SECTION 10

BIFURCATION PHENOMENA IN POPULATION MODELS

BY

G. OSTER AND J. GUCKENHEIMER


Biological systems tend to be considerably more complex than those studied in physics or chemistry. In analyzing models, one is frequently presented with two alternatives: either resorting to brute force computer simulation or to reducing the model further via such drastic approximations as to render it biologically uninteresting. Neither alternative is attractive. Indeed, the former alternative is hardly viable for most situations in ecology since sufficient data is rarely available to quantitatively validate a model. This contrasts starkly with the physical sciences where small differences can often discriminate between competing theories. The situation is such that many ecologists seriously question
whether mathematics can play any useful role in biology. Some claim that there has not yet been a single fundamental advance in biology attributable to mathematical theory. Where complex systems are concerned, they assert that the appropriate language is English, not mathematical. A typical attitude among biologists is that models are useful only insofar as they explain the unknown or suggest new experiments. Such models are hard to come by.

In the face of such cynicism, perhaps mathematicians who would dabble in biology should set themselves more modest goals. Rather than presenting the biological community with an exhaustive analysis of an interesting model, it might be better to produce a "softer" analysis of a meaningful model. From this viewpoint, the role of mathematics is not to generate proofs, but to act as a guide to one's intuition in perceiving what nature is up to. This is no excuse for avoiding hard analysis where it can be done, but as models mimic nature more closely it becomes harder to prove theorems.

In this spirit, we shall discuss several instances where some concepts of bifurcation theory have proved useful in ecological modelling. We shall discuss (briefly) bifurcation phenomena in three kinds of population models: (i) discrete generation populations modelled by difference equations, (ii) continuously breeding populations modelled by ordinary differential equations, and (iii) populations with age structure which require partial or functional differential equations.

* Perhaps excluding the Hardy-Weinberg law--which is trivial mathematically.
These represent three successive stages of increasing biological realism as well as mathematical intractibility. Thus we shall proceed from less realistic models based upon solid mathematical foundations to more realistic models based upon mathematical intuition. In all cases, however, the usefulness of bifurcation theory transcends our ability to cite theorems. By furnishing a qualitative modelling mechanism, it provides a conceptual framework within which we can view a number of important ecological processes.


(2.1) Consider an insect population which breeds once a year. A plot of the total number of individuals as a function of time might look like Figure 10.1a:

If we are only interested in either the mean, total or average number each year, we might consider an approximate difference equation model as shown in Figure 10.1b:
i.e., an equation of the form:

\[ N_{t+1} = F(N_t). \] (2.1)

Models of this kind are commonly employed in entomology (Hassell & May, [1]; Varley, Gradwell & Hassell, [1]). In general, \( F(\cdot) \) will have the shape shown in Figure 10.2:

The reason for this is that as the population density increases crowding effects, such as competition for food, tend to increase death rates and decrease birth rates.
Typical functional forms that have been employed in modelling insect populations are:

\[ N_{t+1} = N_t \frac{r(1-N_t/K)}{N_t + r} \]  \hspace{1cm} (2.2a)

\[ N_{t+1} = N_t \frac{\lambda}{(1+N_t)^b} \]  \hspace{1cm} (2.2b)

\[ N_{t+1} = \frac{N_t}{1+e^{-a(1-N_t/K)}} \]  \hspace{1cm} (2.2c)

\[ N_{t+1} = \begin{cases} \lambda N_t, & N_t < 1 \\ \lambda N_t^{1-b}, & N_t > 1 \end{cases} \]  \hspace{1cm} (2.2d)

Each of these models has the origin as a fixed point and have the "l-hump" characteristic of Figure 10.2, i.e., single critical point less than the positive fixed point. Beyond this, however, they are largely empirical, generated ad hoc by regression of one generation on the next. By and large, however, such simple-minded models have been surprisingly effective in reproducing the generation-to-generation variations in population levels. (Auslander, Oster, Huffaker, Varley, et. al., op. cit.)

