

Hence show that $r = 2$ is a bifurcation value and that as $r \rightarrow 2$ the steady state bifurcates to a periodic solution of period 6.

- 8 A basic delay model used by the International Whaling Commission (IWC) for monitoring whale populations is

$$u_{t+1} = su_t + R(u_{t-T}), \quad 0 < s < 0,$$

where $T \geq 1$ is an integer.

- (i) If u^* is a positive equilibrium show that a sufficient condition for linear stability is $|R'(u^*)| < 1 - s$. [Hint: Use Rouché's theorem on the resulting characteristic polynomial for small perturbations about u^* .]
- (ii) If $R(u) = (1 - s)u[1 + q(1 - u)]$, $q > 0$ and the delay $T = 1$, show that the equilibrium state is stable for all $0 < q < 2$. [With this model, T is the time from birth to sexual maturity, s is a survival parameter and $R(u_{t-T})$ the recruitment to the adult population from those born T years ago.]
- 9 Consider the effect of regularly harvesting the population of a species for which the model equation is

$$u_{t+1} = \frac{bu_t^2}{1 + u_t^2} - Eu_t = f(u_t; E), \quad b > 2, \quad E > 0,$$

where E is a measure of the effort expended in obtaining the harvest, Eu_t . [This model with $E = 0$ is a special case of that in Exercise 5.] Determine the steady states and hence show that if the effort $E > E_m = (b - 2)/2$, no harvest is obtained. If $E < E_m$ show, by cobwebbing $u_{t+1} = f(u_t; E)$ or otherwise, that the model is realistic only if the population u_t always lies between two positive values which you should determine analytically.

With $E < E_m$ evaluate the eigenvalue of the largest positive steady state. Demonstrate that a tangent bifurcation exists as $E \rightarrow E_m$.

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3. Models for Interacting Populations

When species interact the population dynamics of each species is affected. In general there is a whole web of interacting species, sometimes called a trophic web, which makes for structurally complex communities. We consider here systems involving 2 or more species, concentrating particularly on two-species systems. The book by Kot (2001) discusses such models (including age-structured interacting population systems) with numerous recent practical examples. There are three main types of interaction. (i) If the growth rate of one population is decreased and the other increased the populations are in a *predator-prey* situation. (ii) If the growth rate of each population is decreased then it is competition. (iii) If each population's growth rate is enhanced then it is called *mutualism* or *symbiosis*.

All of the mathematical techniques and analytical methods in this chapter are directly applicable to Chapter 6 on reaction kinetics, where similar equations arise; there the 'species' are chemical concentrations.

3.1 Predator-Prey Models: Lotka-Volterra Systems

Volterra (1926) first proposed a simple model for the predation of one species by another to explain the oscillatory levels of certain fish catches in the Adriatic. If $N(t)$ is the prey population and $P(t)$ that of the predator at time t then Volterra's model is

$$\frac{dN}{dt} = N(a - bP), \quad (3.1)$$

$$\frac{dP}{dt} = P(cN - d), \quad (3.2)$$

where a, b, c and d are positive constants.

The assumptions in the model are: (i) The prey in the absence of any predation grows unboundedly in a Malthusian way; this is the aN term in (3.1). (ii) The effect of the predation is to reduce the prey's per capita growth rate by a term proportional to the prey and predator populations; this is the $-bNP$ term. (iii) In the absence of any prey for sustenance the predator's death rate results in exponential decay, that is, the $-dP$ term in (3.2). (iv) The prey's contribution to the predators' growth rate is cNP ; that is, it is proportional to the available prey as well as to the size of the predator population. The NP terms can be thought of as representing the conversion of energy from one source

to another: bNP is taken from the prey and cNP accrues to the predators. We shall see that this model has serious drawbacks. Nevertheless it has been of considerable value in posing highly relevant questions and is a jumping-off place for more realistic models; this is the main motivation for studying it here.

The model (3.1) and (3.2) is known as the *Lotka–Volterra model* since the same equations were also derived by Lotka (1920; see also 1925) from a hypothetical chemical reaction which he said could exhibit periodic behaviour in the chemical concentrations. With this motivation the dependent variables represent chemical concentrations; we touch on this again in Chapter 6.

