Module 764

Of Mites and Models:
A Temperature-Dependent Model of a Mite Predator–Prey Interaction

John B. Collings
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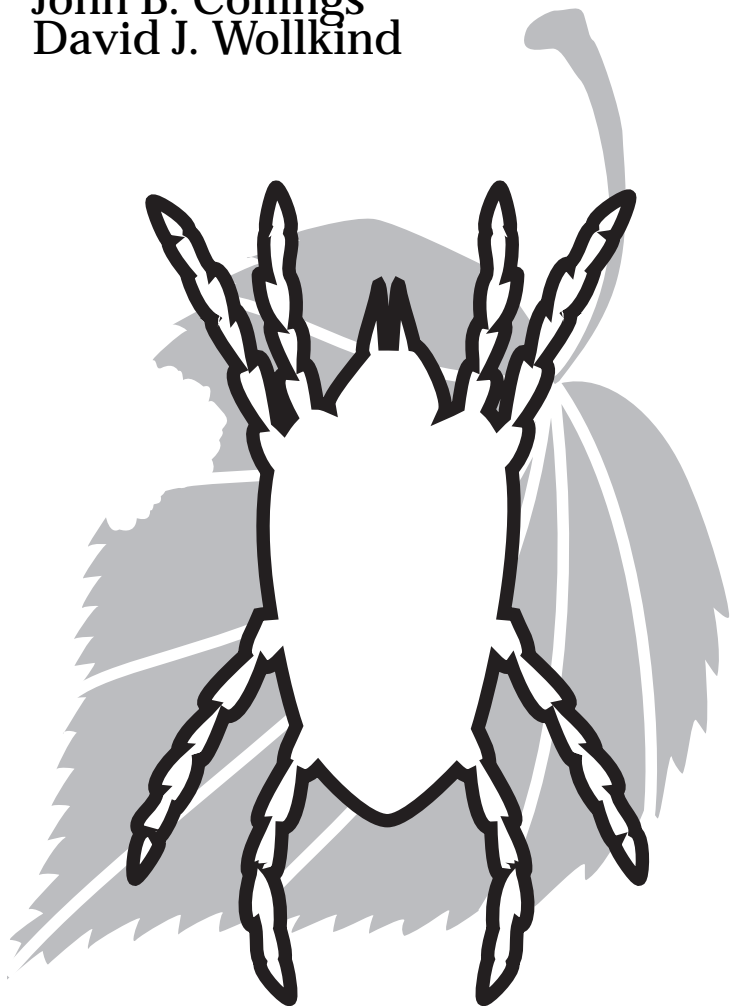
Applications of Mathematical Modeling and Differential Equations

INTERMODULAR DESCRIPTION SHEET:	UMAP Unit 764

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MATHEMATICAL FIELD:

Mathematical modeling, differential equations

APPLICATION FIELD:

Population biology

TARGET AUDIENCE:

Students in differential equations or mathematical modeling courses that cover phase-plane analysis.

ABSTRACT:

We analyze the qualitative behavior of a model for a mite predator-prey interaction. This model is based on a simple system of differential equations, and the model parameters are assigned values determined for a specific interaction between two species of mites. Several of these parameters are functions of temperature, and temperature is treated as a bifurcation parameter in the analysis of the model. It is shown that, depending on the temperature value, the model exhibits a stable fixed point, a stable limit cycle, or both (bistability). The model is used to illustrate population outbreaks.

PREREQUISITES:

Familiarity with the qualitative analysis of systems of differential equations (phase-plane analysis), and availability of an ODE solver with an adaptive step size (e.g., a Runge-Kutta-Fehlberg method).

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MODULES AND MONOGRAPHS IN UNDERGRADUATE
MATHEMATICS AND ITS APPLICATIONS (UMAP) PROJECT

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications, to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and now is supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a nonprofit corporation engaged in research and development in mathematics education.

Paul J. Campbell   Editor
Solomon Garfunkel   Executive Director, COMAP

1. Introduction

This Module, based on the work of Wollkind et al. [1988], analyzes a simple differential equations-based model for a predator-prey interaction between two species of mites. Mites are minute arthropods related to spiders and ticks. There are many species of mites, and mites are found in a variety of habitats, including plants, animals, stored food, and house dust. While most mite species are relatively benign, a number of species are agricultural pests, some are disease vectors, and dust mites are a common cause of allergies.

The population interaction that we consider below is between the predacious mite *Metaseiulus occidentalis* Nesbitt and its spider mite prey *Tetranychus mcdanieli* McGregor, an interaction that is common on apple trees in the state of Washington. The spider mite feeds on the leaves of the apple tree; and when population densities reach moderate levels (approximately 50 mites per leaf), there can be economically significant damage to the apple crop. Extended periods of high spider mite densities can harm the trees. Spider mites are known to rapidly develop resistance to pesticides, so maintaining their population densities at low levels using natural methods such as predators (an example of *biological control*) is of interest. The predator *M. occidentalis* can be an effective control of *T. mcdanieli*, and hence the interaction between these two mites is of some interest.

Understanding how populations change over time is an important problem in population biology, and much work has been done on formulating and analyzing models of population dynamics. The extensive literature on this subject includes descriptions of models ranging from very simple single-species models to very complicated models of entire ecosystems. The dynamics of a population of organisms are influenced by a variety of factors, including climate, habitat, ages of the organisms, and the species present. Some of these factors are deterministic and some are stochastic, and models that include even a few of these diverse factors can be very difficult to analyze. It is common, at least as a starting point, to consider simplified models that sacrifice some of the details but still provide insight (it is hoped) into the qualitative behavior of the population dynamics. In the formulation of the model analyzed below, we adopt such a parsimonious point of view.

