often lead to a nonoptimal harvesting
effort. Let the price per unit fish be p and the cost per unit effort
be c, both assumed to be constants. Then the total cost (per unit
time) is cE, while the revenue from the harvest (per unit time) is
pH. In a sustained-yield situation, the break-even point would be the
intersection of $pH_2^*(E)$ and cE.

The break-even point occurs (when $H_2^*(E) = (c/p)E$) at $E = E_{be} = \frac{r}{q} \cdot (1 - \frac{(c/p)}{qK})$. See Figure 6.6.
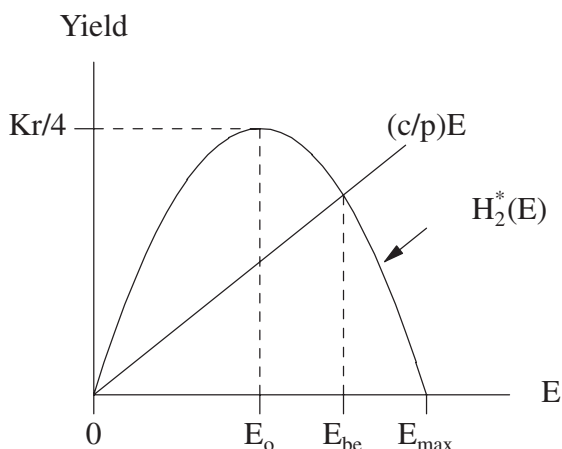
Figure 6.6. $E_{max} = r/q$ is the maximum effort beyond which the fish population will become extinct. E_{be} is the break-even effort for a given cost c and price p.

For higher priced fishes, this break-even effort occurs for an E closer and closer to E_{max}. But since the yield for these values of E is getting closer and closer to zero, the effort E will never get to E_{max} unless $c/p \to 0$. So, for a fish whose price is finite (i.e., $c/p > 0$), E_{be} is less than E_{max} by some finite amount.

If the current level of effort expended is $E < E_{be}$, i.e., less than the break-even level, then there would still be profit to be made for additional effort. There is, however, no economic incentive to expend an effort greater than the break-even point E_{be}. Since, as we have pointed out earlier, E_{be} is less than E_{max} by a finite amount, the fish will not go extinct.

6.6 Depensation Growth Models

The above conclusion does not seem to be consistent with our experiences: along the Pacific coast there were collapses of the sardine fishery near San Francisco and the anchovy fishery in Peru. This forces us to re-examine our model.

It is known that clupeids (such as sardines, anchovies, and herrings) form large and closely packed schools. Natural predators, which are not similarly concentrated, may be less efficient at decimating the prey population. On the other hand, if their population density gets too low these prey species are unable to reproduce rapidly enough to compensate for predator mortality. These populations grow only
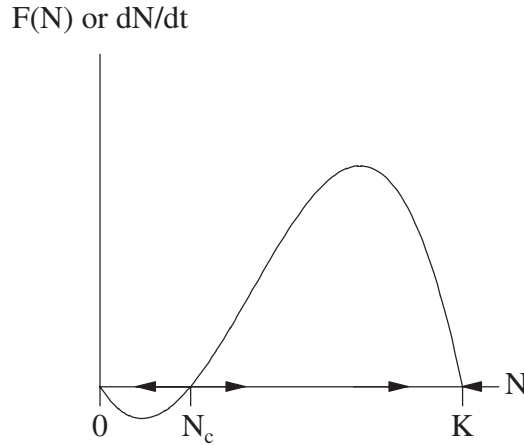
Figure 6.7. Depensation growth model without harvesting.

when their N lies between a (critical mass) value, N_c, and the carrying capacity, K. An example of such "depensation" growth models is

$$F(N) = r N \cdot (N/N_c - 1) \cdot (1 - N/K). \qquad (6.7)$$

There are now three equilibrium solutions (see Figure 6.7), with $N = 0$ being a *stable* equilibrium (compare this situation with the earlier logistic model, where $N = 0$ is an unstable equilibrium). If the population falls below its critical mass value, N_c, it will head to $N = 0$. Extinction is a stable equilibrium.

With the harvest term put back in, we now have

$$\frac{d}{dt} N = -r \cdot N \cdot (1 - N/N_c) \cdot (1 - N/K) - q E N. \qquad (6.8)$$

There are three equilibria: $N_1^* = 0$ and N_3^* are stable, and N_2^* is unstable. These equilibria are obtained by setting $dN/dt = 0$ in Eq. (6.8), and solving

$$N^* \cdot [r (N^*/N_c - 1)(1 - N^*/K) - q E] = 0.$$

Alternatively, they can be obtained as points of intersection of the harvesting line, $q E N$, and the growth rate, $F(N)$, in Figure 6.8.