As a first step in analysing the Lotka–Volterra model we nondimensionalise the system by writing

$$u(\tau) = \frac{cN(t)}{d}, \quad v(\tau) = \frac{bP(t)}{a}, \quad \tau = at, \quad \alpha = d/a, \quad (3.3)$$

and it becomes

$$\frac{du}{d\tau} = u(1 - v), \quad \frac{dv}{d\tau} = \alpha v(u - 1). \quad (3.4)$$

In the u, v phase plane (a brief summary of basic phase plane methods is given in Appendix A) these give

$$\frac{dv}{du} = \alpha \frac{v(u - 1)}{u(1 - v)}, \quad (3.5)$$

which has singular points at $u = v = 0$ and $u = v = 1$. We can integrate (3.5) exactly to get the phase trajectories

$$\alpha u + v - \ln u^\alpha v = H, \quad (3.6)$$

where $H > H_{\min}$ is a constant: $H_{\min} = 1 + \alpha$ is the minimum of H over all (u, v) and it occurs at $u = v = 1$. For a given $H > 1 + \alpha$, the trajectories (3.6) in the phase plane are closed as illustrated in Figure 3.1.

A closed trajectory in the u, v plane implies periodic solutions in τ for u and v in (3.4). The initial conditions, $u(0)$ and $v(0)$, determine the constant H in (3.6) and hence the phase trajectory in Figure 3.1. Typical periodic solutions $u(\tau)$ and $v(\tau)$ are illustrated in Figure 3.2. From (3.4) we can see immediately that u has a turning point when $v = 1$ and v has one when $u = 1$.

A major inadequacy of the Lotka–Volterra model is clear from Figure 3.1—the solutions are not structurally stable. Suppose, for example, $u(0)$ and $v(0)$ are such that u and v for $\tau > 0$ are on the trajectory H_4 which passes close to the u and v axes. Then any small perturbation will move the solution onto another trajectory which does not lie *everywhere* close to the original one H_4 . Thus a small perturbation can have a very marked effect, at the very least on the amplitude of the oscillation. This is a problem with any system which has a first integral, like (3.6), which is a closed trajectory in the phase plane. They are called *conservative systems*; here (3.6) is the associated ‘conservation

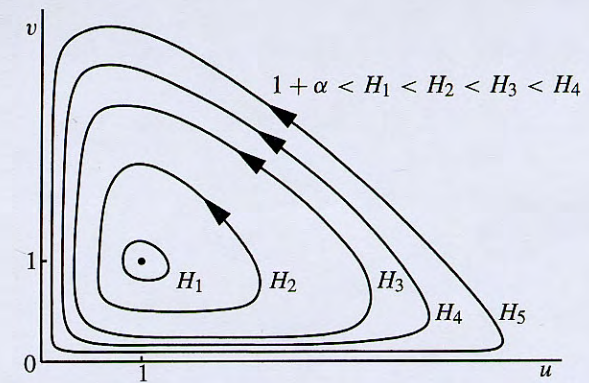


Figure 3.1. Closed (u, v) phase plane trajectories, from (3.6) with various H , for the Lotka–Volterra system (3.4): $H_1 = 2.1$, $H_2 = 2.4$, $H_3 = 3.0$, $H_4 = 4$. The arrows denote the direction of change with increasing time τ .

law.’ They are usually of little use as models for real interacting populations (see one interesting and amusing attempt to do so below). However, the method of analysis of the steady states is typical.

Returning to the form (3.4), a linearisation about the singular points determines the type of singularity and the stability of the steady states. A similar linear stability analysis has to be carried out on equivalent systems with any number of equations. We first consider the steady state $(u, v) = (0, 0)$. Let x and y be small perturbations about $(0, 0)$. If we keep only linear terms, (3.4) becomes

$$\begin{pmatrix} \frac{dx}{d\tau} \\ \frac{dy}{d\tau} \end{pmatrix} \approx \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix}. \quad (3.7)$$

The solution is of the form

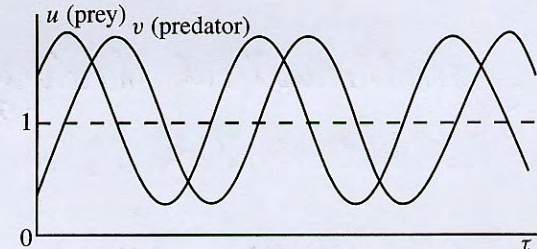


Figure 3.2. Periodic solutions for the prey $u(\tau)$ and the predator $v(\tau)$ for the Lotka–Volterra system (3.4) with $\alpha = 1$ and initial conditions $u(0) = 1.25$, $v(0) = 0.66$.

$$\begin{pmatrix} x(\tau) \\ y(\tau) \end{pmatrix} = \mathbf{B}e^{\lambda\tau},$$

where \mathbf{B} is an arbitrary constant column vector and the eigenvalues λ are given by the characteristic polynomial of the matrix A and thus are solutions of

$$|A - \lambda I| = \begin{vmatrix} 1 - \lambda & 0 \\ 0 & -\alpha - \lambda \end{vmatrix} = 0 \Rightarrow \lambda_1 = 1, \quad \lambda_2 = -\alpha.$$

Since at least one eigenvalue, $\lambda_1 > 0$, $x(\tau)$ and $y(\tau)$ grow exponentially and so $u = 0 = v$ is linearly unstable. Since $\lambda_1 > 0$ and $\lambda_2 < 0$ this is a *saddle point* singularity (see Appendix A).