We start with a system of ordinary differential equations that is easy to analyze. This system possesses a single fixed point in the first quadrant of the phase plane; when this fixed point is unstable, the system exhibits a stable limit cycle.

A criticism that has been offered for such simple differential-equations based models of predator–prey interactions is the lack of biological relevance in the parameter values used to illustrate the mathematical behavior of the model system. In an effort to at least partly address this concern, we incorporate parameter values deduced specifically for the *M. occidentalis–T. mcdanieli* interaction into the system. The resulting model exhibits, depending on the parameter values, a stable fixed point, a stable limit cycle, or both. The simultaneous

existence of two attractors is an example of *bistability*. The model shows good qualitative agreement with field observations for the mite interaction and with laboratory data for related interactions. In order to keep the analysis reasonable, the model does not include spatial dependencies, stochastic influences, or age-related features of the populations.

The first part of the project analyzes the qualitative behavior of the system of differential equations on which the model is based. This includes locating and classifying fixed points and determining a sufficient condition for the presence of a periodic solution. The second part introduces the parameter definitions specific to the *M. occidentalis–T. mcdanieli* interaction. Numerical methods are then used to deduce model behavior for these parameter values.

Several of the model parameters are functions of environmental temperature, and solutions of the model system will be shown to vary with respect to type, value, and stability as temperature varies. Temperature thus serves as a *bifurcation parameter*, and temperature values at which solutions undergo a qualitative change are *bifurcation points*.

The next section provides some background on the development of population models. For readers interested in learning more about the modeling of populations, there are a number of books that can provide a more thorough introduction to the subject. A recent book that is accessible to anyone with a year of calculus is Hastings [1997]. Two other books that may be of interest (and that require even less mathematics) are Kingsland [1985], which discusses the history of population modeling, and Cohen [1995], which discusses the modeling of human populations. Another source of information for readers with network access is the Population Ecology Home Page at `http://viner.ento.vt.edu/~sharov/popechome/welcome.html`. This network site, maintained at Virginia Tech by Alexei Sharov, provides access to a variety of resources pertaining to population ecology and population modeling.

2.   Development of the Model

Simple models for the growth of a single species are often based on the logistic equation,

$$\frac{dh}{dt} = r_1 h \left(1 - \frac{h}{K} \right),$$

where t denotes time and $h = h(t)$ denotes the population density (number per unit area). The per capita growth rate is

$$\frac{1}{h}\frac{dh}{dt} = r_1 \left(1 - \frac{h}{K} \right),$$

and the parameter $r_1 > 0$ denotes the maximum per capita growth rate. The parameter $K > 0$ is the population carrying capacity, which is the maximum population density that the environment can support over some reasonably

long period of time. The logistic equation is simplistic (for example, growth rates and carrying capacities for real populations are generally not constant), but it is easy to analyze (it is a separable equation, discussed in many introductory differential equations texts, such as Borrelli and Coleman [1996]). When the population density is low, growth is almost exponential; but as $h(t)$ increases, the growth rate slows and $h(t)$ approaches the carrying capacity K asymptotically. The constant solution $h(t) = K$ is a stable equilibrium solution.

If the population being modeled experiences some form of harvesting, a harvesting term $\psi \geq 0$ can be incorporated into the logistic equation to get

$$\frac{dh}{dt} = r_1 h \left(1 - \frac{h}{K}\right) - \psi.$$

A number of factors can influence the rate of harvesting, such as the number of harvesters, the efficiency of the harvesters, and the impact of weather on harvesting; so ψ will generally be a function of one or more variables and parameters.

When $h(t)$ denotes the density of a prey species that is being harvested by a predator species, the harvesting term ψ is commonly assumed to be proportional to the density of predators. Denoting the predator density by $p = p(t)$, this assumption gives

$$\psi = p \cdot f(h, p)$$

where $f(h, p)$ denotes the predator per capita rate of predation, called the *functional response*.

A number of functional responses have been proposed in the literature of population biology, many of which assume this per capita predation rate to be independent of the predator density. A simple example is $f(h) = ah$ with a constant. This functional response implies that the rate of predation increases linearly with the prey density, and it does not take into account the fact that there are only so many prey a predator can locate, kill, and consume in any finite interval of time.

A more realistic functional response that accounts for the time necessary to locate and *handle* prey is

$$f(h) = \frac{ah}{h + b}.$$

This functional response shows the per capita predation rate increasing with prey density to a maximal predation rate given by the parameter $a > 0$. The parameter $b > 0$ is related to searching efficiency and prey handling time and corresponds to the prey density necessary for the predator to achieve one-half the maximal rate of predation. This functional response is often used in models of arthropod predation, and it is the one that we will use. Incorporating this functional response into the equation for the prey dynamics yields

$$\frac{dh}{dt} = r_1 h \left(1 - \frac{h}{K}\right) - p\frac{ah}{h + b}. \tag{1}$$

In the interaction that that we are modeling, the lifetime of the predator is similar to that of the prey, so the predator population dynamics must also be considered. We start with a logistic equation for $p(t)$,

$$\frac{dp}{dt} = r_2 p \left(1 - \frac{p}{\Gamma}\right),$$

where $r_2 > 0$ represents the maximal per capita growth rate of the predator and $\Gamma > 0$ represents the carrying capacity of the predator species.