*Note that, for \( r \ll 1 \), equation (2.2a) is

\[ N_{t+1} - N_t = rN_t(1 - \frac{N_t}{K}) \]  \hspace{1cm} (2.2a*)

which is just the forward difference equation corresponding to the familiar logistic equation for population growth:

\[ \frac{dN}{dt} = rN(1 - \frac{N}{K}) \]. Thus, \( r \) in (2.2) can be interpreted as the net generation-to-generation reproductive rate. Although Equation (2.2a) can exhibit bifurcations, (2.2a*) cannot. (i.e., for large \( r \), (2.2a) has a critical point, so it cannot be a finite version of (2.2a*).
Whether or not the population, as modelled by any of equations (2.2), settles down to a steady generation-to-generation level depends on the stability of the fixed point, \( F(N) = N, N > 0 \), and perhaps the initial condition. This, in turn, depends on the particular parameter values, such as \( r \) in (2.2a). Let us consider (2.2a) as the prototype for our discussion. The eigenvalue of \( F(\cdot) \) at the fixed point \( N_0 = K \) is \( A(r) = F'(N) = 1-r \). As the reproduction rate increases past 2, \( A(r) \) moves across the unit circle and \( N_0 \) ceases to be an attractor. However, if \( F \) has a critical point—as we have supposed in the models (2.2)—then the composition of \( F \) with itself will have at least 3 critical points and we can look at the period-2 fixed points:

\[
F^2(N_2) \equiv F \circ F(N_2) = N_2
\]

and the eigenvalues of \( F^2 \) at these points:

\[
\lambda_2(r) = D(F^2)(N_2).
\]

The stability of the pair of period-2 points, which have split off from the original fixed point as \( r \) crosses 2, is determined by the eigenvalues, \( \lambda_2(r) \). Initially stable, these period-2 points bifurcate when \( |\lambda_2(r)| \geq 1 \). In this case, the nature of the bifurcation depends on whether it occurs at +1 or −1. At \( \lambda < -1 \) each period 2 point bifurcates into a pair of stable points with period 4. This process continues as \( r \) increases: bifurcations from \( \lambda_2(r) = -1 \) giving rise to pairs of attracting points of period 2k while bifurcations from \( \lambda_2(r) = +1 \) either create or destroy
periodic points. (c.f., Figure 10.3.)

![Graph showing bifurcations](image)

**Figure 10.3**

The orbit generated by $F(\cdot)$ becomes successively more complicated with each bifurcation—the initially stable fixed point splitting to orbits of successively higher periods. This can continue indefinitely, with bifurcation points occurring closer and closer together. As $r$ is increased past 2, exciting successively stable higher periodic orbits, there can occur a limit point, $r_c$, beyond which completely aperiodic points appear. That is, orbits are generated—which do not tend asymptotically to a periodic orbit. Sufficient conditions for such aperiodic orbits to exist has been given by Li and Yorke [1]. If $F(\cdot)$ folds some interval onto itself as shown in Figure 10.4a, then there exist aperiodic points (i.e., initial conditions which do not lie in the domain of attraction of any stable fixed point).
Alternatively, if the population exhibits a "3-point cycle" wherein the population rises 2 years in succession and then crashes past the original level, then non-periodic motion will ensue, (c.f. Figure 10.4b):

The consequences of this phenomenon for ecological modelling are profound. We can have confidence in a model only if it is subject to experimental validation. If a series of yearly censuses are collected of some population, and they appear
chaotic, exhibiting no perceivable regularities, then we can conclude one of three things: (a) the system is truly stochastic—dominated by random influences; (b) experimental error is of such magnitude that all regularities are obscured; (c) a very simple deterministic mechanism is operating, but is obscured by the phenomenon described above. As an extreme case, the orbit generated by the simple map shown in Figure 10.5 is indistinguishable from a sequence of Bernoulli trials!

Figure 10.5

For systems of 2 interacting populations (e.g., predator-prey, parasite-host, etc.) the situation is even more delicate and little is known about the transition to aperiodic motion. However, May [2] has simulated some 2-population difference equation models. He found that the population trajectories exhibited chaotic behavior for quite reasonable parameter ranges.