Without regulatory control, a catastrophic collapse of the fishery or an outright extinction of the species is a distinct possibility for populations with a depensation growth behavior (see Figures 6.9 and 6.10).
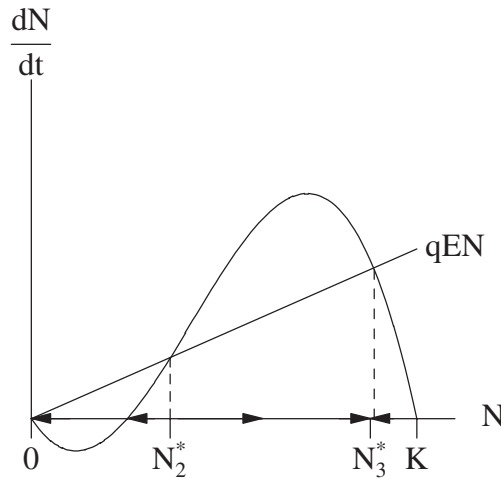
Figure 6.8. Depensation growth model with harvesting.
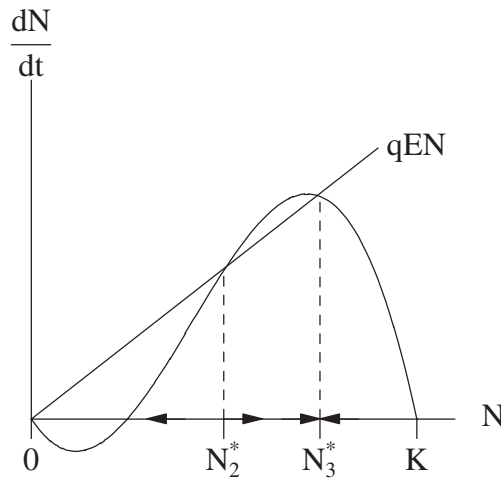
Figure 6.9. At higher levels of effort E, the unstable equilibrium N_2^* and the stable equilibrium N_3^* come closer to each other.

To see this in more detail, consider the sustained yield,

$$H_3^* \equiv H(N_3^*) = qE N_3^*,$$

as a function of E (see Figure 6.11). (Remember that N_3^* is a function of E also.) Let $E = E_{\max}$ be the largest effort beyond which the fish population will head for extinction. In this case, this occurs when
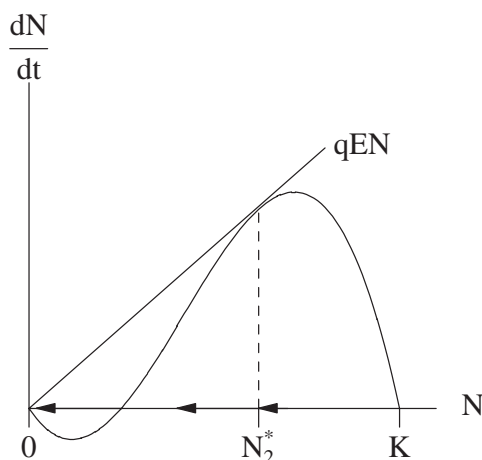
Figure 6.10. Until $N_2^* = N_3^*$. Then suddenly the stability properties of the equilibria change. N_3^* becomes *unstable*. All solutions will head to the only stable equilibrium, $N_1^* = 0$.
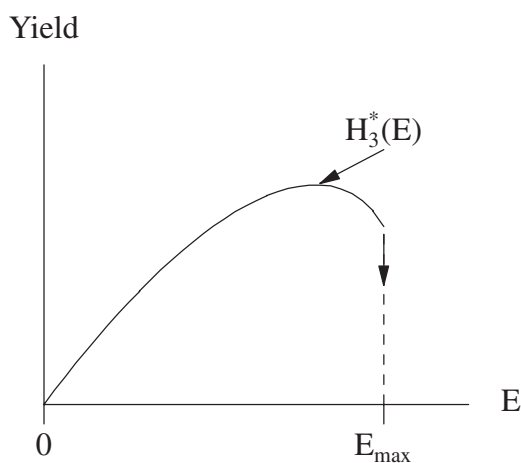
Figure 6.11. Sustained yield curve for the depensation growth model.

$N_3^* = N_2^*$, giving, as can be shown,

$$E_{max} = \frac{r}{q} \left[\frac{\left(\frac{K+N_c}{2}\right)^2}{N_c \cdot K} - 1 \right].$$

At this level of harvesting, the yield is still quite high (in contrast to the previous model, where the yield is zero at E_{max}). A fishery

producing a high yield (and possibly at a comfortable profit) may, without knowing it, allow a harvesting effort exceeding E_{max}. Suddenly the yield is not sustainable and the fish population declines monotonically to zero.