In an interaction in which the predator is totally dependent on a single prey species (i.e., one in which predators have no other source of sustenance and will starve to death if deprived of the prey), it is reasonable to assume that Γ depends on the density of the prey species. The simplest relationship is to let

$$\Gamma = \gamma h,$$

where the proportionality constant γ represents a measure of the food quality of the prey for conversion into predator births. The predator dynamics are then determined by the equation

$$\frac{dp}{dt} = r_2 p \left(1 - \frac{p}{\gamma h}\right). \tag{2}$$

Equations **(1)** and **(2)** together define the system of differential equations

$$\frac{dh}{dt} = r_1 h \left(1 - \frac{h}{K}\right) - p\frac{ah}{h + b}, \tag{3a}$$

$$\frac{dp}{dt} = r_2 p \left(1 - \frac{p}{\gamma h}\right), \tag{3b}$$

which provides the framework for our predator–prey model. This simple system was first proposed as a model of predator–prey dynamics by May [1973], and it was used shortly thereafter by Caughley [1976] to model successfully the population interaction between the moth *Cactoblastis cactorum* and the prickly-pear cactus in Australia. The first part of the project examines the qualitative behavior of system **(3)**. A discussion of the qualitative behavior of this model system can also be found in several books (Arrowsmith and Place [1982], Beltrami [1987], and Renshaw [1991]), but none of these applies the model to a specific interaction or discusses the possibility of bistability.

3.   Analysis of the Model, Part I

The analysis of system **(3)** can be simplified by introducing dimensionless variables and parameters, which will replace the six model parameters by three parameter groups and also scale the dependent variables so that their magnitudes are smaller than 1. This process of *scaling* is common in mathematical modeling and is based on changing the dependent and independent variables (e.g., see Borrelli and Coleman [1996]).

Exercises

1. Show that introducing the variables and parameters

$$\tau = r_1 t, \quad H = \frac{h}{K}, \quad P = \frac{p}{\gamma K}, \quad D = \frac{b}{K}, \quad \theta = \frac{r_2}{r_1}, \quad \phi = \frac{a\gamma}{r_1}$$

transforms system **(3)** into the nondimensional system

$$\frac{dH}{d\tau} = H(1 - H) - P\frac{\phi H}{H + D}, \tag{4a}$$

$$\frac{dP}{d\tau} = \theta P \left(1 - \frac{P}{H}\right). \tag{4b}$$

2. Sketch the prey *nullcline* in that portion of the HP plane on which system **(4)** is defined. (Also called a $0-isocline$, this is the curve on which $dH/d\tau = 0$.) On the same graph, sketch the predator nullclines. Show that system **(4)** has exactly one *community equilibrium point* (i.e., fixed point in the first quadrant), and that this point is given by (H_e, P_e) where $P_e = H_e$ and

$$H_e = \frac{1}{2}(\Delta + 1 - \phi - D), \quad \text{for} \quad \Delta = \sqrt{(1 - \phi - D)^2 + 4D}. \tag{5}$$

The process of scaling used to obtain system **(4)** from system **(3)** does not affect the existence or stability of solutions, so we know that system **(3)** also has a single community equilibrium point. We denote this point by (h_e, p_e) and note that $h_e = KH_e$ and $p_e = \gamma K H_e$. From the nullclines sketched in **Exercise 2**, it is clear that $H_e < 1$, and so $h_e = KH_e < K$. This means that the prey equilibrium density is less than the prey carrying capacity. In the absence of predators, the prey density approaches carrying capacity, and so we can conclude that predation acts to lower the prey density.

Exercises

3. Show that the only other fixed point with nonnegative population densities is $(1, 0)$, and show that this point is always a saddle point. Find the *principal directions* associated with the *stable* and *unstable manifolds* of the linearization of system **(4)** about the fixed point $(0, 1)$. These principal directions are defined by the eigenvectors of the linearized system.

4. Show that at $(1, 0)$, the slope of the unstable manifold is less than the slope of the prey nullcline. This implies that in a sufficiently small neighborhood of $(1, 0)$ in the first quadrant, the unstable manifold of the saddle point lies above the prey nullcline, as illustrated in **Figure 1**. This unstable manifold is useful in determining a sufficient condition for the existence of a periodic solution (see **Exercise 8**).
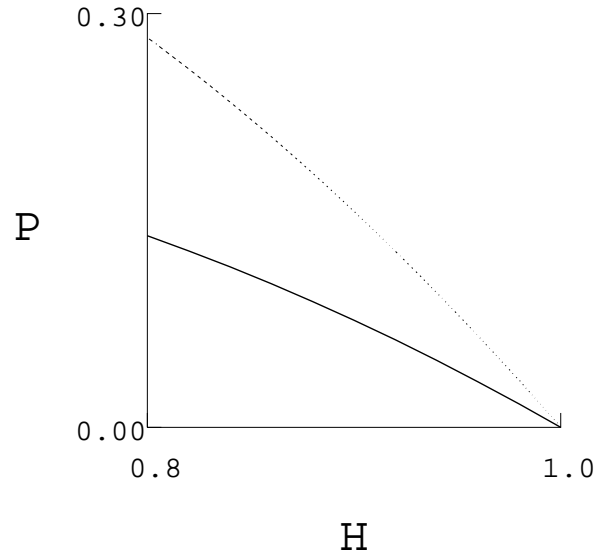
Figure 1. A plot of the prey nullcline (solid line) and the unstable manifold (broken line) near the saddle point $(1, 0)$. The slope of the unstable manifold at this point is determined by the eigenvector associated with the positive eigenvalue.