(3.1) If a population breeds continuously, so that the
generations overlap, then the appropriate model is an ordinary differential equation of the form

\[
\frac{dN}{dt} = N f(N) = N \left[ \left( \frac{\text{per capita birth rate}}{\text{per capita}} \right) - \left( \frac{\text{per capita death rate}}{\text{per capita}} \right) \right]
\]  

(3.1)

The number of such models in the literature is legion, and we shall comment only briefly on certain aspects pertaining to their bifurcation behavior.

(3.2) A recurrent theme in ecology is the phenomenon of population oscillations. The earliest prototype was the predator-prey equations of Volterra and Lotka (see, for example, May, [1]):

\[
\begin{align*}
\dot{N}_1 &= N_1 f_1(N_1, N_2) = N_1 \left( c_1 - c_2 N_2 \right) \\
\dot{N}_2 &= N_2 f_2(N_1, N_2) = N_2 \left( -c_3 + c_4 N_1 \right).
\end{align*}
\]  

(3.2)

The solutions to (3.2) are indeed periodic (Hirsch and Smale, [1]), but are neutrally stable, the amplitude of the oscillations depending on the initial conditions.

Recently, May [1,2] has shown that virtually all of the models for predator-prey systems possess either a stable equilibrium or a stable limit cycle (in the first quadrant). His demonstration hinges on showing that most models fall within the purview of a theorem by Kolmogorov [1], which is essentially an application of the Poincaré-Bendixson Theorem to systems of the form (1). [Essentially, any population model such that 1) there is a single unstable singularity in the first quadrant and 2) the axes are invariant (e.g.,}
\( \dot{N} = Nf(N) \) will have a limit cycle since large radius orbits must be directed inward due to the finite population limitation that must be imposed on any realistic model.

A typical predator-prey system which exhibits limit cycle behavior is: (Rosenzweig, [1]; May, [1]):

\[
\begin{align*}
\dot{N}_1 &= N_1 \left[ r \left( 1 - \frac{N_1}{K} \right) \right] - kN_2 \left( 1 - e^{-cN_1} \right) \\
\dot{N}_2 &= N_2 \left[ -b + \beta \left( 1 - e^{-fN_1} \right) \right]
\end{align*}
\tag{3.3}
\]

The interpretation is that the prey, \( N_1 \), in the absence of the predator, grows logistically and the predator, in the absence of prey, dies out exponentially. The second term in the first equation models a predator population whose capacity to capture prey gradually satiates.

The equilibrium point of equation (3.3) can be computed explicitly:

\[
\begin{align*}
\bar{N}_1 &= \ln(1 + \frac{b}{\beta})^{-1/f} \\
\bar{N}_2 &= r\bar{N}_1 \left( 1 - \frac{\bar{N}_1}{K} \right)/k \left[ 1 - (1+ \frac{b}{\beta})^{c/f} \right]
\end{align*}
\]

Then, computing the Jacobian at the equilibrium it is easy to check that the signs of the determinant and trace depend on the magnitude of the parameters \( \{r,K,k,c,b,\beta,f\} \). Thus, there exists a family of curves, parametrized by some combination of members of \( \pi \), carrying the eigenvalues into the RHP (c.f. Figure 10.6). Since large radius orbits move inward, the limit cycles are indeed generated by the Hopf mechanism. We also note that, since the eigenvalue trajectories are controlled by more than one parameter, the limit
cycle can appear at finite, rather than zero amplitude.

\[ \text{Figure 10.6} \]

(3.3) Predator-prey type equations have been used by Bell [1] to model "populations" of antibody and antigen in the immune response. Using Friedrichs' [1] version of the bifurcation theorem, Pimbly [1] demonstrated that Bell's equations exhibit periodic behavior which can be interpreted biologically in terms of the mechanism controlling infection.