6.7 Comments

Myers et al. (1995) analyzed data from 128 fish stocks in order to determine if depensatory dynamics are common among exploited fish populations. Of the 128 fish stocks examined, they found statistically significant depensation only in an Icelandic herring stock and two Pacific salmon stocks. In all cases there was evidence of environmental effects that probably underlie the reduced rate of population increase. (On the other hand, critics point to the fact that 80% of the 128 fish stocks considered by Myers et al. yield inconclusive results because of a lack of statistical power.)

6.8 Exercises

1. *Regulated harvesting*

   Study Eq. (6.3) for a constant harvesting rate H in two ways:

   a. Use phase planes to find graphically the equilibria and their stability.

   b. Solve Eq. (6.3) exactly using the method of separation of variables.

2. *SI model of epidemiology*

   Derive a differential equation modeling the spread of flu among individuals in a fixed population of N. That is, express the rate of increase of the number of infected individuals ($I(t)$) in terms of $I(t)$:

   $$\frac{dI}{dt} = \cdots .$$

   You can assume that (a) the disease is nonfatal, and so N is constant; (b) the number of susceptible individuals $S(t)$ is the same as the number of uninfected individuals at time t; and (c) the rate of increase of infected individuals is proportional to the number of infected times the number of susceptible individuals at any given time. Obtain a single equation for $I(t)$ by eliminating $S(t)$.

3. Solve via separation of variables the following logistic equation for $I(t)$

$$\frac{dI}{dt} = rI \cdot \left(1 - \frac{I}{K}\right), \quad I(0) = I_0,$$

where r and K are positive constants. Find also the limit of $I(t)$ as $t \to \infty$.

4. Obtain the explicit solution to the harvesting problem

$$\frac{dN}{dt} = rN(1 - N/K) - H(N), \quad H = qEN,$$

subject to the initial condition $N(0) = N_0$. Here $N = N(t)$. The parameters r, K, q, and E are positive constants. Deduce the two limiting behaviors as $t \to \infty$.

5. There are many important classes of species whose birthrate is not proportional to the population size $N(t)$. Suppose, for example, that each member of the population requires a partner for reproduction and that each member relies on chance encounters to meet a mate. If the expected number of encounters is proportional to the product of the numbers of males and females, and if these are equally distributed in the population, then the number of encounters, and hence the birthrate, is proportional to $N(t)^2$. The death rate is still proportional to $N(t)$. Consequently, the population size $N(t)$ satisfies the differential equation

$$\frac{dN}{dt} = bN^2 - aN;$$

a, b are positive constants.

a. Solve for $N(t)$ given $N(0)$.

b. Find the long-time behavior by taking $t \to \infty$ in your solution in (a). Do this for the case $N(0) < a/b$.

6. *Right-handed snails*

D'Arcy Wentworth Thompson, a noted scientist of natural history, wrote in his book, *On Growth and Form* (1917): "But why, in the general run of shells, all the world over, in the past and in the present, one direction of twist is so overwhelmingly commoner than the other, no man knows." Most snail species are *dextral* (right-handed) in their shell pattern. *Sinistral* (left-handed) snails are exceedingly rare.

A plausible model for the appearance of such a bias in population handedness can be as follows: let $p(t)$ be the ratio of dextral snails in

the population of snails. $p = 1$ means that all snails are right-handed, and $p = 0$ means that all snails are left-handed. A model equation for $p(t)$ can be

$$\frac{d}{dt} p = \alpha p \cdot (1 - p) \cdot \left(p - \frac{1}{2} \right),$$

which has no left–right bias.

a. Locate the equilibria of p and determine their stability.

b. Suppose that at $t = 0$ (which is a very long time ago, perhaps a few hundred million years ago), $p(0) = \frac{1}{2}$; that is, the dextral and sinistral snails are evenly divided. Describe what will happen a few hundred million years later. Argue that we should not expect that $p(t) = \frac{1}{2}$ as $t \to \infty$ (i.e., an equal number of dextral and sinistral snails at the present time), and argue that our present state of affairs (mostly dextral snails) is an accident (i.e., we could just as well have mostly sinistral snails now).

7. Firefly synchrony

Philip Laurent wrote in *Science* in 1917 about a phenomenon he saw in Southeast Asia: "Some twenty years ago I saw, or thought I saw, a synchronal or simultaneous flashing of fireflies. I could hardly believe my eyes, for such a thing to occur among insects is certainly contrary to all natural laws."

Joy Adamson wrote in 1961 about an African version of the same phenomenon: "A great belt of light, some ten feet wide, formed by thousands upon thousands of fireflies whose green phosphorescence bridges the shoulder-high grass ... One is left wondering what means of communication they possess which enables them to coordinate their shining as though controlled by a mechanical device."