5. Linearize system **(4)** at the equilibrium point (H_e, P_e), and show that the Jacobian for system **(4)** evaluated at this fixed point is

$$
J_e = \begin{pmatrix} 1 - 2H_e - \dfrac{\phi D H_e}{(H_e + D)^2} & \dfrac{-\phi H_e}{H_e + D} \\[2em] \theta & -\theta \end{pmatrix}. \tag{6}
$$

6. The fixed point (H_e, P_e) is locally stable if and only if $\det(J_e) > 0$ and $\operatorname{tr}(J_e) < 0$. Show that the condition $\det(J_e) > 0$ is always satisfied, and so deduce that (H_e, P_e) is locally stable if and only if $\theta > \theta_c$, where

$$
\theta_c = \frac{H_e(1 - D - 2H_e)}{H_e + D}. \tag{7}
$$

Hint: A community equilibrium point lies on the prey nullcline, so

$$
1 - H_e = \frac{\phi H_e}{H_e + D}. \tag{8}
$$

A simpler expression for θ_c can be derived as follows. It can be shown that at equilibrium,

$$
\frac{H_e}{H_e + D} = \frac{1}{H_e + D + \phi}, \tag{9}
$$

6

and **(7)** and **(9)** imply that

$$\theta_c = \frac{1 - D - 2H_e}{H_e + D + \phi}.$$ (10)

From **(5)** and **(10)** we then get, after simplifying,

$$\theta_c = \frac{2(\phi - \Delta)}{1 + \phi + D + \Delta}.$$ (11)

Exercises

7. Use **(11)** and **(5)** to show that if $D < 1$, then values of $\phi > 0$ exist for which $\theta_c > 0$. For such values of D and ϕ, the community equilibrium point can be made stable or unstable by "tuning" θ. Conversely, if $D > 1$, then the community equilibrium point is always stable since $\theta_c < 0$ while $\theta > 0$.

8. Use the Poincaré-Bendixson Theorem to show that when (H_e, P_e) is unstable, the system exhibits a closed trajectory corresponding to a periodic solution. *Hint:* Use part of a trajectory following the unstable manifold of the saddle point at $(1, 0)$ and a portion of the prey nullcline to bound a closed region containing the unstable equilibrium point, and show that this region is positively invariant.

At this point, you have established that system **(4)** possesses a single community equilibrium point, and that the instability of this point is a sufficient condition for the existence of a periodic solution. The process of scaling used to obtain system **(4)** from system **(3)** does not affect the existence or stability of solutions, and so the same conclusions apply to system **(3)**.

The next section uses numerical methods to examine the behavior of system **(3)** with parameter values defined specifically for the *M. occidentalis–T. mcdanieli* predator–prey interaction. While much of the behavior can be deduced from the analysis in the present section, the numerical analysis reveals the presence of two stable solutions for some values of the model parameters. This example of *bistability* involves both a fixed point and a periodic solution, and it is a situation that is not easy to show using only analytical methods.

4.   Analysis of the Model, Part II

System **(3)** can be used to model the interaction between the predacious mite *M. occidentalis* and its spider mite prey *T. mcdanieli* by assigning to the model parameters values appropriate for this interaction. We first note that time $t > 0$ is measured in days and prey and predator densities ($h > 0$ and $p \geq 0$ respectively) are measured in mites per leaf. Temperature has been identified as the most important environmental variable affecting this interaction,

so temperature is incorporated explicitly into the parameters r_1, r_2, and a. In particular, Wollkind et al. [1988] adopt for the per capita growth rates per day of *T. mcdanieli* and *M. occidentalis*, respectively, the functions

$$r_1(T) = 0.048\big[\exp\big(0.103(T - 10)\big) - \exp\big(0.369(T - 10) - 7.457\big)\big],$$
$$r_2(T) = 0.089\big[\exp\big(0.055(T - 10)\big) - \exp\big(0.483(T - 10) - 11.648\big)\big],$$

for $T \in [10, T_M)$, where T represents environmental temperature measured in degrees Celsius and $T_M = 37.2°$ C is the *predator lethal maximum temperature* above which life processes cannot be maintained for an extended period of time. (These growth rate expressions were determined by using simulation models of mite development that incorporated life history data for the species under consideration.) Wollkind et al. [1988] define the maximal predator per capita predation rate a by the function

$$a(T) = \frac{16\, r_2^2(T)}{r_1(T)}.$$

The remaining parameters are given values typical for such a mite interaction, with $\gamma = 0.15$, $K = 300$ mites per leaf, and $b = 0.04$ mites per leaf (or one mite per 25 leaves; field observations often find mite densities much less than 1 mite per leaf).

Exercises

9. Differentiate equation **(8)** implicitly with respect to T, to show that

$$\frac{dH_e}{dT} = \left[\frac{-H_e(H_e + D)}{(H_e + D)^2 + \phi D}\right]\frac{d\phi}{dT}. \tag{12}$$

   Use the fact that $d\phi/dT < 0$ to conclude that the equilibrium prey densities increase with temperature (recall that $h_e = KH_e$). In the field, an increase in temperature often leads to an increase in the density of the spider mite population.

10. From **Exercise 6**, we know that the community equilibrium point is stable if and only if $\theta > \theta_c$. Plot θ and θ_c as functions of T for $T \in (10, T_M)$ and note that these two curves intersect twice, at values of T that we will denote by T_1 and T_2 (with $T_1 < T_2$). Conclude that the community equilibrium point is stable for $T \in (10, T_1)$ and $T \in (T_2, T_M)$, and unstable for $T \in (T_1, T_2)$.

By using numerical methods to solve the equation $\theta(T) = \theta_c(T)$, we find that $T_1 \approx 30.89$ and $T_2 \approx 35.56$. From **Exercise 8**, we know that $T \in (T_1, T_2)$ is a sufficient condition for the existence of a periodic solution; and it can be shown that T_1 and T_2 are *Hopf bifurcation points*. (In general, if μ_c denotes a Hopf bifurcation point for a parameter μ, when $|\mu - \mu_c|$ is sufficiently small,

a periodic solution exists either for $\mu < \mu_c$ or for $\mu > \mu_c$, and as $\mu \to \mu_c$ the amplitude of the periodic solution approaches zero; see, e.g., Beltrami [1987].)

The following two exercises produce a diagram that illustrates how solutions change with respect to type, value and stability as the value of the parameter T changes. Such a diagram is called a *bifurcation diagram*, and T is the *bifurcation parameter*.