(3.4) For systems of 3 or more species the possibility of higher order bifurcations raises the same operational problems as we encountered for difference equation models. Successive bifurcations beyond the first occur when the eigenvalues of the Poincaré map passes outside the unit circle (Hirsch and Smale, [1]), thus higher periods, (and aperiodic behavior) of this difference equation will produce quite chaotic-looking population records. This phenomenon is quite well known in Hamiltonian systems (Arnold and Avez, [1]). Since it is generally much more difficult to obtain a reliable experimental record for population systems, the
existence of such "strange attractors" would imply that the model may well not be experimentally verifiable.

Thus we find that bifurcation in model equations are a mixed blessing, explaining some phenomena and obscuring others.

4. Age-Structured Populations.

(4.1) By using ordinary differential and difference equation models we have taken a naive view of population dynamics by assuming that the state of the population is specified by total population number alone. A moment reflection shows that, in order to predict the growth of a population, account must be taken of internal variables such as age and size distributions. Clearly a thousand individuals past breeding age, or all of one sex do not constitute a viable population. In this section we shall illustrate some of the consequences of including the population age structure as a state variable.

(4.2) The equation of motion for an age-structured population is easy to write down. Let \( n(a,t) \) = population age density function, i.e., \( N(t) = \int_0^\infty n(a,t)\,da \) = total population. Then a conservation equation can be written for \( n \):

\[
\frac{\partial n}{\partial t} + \text{div } J = \text{loss by deaths.} \tag{4.1}
\]

Since the flux of individuals, \( J_n \), through age-time is just \( v_n \), where \( v = \frac{da}{dt} = 1 \), we can write

\[
\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -v_n \tag{4.2}
\]
where $\mu(a,t,')$ is the age-specific death rate. The special feature of the equation is the boundary condition giving the birthrate,

$$n(0,t) = \int_{0}^{\infty} b(a,t,')n(a,t)da$$

(4.3)

where $b(a,t,')$ is the age-specific birth rate. As we have indicated, the birth and death rates are functions of other variables as well. For example, population density frequently affects mortality and fecundity, so that

$$\mu = \mu(a,t,N)$$

(4.4a)

$$b = b(a,t,N)$$

(4.4b)

where

$$N = \int_{0}^{\infty} n(a,t,N)da.$$ 

(4.5)

is the total population. With appropriate smoothness and boundedness assumptions, Gurtin and MacCamy [1] proved existence and uniqueness for the system (4.2) - (4.5). We note that in engineering terms the age equations constitute a "distributed parameter positive feedback system." This easily implies that, as birthrates increase and/or deathrates decrease, the system will pass from a stable to an unstable regime. In the next subsection we examine the bifurcation behavior of a single population feeding off a single resource. Then we model a host-parasite system by coupling two age systems together. In both cases the existence of bifurcations must be inferred from qualitative and numerical arguments, since direct verification is unavailable. Nevertheless, we shall gain significant insights into some interesting ecological phenomena via our models.
In one of the best known experiments in ecology, the Australian entomologist A. J. Nicholson maintained a population of sheep blowflies on a diet of chopped liver and sugar for several years. In Figure 10.7 we have reproduced a portion of his data. The biological explanation for the violent oscillations is straightforward: Nicholson deliberately kept the food supply to the adult flies below the level required to sustain a population the size of one of the peaks. At moderate population levels competition prevents any individual from obtaining enough protein. Protein starvation, in turn, reduces the fecundity of each adult fly so that the next generation is much smaller. For this smaller generation the food supply is adequate and the fecundity rebounds to its maximum level.