It is the males that flash to attract females. Individual males have their own light-emitting oscillators, with a natural period of about 0.9 second, but also have some ability to change the period to mimic the flashing of a particularly strong neighbor, thus increasing their own attractiveness to the females. Some species of fireflies can do this better than others, being able to change the frequency of their flashing by up to 15% in response to an external stimulus.

Let $\theta_e(t)$ be the phase (of the angle in radians) in the flashing of the external stimulus at time t (e.g., an attractive male neighbor). The frequency ω_e of the flashing is assumed to be given and fixed with

$$\frac{d\theta_e}{dt} = \omega_e.$$

Let $\theta(t)$ be the phase of a particular firefly under consideration at the same time t. If $\theta(t)$ is ahead of $\theta_e(t)$, it will try to slow down. If $\theta(t)$ is behind, it will try to speed up. So a model for $\frac{d}{dt}\theta$ is given by:

$$\frac{d\theta}{dt} = \omega + \alpha \sin(\theta_e - \theta).$$

The size of the external stimulus is measured by the parameter α, and ω is the natural frequency of this firefly in the absence of an external stimulus. So if θ_e is slightly ahead of θ, θ will increase so that $\frac{d}{dt}\theta > \omega$. It will slow down ($\frac{d}{dt}\theta < \omega$) if θ_e is slightly behind θ. Let $\phi(t) = \theta_e - \theta$ be the relative phase, $\tau = \alpha t$, and $\delta = (\omega_e - \omega)/\alpha$. The above equation becomes

$$\frac{d\phi}{d\tau} = \delta - \sin\phi,$$

involving only one parameter, δ. δ can be positive or negative; we consider the positive case below. The negative case is similar.

a. Plot the phase diagram (of $\frac{d\phi}{d\tau}$ vs. ϕ) schematically for the three different cases ($\delta = 0, 0 < \delta \leq 1, \delta > 1$) and for the range $-\pi \leq \phi \leq \pi$.

b. Describe the equilibria in the three cases and their stability (using arrows to indicate the direction of increasing ϕ).

c. Describe what happens to $\theta(t)$ eventually in the three cases: (i) for the very strong stimulus case, $\delta = 0$; (ii) for the weak stimulus case, $\delta > 1$; and (iii) for the moderate and realistic case, $0 < \delta \leq 1$. We call the case of nonsynchronous change in phase a phase drift, and we call the establishment of a steady phase relative to the external phase a phase locking. When phase locking occurs, the fireflies flash at the same frequency.

d. Derive the condition (an inequality among ω, α, and ω_e) for phase locking.

8. **Flu epidemic**

A flu epidemic starts in an isolated population of 1,000 individuals. When 100 individuals are infected the rate at which new infections are occurring is 90 individuals per day. If 20 individuals are infected at time $t = 0$, when will 90% of the population be infected?

(*Hints and assumptions*: Let $I(t)$, $N(t)$ be the number of infected and noninfected individuals at time t, respectively. The number of noninfected individuals is $N(t) = 1000 - I(t)$. The rate at which $I(t)$ is increasing should be proportional, $I(t)N(t)$.)

9. *Modeling the spread of technology*

Let N^* be the total number of ranchers in Uruguay, and $N(t)$ be the number of ranchers who have adopted an improved pasture technology there. Assume that the rate of adoption, $\frac{dN}{dt}$, is proportional to both the number who have adopted the technology and the fraction of the ranchers who have not (and so are susceptible to conversion). Let a be the proportionality constant.

a. Write down the differential equation for $N(t)$.

b. According to Banks (1993), $N^* = 17{,}015$, $N(0) = 141$, $a = 0.490$ per year. Determine how long it takes for the improved pasture technology to spread to 80% of the population of the ranchers.

10.

For a fish population modeled by a depensation growth model, we have, when there is harvesting,

$$\frac{d}{dt}N = F(N) - H(N),$$

where

$$F(N) = r N \cdot (N/N_c - 1)(1 - N/K)$$

and $H(N) = qEN$.

a. Find (and plot, freehand) the sustained yield $H(N_3^*)$ as a function of effort E, and the unsustainable yield $H(N_2^*)$, also as a function of E (and plot on the same figure). Here N_3^* is the nontrivial stable equilibrium of N and N_2^* is the unstable equilibrium.

b. Find the $E(= E_{\max})$, where the two curves in (a) merge (this happens when $N_2^* = N_3^*$). What happens to the fishery and the fish population when $E = E_{\max}$?

c. Suppose harvesting is done at effort level $E = E_{\max}$ for a while so that the fish population is below what was thought of as the "sustainable" N_3^* (which is equal to N_2^*, so actually it is not really sustainable). Realizing that there is a problem, the government puts in a fishing limit that reduces the effort E to slightly below $E_{\max}$. Can the fishery recover?