Exercise

11. Plot h_e as a function of T for $T \in (28, 37)$ (recall that $h_e = KH_e$). Indicate on this plot the location of the Hopf bifurcation points. Also indicate for which values of T the fixed point (h_e, p_e) is stable and for which values it is unstable. (A common method is to use a solid line to represent the fixed point when it is stable and a broken line when it is unstable. A Hopf bifurcation point is indicated by a solid square.)

Similar information for the periodic solutions can be added to the bifurcation diagram by plotting a measure (such as a norm) of such solutions for different values of T. A useful measure in this case is the maximum prey level attained during one period of such an oscillation. That is, for each fixed value of T a periodic solution $h(t; T)$ can be represented by the value

$$\max_{t \in [0, \Omega]} h(t; T),$$

where Ω is the period of oscillation.

Exercise

12. Numerically estimate the maximum prey value associated with the periodic solution when $T = 35.5$ and plot this value on the bifurcation diagram. (This value can be estimated from the graph of the periodic solution in the phase plane, or from a plot of $h(t)$, after transients have decayed.) Repeat, for $T = 34.5, 33.5, 32.5, 31.5$. What happens at $T = 30.5$? $T = 30$? (Recall that the fixed point is locally stable for $T < 30.89$.)

It can be shown that the lowest temperature value at which the system exhibits a periodic solution is $T_0 \approx 29.95$. At T_0, there is a *saddle node bifurcation* of periodic solutions. For $T < T_0$, there are no periodic solutions; but as T increases through T_0, both stable and unstable periodic solutions come into existence. For $T \in (T_0, T_1)$, the system exhibits both a stable limit cycle and a stable fixed point, an example of bistability.

Exercise

13. Plot the phase portrait for the system at $T = 30$ and show that an unstable limit cycle acts as the *separatrix* between the *basins of attraction* of the stable fixed point and stable limit cycle. Initial conditions in the region bounded by the unstable limit cycle give rise to trajectories that approach the stable community equilibrium point, while initial conditions outside this region yield trajectories that approach the stable limit cycle. (A plot of the unstable limit cycle can be obtained by letting $t \to -\infty$.)

There are unstable limit cycles for all $T \in (T_0, T_1)$. A curve representing these solutions can be added to the bifurcation diagram, as illustrated in **Figure 2** by the curve of unfilled circles.
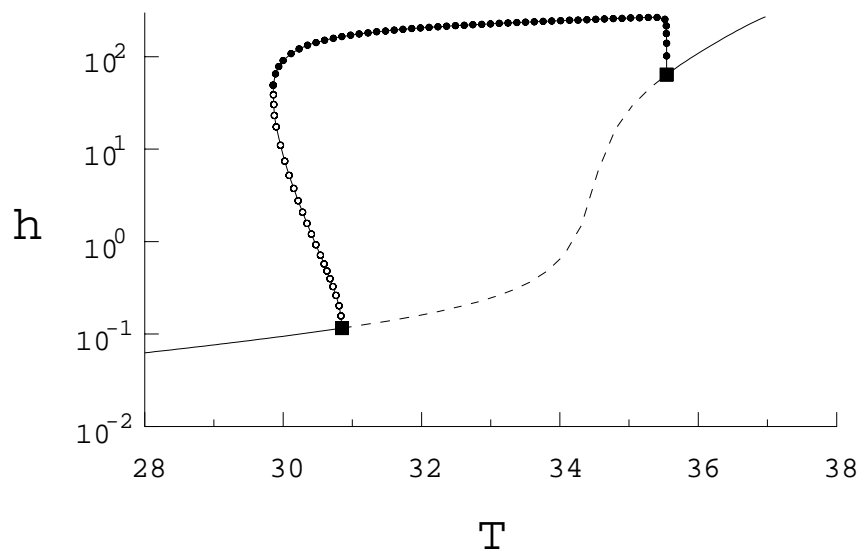

Figure 2. The complete bifurcation diagram for system **(3)** for $T \in (28, 37)$. The vertical axis uses a logarithmic scale to better show the details. (The bifurcation diagram produced in **Exercises 11** and **12** will contain a subset of the information shown in this figure.)

The bifurcation diagram in **Figure 2** gives a graphical representation of how the system behavior depends on the temperature parameter.

- For each $T \in (10, T_0)$, the system has a globally stable community equilibrium point with a very low prey density.

- For each $T \in (T_2, T_M)$, there is a globally stable community equilibrium point with a relatively high prey density.

- For each $T \in (T_1, T_2)$, the system exhibits a globally stable limit cycle with a significant prey maximum.

If we interpret T as mean daily temperature, this model behavior is in qualitative agreement with field observations, which generally find that spider mite

densities are higher and population oscillations are more likely later in the growing season when temperatures are higher. The interval (T_0, T_1) is characterized by bistability, which we discuss below. Before doing so, we mention that the process of determining the bifurcation diagram for a system of differential equations can be automated through the use of numerical methods for continuing solution curves as a parameter varies, and in fact several computer packages produce these diagrams (**Figure 2** was produced using the program AUTO; see the **Software Notes**).

Exercise

14. Let $T = 30$, and plot the prey equilibrium density $h(t) = h_e(T)$ for $0 \leq t \leq 100$. Use a differential equation solver to plot, for $0 \leq t \leq 100$, the prey density $h(t)$ obtained by using initial conditions that are 10% of the equilibrium values, i.e., set

$$\big(h(0), p(0)\big) = 0.1\big(h_e(T), p_e(T)\big).$$

Compare these two solutions, and in particular note the difference in maximum densities.