A model for this situation must include some accounting for the nutritional state of the adult flies since this governs the rate of egg laying. Accordingly, we shall define a variable, $\xi$, which measures the nutritional state (e.g., mass, "health") (Oster and Auslander, [1]). A conservation equation in $(t,a,\xi)$ coordinates takes the form

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} + \frac{\partial}{\partial \xi} (gn) = -\mu n$$

where

$$\frac{d\xi}{dt} = g(t,a,\xi,f)$$

is the growth rate of $\xi$, which depends on the food supply, $f(t)$. The birthrate is then

$$n(0,t,\xi) = \iint da\ d\xi'\ nb(t,a,\xi',\xi).$$

The equation for the food abundance is
Figure 10.7. Top: periodically forced system Bottom: constant food supply
\[ \frac{df}{dt} = u(t) - C(t,a,n) \]  \hspace{1cm} (4.8)

where \( u(t) \) is the rate food is supplied to the population and \( C(\cdot) \) is the consumption rate by the adult flies. Reasonable empirical forms for the functions \( b(\cdot), \mu(\cdot), C \) are shown in Figure 10.8. A careful numerical simulation of this model shows reasonable agreement with experiment, Figure 10.9 (Oster and Auslander, [1]). However, we would like to see how the model generates these oscillations; naturally, the mechanism of bifurcations suggests itself. In order to examine this mechanism let us consider the simpler population-resource system.

![Diagram](image-url)

(a) fecundity  \hspace{1cm} (b) mortality

\[ C(f) \]

(c) consumption

Figure 10.8. Constitutive Relations
Figure 10.9
Comparison of simulated results with experimental data.

\[ \frac{3n}{\partial t} + \frac{3n}{\partial a} = -\mu n \]  
(4.9a)

\[ n(0,t) = \int b(a,R)n \, da \]  
(4.9b)

\[ \frac{dR}{dt} = F(R,n). \]  
(4.9c)

Regardless of the form of the functions the equations, linearized about an equilibrium state, will take the form (Oster and Takahashi, [1])

\[ \frac{3x}{\partial t} + \frac{3x}{\partial a} = -\bar{\mu}x \]  
(4.10a)

\[ x(0,t) = gR(t) + \int_{a}^{a+\gamma} x(t,a) \, da \]  
(4.10b)

\[ \frac{dR}{dt} = -AR(t) - By(t) + Cu(t) \]  
(4.10c)
where \( g, A, B, C, \overline{\mu} \) and \( E \) are linearization constants and \( y(t) = \int_{0}^{t} x \, dt \). One way to obtain the response of system (4.10) to various food supply schedules, \( u(t) \), is to compute the "transfer function" (Takahashi, Rabins, Auslander, [1]). That is, equation (4.10a) can be written as \( \frac{dx}{dt} = Lx \) where \( L \) is a linear operator. Note that the initial conditions for the linearized system are zero, thus taking the Laplace Transform with respect to time is equivalent to the eigenvalue equation \( Lx(a,s) = sx(a,s) \), where \( s \in \mathbb{C} \). Therefore, we can compute the spectrum of the system (4.10) as follows. Taking the Laplace Transform of system (4.10) we obtain

\[
X(a,s) = e^{-(s+\overline{\mu})a}G(s)R(s) \quad (4.11)
\]

\[
R(s) = \frac{C}{S+A+\frac{B}{S+\overline{\mu}}} U(s) \quad (4.12)
\]

where \( X(a,s), R(s) \) and \( U(s) \) are the transformed variables and

\[
G(s) = \frac{g}{1 - \frac{\overline{\mu}}{\sigma} \{ e^{-(s+\overline{\mu})\alpha} - e^{-(s+\overline{\mu})(\alpha+\gamma)} \}} . \quad (4.13)
\]

Thus, the response, or "output", \( X(s,a) \) can be expressed in terms of the input, \( U(s) \), as

\[
X(a,s) = g(s)U(s) \quad (4.14)
\]

where \( g(s) = e^{-(s+\overline{\mu})a}G(s) \) is the "transfer function". The response of the total population to food supply can be written

\[
Y(s) = \frac{1}{s+\overline{\mu}} G(s)R(s) \quad (4.15)
\]
where \( Y(s) = \int_0^\infty X(a,s)da \). The characteristic equation for the system is given by the denominator of equation (4.1):

\[
1 + \frac{Bg}{(s+\alpha)(s+\mu)(1-b*e^{-(s+\mu)\alpha})} = 0. \tag{4.16}
\]