From **Exercise 14**, we can deduce that if populations at equilibrium are subjected to some external force that kills a sufficient portion of the populations, then population densities will rebound dramatically as the stable equilibrium densities are replaced by stable oscillations, as illustrated in **Figure 3**.
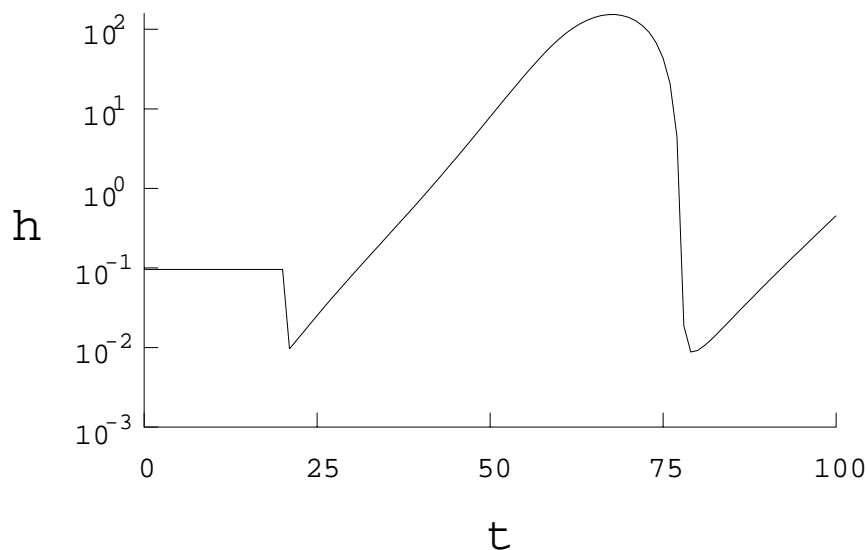

Figure 3. A plot of $h(t)$ illustrating an outbreak. The equilibrium density at $T = 30$, $h(t) = h_e(30)$, is shown for $0 < t < 20$, at which time both prey and predator densities are reduced to 10% of their equilibrium levels. This is followed by a dramatic increase in the prey density, i.e., an outbreak. A logarithmic scale is used on the vertical axis to better show the details.

From a population dynamics point of view, this is an example of a *population outbreak*, wherein the population density of a species undergoes an increase of several orders of magnitude over a short period of time. Such behavior has been observed in the field, associated with the use of pesticides. A typical pesticide-induced outbreak scenario starts with the application of a pesticide that causes an immediate reduction in the population densities of both predator and prey (pesticides often kill more than just the intended pest species). This is followed by a quick resurgence of the spider mite population, often to densities much higher than those prior to the application. The predator population may then increase, but rather than controlling the prey the predator may overexploit its prey (i.e., the predators kill too many prey to be able to sustain their own numbers), leading to a population crash. Population outbreaks and crashes can occur in a cyclic fashion. Pesticide-induced outbreaks have been documented in a variety of agricultural interactions (e.g., see DeBach and Rosen [1991]).

Another mechanism for causing an outbreak involves increasing the temperature parameter. In particular, when $T < T_0$ the system exhibits a globally stable community equilibrium point. As T increases through T_1 this equilibrium solution becomes unstable, and trajectories spiral out to a stable limit cycle with a maximum prey density much larger than the equilibrium densities found for $T < T_0$, as illustrated in **Figure 4**. Note that a subsequent decrease in T through T_1 does not lead to a collapse to the stable fixed point unless T is actually decreased below T_0. This is an example of *hysteresis*, a lack of reversibility as T is varied near T_1. This hysteresis, as well as the potential to model outbreaks, is a direct consequence of the interval of bistability for $T \in (T_0, T_1)$.
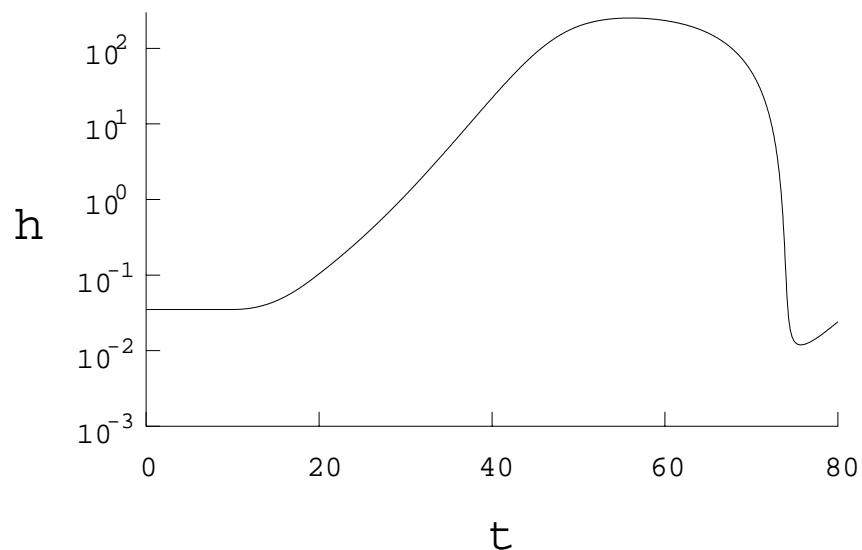

Figure 4. A plot of $h(t)$ illustrating an outbreak as T is increased from 25 to 35 over the course of 10 days, beginning at $t = 10$. The populations were started at the equilibrium densities $(h_e(25), p_e(25))$. A logarithmic scale is used on the vertical axis to show the details better.

5. Software Notes

The project requires the use of numerical methods to obtain periodic solutions of the system of differential equations. Due to the nature of the system, we recommend using a differential equations solver with an adaptive step size, and some experimentation with tolerance values and maximum step size may be necessary. We have had good results using the Runge-Kutta-Fehlberg method provided with the Midshipman Differential Equations Program (MDEP) (a freeware program for DOS machines available from J.L. Buchanan, Mathematics Dept., United States Naval Academy, 572 Holloway Road, Annapolis, Maryland, 21402–5002).