The roots of (4.16) yield the system eigenvalues, as can be verified directly by substitution into (4.10). The product \( Bg \) can be interpreted as measuring (effect of population on food level) \( \times \) (effect of food level on birthrate). Thus, by varying the "gain", \( Bg \), each of the infinite number of eigenvalues traces out a path on the complex plane. Clearly the system is asymptotically stable for \( u(t) = 0 \), for the population will eventually starve. For \( u(t) > 0 \), the dynamics are controlled by, the parameter \( (Bg) \). We can get some idea of the effect of varying \( (Bg) \) on the system eigenvalues by examining the special case of \( b(a) = b^*\delta(a-\alpha) \), i.e., all births occur at age \( \alpha \). The characteristic equation then becomes:

\[
1 + \frac{Bg}{(s+\alpha)(s+\mu)(1-b*e^{-(s+\mu)\alpha})} = 0. \tag{4.17}
\]

At \( Bg = 0 \), (4.17) has roots as \( s = -\alpha \), \( s = -\mu \), and those satisfying

\[
e^{(s+\mu)\alpha} = b^*. \tag{4.18}
\]

Setting \( s = \sigma + i\omega \), the roots of (4.18) are seen to be at \( \sigma = \rho \), \( \omega = \frac{2n\pi}{\alpha} \), \( n = 1,2,... \), where \( \sigma = \rho \) is the real root of (4.18). In Figure 10.10 we sketch the "root locus" (Takahashi, Rabins and Auslander, [1]) for equation (4.17) as \( (Bg) \) is varied from 0 to \( \infty \) (Oster and Takahashi, [1]).
The branches start at \( B_g = 0 \) (denoted by \( x \)) and, as \( B_g \to \infty \), approach the asymptotes \( \omega = \pm \frac{2n\pi}{\alpha} \), \( n = 0, 1, \ldots \).

What is apparent from Figure 10.9 is that there is some range of parameter values for which the linearized model passes from stability to instability. That is, as the interaction parameter \( B_g \) is varied in the appropriate range the leading pair of eigenvalues cross the imaginary axis. At this point the linearized system begins to exhibit small amplitude oscillations, which grow as the parameter is further increased. (Of course, sooner or later other root pairs cross to the RHP; these are associated with secondary frequencies, and will not concern us here.)

Simulation studies of the model system (4.5 - 4.8) indicate that the oscillations do not grow from zero amplitude, but bifurcate to finite amplitude oscillations. This suggests that the bifurcation is controlled by 2 parameters rather than 1. (c.f. Takens [1]) as shown in Figure 10.11.
We can use the age model to answer a puzzling question in the ecological literature. Over a period of several years Professor C. B. Huffaker maintained an experimental ecosystem containing a parasitic wasp which lays its eggs in the larvae of a certain moth. He noticed that, very quickly after initiation, the populations settled into stable oscillations. These oscillations were characterized by age structures which were practically discrete generations. Conventional predator-prey models do not suffice to explain these oscillations since phase plane trajectories cross—the explanation lies in the age structure dynamics. We can couple two conservation equations like (4.2) by an age specific interaction that models the searching behavior of the parasite. The resulting model looks like:

\[
\frac{\partial p}{\partial t} + \frac{\partial p}{\partial a} = -\mu_p(a,t)p \tag{4.19}
\]
\[ p(0,t) = \int_{a_p}^{\infty} b_p(a',t,H_0) p(a',t) da' \]  
(4.20)

\[ \frac{dh}{dt} + \frac{h}{3a} = -y_h(a,t,H,H_0,P_1) h \]  
(4.21)

\[ h(0,t) = \int_{a_h}^{\infty} b_h(t,a',H_1(t-t)) h(a',t) da' \]  
(4.22)

where

\[ H_0(t) = \int_{\beta}^{\beta+\delta} h(a',t) da' = \text{no. host larvae} \]  
(4.23)

\[ H_1(t) = \int_{a_h}^{\infty} h(a',t) da' = \text{no. host adults} \]  
(4.24)

\[ H(t) = \int_{0}^{\infty} h(a',t) da' = \text{total no. hosts} \]  
(4.25)

\[ P_1(t) = \int_{a_p}^{\infty} p(a',t) da' = \text{no. parasite adults}. \]  
(4.26)