Two commercially available programs that we have also used successfully on the model system are Mathematica (available from Wolfram Research, Inc., 100 Trade Center Drive, Champaign, IL, 61820–7237) and PSI-Plot (available from Poly Software International, P.O. Box 526368, Salt Lake City, UT 84152). PSI-Plot is a software package for technical plotting (it was used to produce the figures in this paper), but it also provides a number of ODE solvers.

AUTO is a FORTRAN software package for solving continuation and bifurcation problems for systems of autonomous differential equations, written by Eusebius Doedel (now at Concordia University in Montreal) (available from Applied Mathematics 217–50, California Institute of Technology, Pasadena, CA, 91125). AUTO is also available as part of a larger software package, XPPAUT (available from G. Bard Ermentrout at the University of Pittsburgh). XPPAUT, designed for UNIX machines, is available over the Internet at `http://www.pitt.edu/~phase/` . In addition to AUTO, it provides solvers for systems of differential equations, including adaptive-step-size methods. (XPPAUT is now available for Windows 95/NT from the same Internet location.)

6. Solutions to the Exercises

1. The chain rule gives:

$$\frac{dH}{d\tau} = \frac{dH}{dt}\frac{dt}{d\tau} = \frac{dH}{dh}\frac{dh}{dt}\frac{dt}{d\tau} = \frac{1}{r_1}\frac{1}{K}\frac{dh}{dt}.$$

2. The predator nullclines are the H-axis and the line $P_1(H) = H$, and the prey nullcline is the parabola $P_2(H) = (1 - H)(H + D)/\phi$. (For the graphs of the nullclines, see **Figure 5**.) The community equilibrium point is the point in the first quadrant at which $P_1(H)$ intersects $P_2(H)$, and the value of H at this intersection is then given by the positive root of the equation
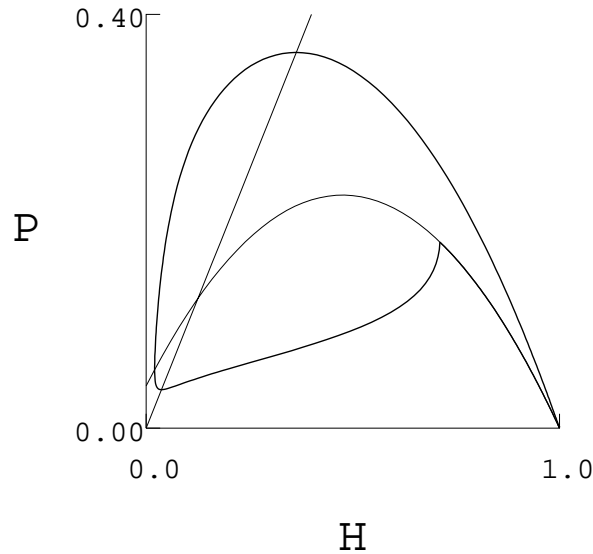
$$D + (1 - D - \phi)H - H^2 = 0.$$

Figure 5. A plot of the prey and predator nullclines (thin lines), and the boundary (thick line) of an invariant region containing the community equilibrium point.

3. If $P \neq H$, the only other value of P for which $dP/d\tau = 0$ is $P = 0$. In this case, $dH/d\tau = 0$ implies that $H = 1$, and so the only other feasible fixed point is $(1, 0)$. The Jacobian matrix for system **(4)** is

$$J = \begin{pmatrix} 1 - 2H - \dfrac{\phi DP}{(H+D)^2} & \dfrac{-\phi H}{H+D} \\ \\ \theta\dfrac{P^2}{H^2} & \theta - 2\theta\dfrac{P}{H} \end{pmatrix}. \tag{13}$$

Evaluation of J at the point $(1, 0)$ gives

$$J_{|_{(1,0)}} = \begin{pmatrix} -1 & \dfrac{-\phi}{1+D} \\ \\ 0 & \theta \end{pmatrix}.$$

The eigenvalues of $J_{|_{(1,0)}}$ are -1 and θ, and so $(1, 0)$ is a saddle point. The eigenvectors associated with these eigenvalues are

$$\begin{pmatrix} 1 \\ 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 1 \\ -(1+\theta)(1+D)/\phi \end{pmatrix},$$

respectively.

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4. The slope of the prey nullcline is

$$P_2'(H) = (1 - 2H - D)/\phi,$$

and at the saddle point $(1, 0)$ the slope is $P_2'(1) = -(1+D)/\phi$. The slope of the unstable manifold at this point is the slope S of the eigenvector associated with the eigenvalue $\theta > 0$, and $S = -(1 + \theta)(1 + D)/\phi < P_2'(1)$.

5. J_e given by **(6)** is obtained by evaluating **(13)** at the point (H_e, P_e).

6. J_e can be rewritten by using the hint **(8)** to get

$$J_e = \begin{pmatrix} 1 - 2H_e - \dfrac{D(1 - H_e)}{(H_e + D)} & -(1 - H_e) \\ \\ \theta & -\theta \end{pmatrix}.$$

Then

$$\det(J_e) = \theta \left(H_e + \frac{D(1 - H_e)}{H_e + D} \right) > 0,$$

since $0 < H_e < 1$. The requirement $\mathrm{tr}(J_e) < 0$ then gives the local stability criterion $\theta > \theta_c$, where

$$\theta_c = 1 - 2H_e - \frac{D(1 - H_e)}{(H_e + D)},$$

which simplifies to **(7)**.

7. We have $\theta_c > 0$ when $\phi > \Delta$; and since $\phi > 0$ and $\Delta > 0$, an equivalent requirement is that $\phi^2 > \Delta^2$. From this, we find that $\theta_c > 0$ when

$$2(1 - D)\phi > (1 + D)^2. \tag{14}$$

If $D < 1$, then $\theta_c > 0$ when

$$\phi > \frac{(1 + D)^2}{2(1 - D)}.$$

If $D \geq 1$, then **(14)** cannot be satisfied for any $\phi > 0$, and so in this case $\theta_c < 0$.