The form of the interaction between the populations can be derived by assuming a random search by each parasite for host larvae and employing a mean "area of discovery," A, for each. If the hosts are distributed randomly (Poisson) in a plane, the inter-arrival times are distributed exponentially. Thus the interaction takes the form: (Auslander, Oster, Huffaker, op. cit.)

\[ \text{[no. hosts parasitized]}(a) = bh(a)(1-e^{-A(s)P_1}) \]  
(4.27)

This is added to the natural mortality (assumed constant) to obtain the total host mortality. As indicated in equation (4.22) the host birthrate includes a delayed effect that depends on the nutritional history of the host. This is because fecundity is a function of adult size, which depends
on the available food.

The above model was simulated numerically using Huffaker's data (Auslander, Oster and Huffaker, op. cit.), and some of the results are shown in Figure 10.12. First of all, as the strength of the interaction is increased (e.g. by increasing the area of discovery, A) the system undergoes a transition from a state wherein all age classes are represented in both populations to one wherein only a few age classes are represented. That is, the age profiles of both species condense into "travelling waves," which propagate through the age structure in such a fashion that in a "stroboscopic photograph," the generations appear virtually discrete. The phase relationship of the population waves in each population determine the extent to which the populations can coexist. If the parameters are adjusted so that all age classes are represented, then the populations do not coexist: the parasite eliminates the host and then dies out itself.

Following the same procedure outlined for the single population model, we can linearize equations (4.19) - (4.26), Laplace transform and examine the roots of the characteristic equation as the coupling parameter is increased. Clearly, at zero coupling the parasite system is stable about the zero solution while the host population approaches a stable age distribution. Simulation indicates that a stationary age profile also exists with all age classes represented in both populations (continuous generations). Furthermore, at sufficiently high coupling strength the system is stable at zero. Thus, a root locus study, which reveals a leading root pair crossing the imaginary axis as the coupling is increased,
Evolution of the host population toward a stable age distribution in the absence of the parasite. The initial waves were induced by the periodic addition of adult females.

Stroboscopic shot at one generation-time intervals (~51 days) of a "pulse" of hosts which evolves to a stable periodic solution.

Figure 10.12. Simulation of Host-Parasite System
leads us to conclude that an intuitive explanation for the
population waves is a bifurcation phenomenon. Moreover, it is
this mechanism which gives us a satisfying explanation for how
the two populations are able to coexist in a homogeneous en-
vironment—the bifurcation phenomenon creates a "phase niche"
within which the host can escape total annihilation by the
parasite.

(4.5) Two other phenomena involving the age structure
deserve comment. First, an examination of Figure 10.7b shows
that if a periodic signal (in this case a periodic food sup-
ply) is applied to the population system, the forcing fre-
quency interacts with the natural resonant frequency to pro-
duce a "beat" frequency with a wavelength longer than either
component (Oster and Auslander, [1]). This suggests a pos-
sible explanation for certain population periodicities ob-
served in nature which do not appear to track any apparent en-
vironmental cycle. Secondly, there appear to be component
frequencies higher than that of the major resonance. This
suggests that secondary bifurcations from the basic cycle may
play a role in the dynamics. If the age system is discretized
along the characteristics, the resulting set of difference
equations corresponds to the Leslie model well known to demo-
graphers. Beddington and Free [1] simulated such a discrete
age class model and found that, as certain parameters are
varied, transitions to chaotic behavior occurred reminiscent
of the aperiodic orbits discussed in Section 2 for single dif-
ference equations. Thus it appears that the bifurcation
phenomenon can supply a satisfying mathematical mechanism for
explaining not only cyclic regularities in population dynamics, but perhaps some of the irregularities as well.