8. In **Figure 5**, the thick solid line is the boundary of an invariant region containing the (unstable) community equilibrium point, and consists of a portion of the trajectory following the unstable manifold of $(1, 0)$ and part of the prey nullcline. If the community equilibrium point is unstable, then trajectories in this region must approach a periodic solution.

9. H_e and ϕ are both functions of T. Equation **(12)** can be obtained by differentiating

$$1 - H_e(T) = \frac{\phi(T)H_e(T)}{H_e(T) + D}$$

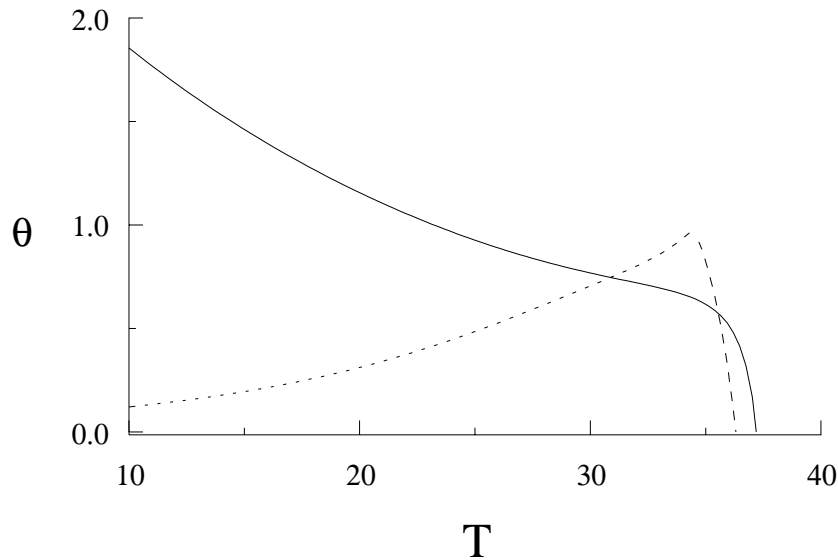with respect to T.

10. See **Figure 6**.

Figure 6. A plot of θ (solid line) and θ_c (broken line) as functions of T.

11. and **12. Figure 2** shows the bifurcation diagram obtained using the software package AUTO, and with a logarithmic scale used on the vertical axis to better show the details. **Figure 7** shows that part of the bifurcation diagram corresponding to the directions in the exercises (and without logarithmic scaling). As in **Figure 2**, the fixed point values h_e are represented by a line, solid where stable and broken where unstable, and the maximal prey values of the periodic solutions are represented by lines of circles.
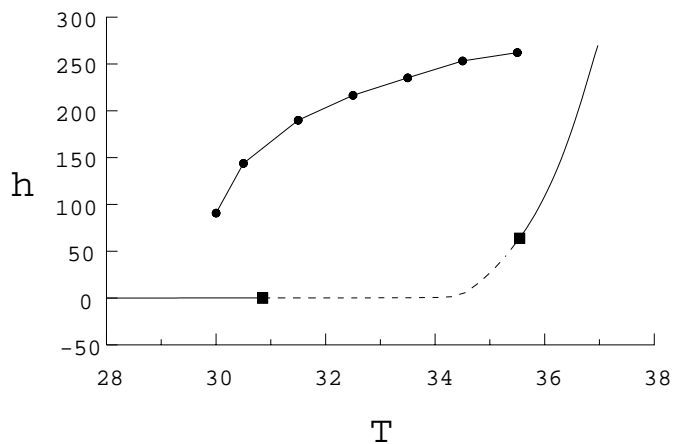
12. See **Figure 8**.

13. See **Figure 3**.

Figure 7. A (partial) bifurcation diagram for system **(3)**, from **Exercises 11** and **12**.
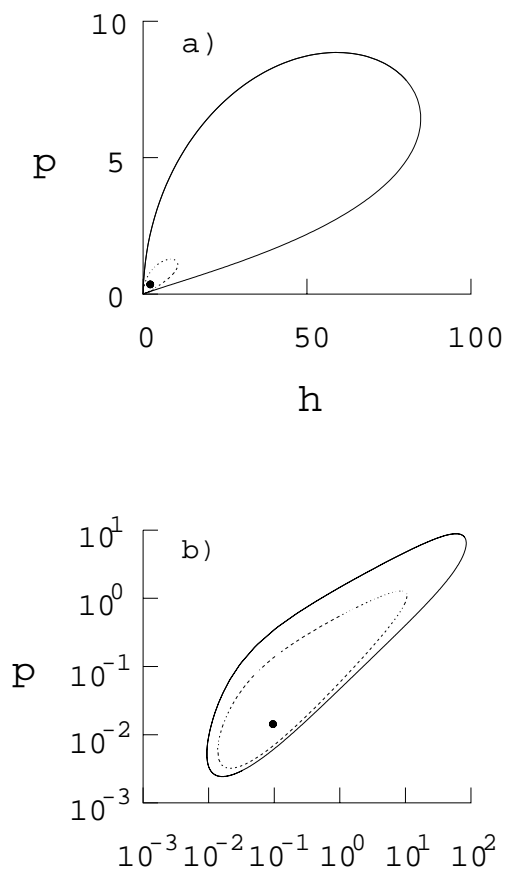

Figure 8. The phase plane at $T = 30$. Plot **a)** uses linear scaling on the axes, while plot **b)** uses logarithmic scaling. In each, the solid line represents the stable limit cycle, the broken line represents the unstable limit cycle (almost invisible in plot **a)**), and the dot represents the stable fixed point. The location of the dot in **a)** is only approximate so that it can be distinguished from the limit cycle curve.

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