Linearising about the steady state $u = v = 1$ by setting $u = 1 + x$, $v = 1 + y$ with $|x|$ and $|y|$ small, (3.4) becomes

$$\begin{pmatrix} \frac{dx}{d\tau} \\ \frac{dy}{d\tau} \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix}, \quad A = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix} \quad (3.8)$$

with eigenvalues λ given by

$$\begin{vmatrix} -\lambda & -1 \\ \alpha & -\lambda \end{vmatrix} = 0 \Rightarrow \lambda_1, \lambda_2 = \pm i\sqrt{\alpha}. \quad (3.9)$$

Thus $u = v = 1$ is a *centre* singularity since the eigenvalues are purely imaginary. Since $\text{Re } \lambda = 0$ the steady state is *neutrally stable*. The solution of (3.8) is of the form

$$\begin{pmatrix} x(\tau) \\ y(\tau) \end{pmatrix} = \mathbf{l}e^{i\sqrt{\alpha}\tau} + \mathbf{m}e^{-i\sqrt{\alpha}\tau},$$

where \mathbf{l} and \mathbf{m} are eigenvectors. So, the solutions in the neighbourhood of the singular point $u = v = 1$ are periodic in τ with period $2\pi/\sqrt{\alpha}$. In dimensional terms from (3.3) this period is $T = 2\pi(a/d)^{1/2}$; that is, the period is proportional to the square root of the ratio of the linear growth rate, a , of the prey to the death rate, d , of the predators. Even though we are only dealing with small perturbations about the steady state $u = v = 1$ we see how the period depends on the intrinsic growth and death rates. For example, an increase in the growth rate of the prey will increase the period; a decrease in the predator death rate does the same thing. Is this what you would expect intuitively?

In this ecological context the matrix A in the linear equations (3.7) and (3.8) is called the *community matrix*, and its eigenvalues λ determine the stability of the steady states. If $\text{Re } \lambda > 0$ then the steady state is unstable while if both $\text{Re } \lambda < 0$ it is stable. The critical case $\text{Re } \lambda = 0$ is termed *neutral stability*.

There have been many attempts to apply the Lotka–Volterra model to real-world oscillatory phenomena. In view of the system's structural instability, they must essentially all fail to be of quantitative practical use. As we mentioned, however, they can be important as vehicles for suggesting relevant questions that should be asked. One particularly interesting example was the attempt to apply the model to the extensive data

on the Canadian lynx–snowshoe hare interaction in the fur catch records of the Hudson Bay Company from about 1845 until the 1930's. We assume that the numbers reflect a fixed proportion of the total population of these animals. Although this assumption is of questionable accuracy, as indicated by what follows, the data nevertheless represent one of the very few long term records available. Figure 3.3 reproduces this data. Williamson's (1996) book is a good source of population data which exhibit periodic or quasi-periodic behaviour.

Figure 3.3 shows reasonable periodic fluctuations and Figure 3.3(c) a more or less closed curve in the phase plane as we now expect from a time-periodic behaviour in the variables. Leigh (1968) used the standard Lotka–Volterra model to try to explain the data. Gilpin (1973) did the same with a modified Lotka–Volterra system. Let us examine the results given in Figure 3.3 a little more carefully. First note that the *direction* of the time arrows in Figure 3.3(c) is clockwise in contrast to that in Figure 3.1. This is reflected in the time curves in Figures 3.3(a) and (b) where the lynx oscillation, the predator's, precedes the hare's. The opposite is the case in the predator–prey situation illustrated in Figure 3.2. Figure 3.3 implies that the hares are eating the lynx! This poses a severe interpretation problem! Gilpin (1973) suggested that perhaps the hares could kill the lynx if they carried a disease which they passed on to the lynx. He incorporated an epidemic effect into his model and the numerical results then looked like those in Figure 3.3(c); this seemed to provide the explanation for the hare “eating” the lynx. A good try, but no such disease is known. Gilpin (1973) also offered what is perhaps the right explanation, namely, that the fur trappers are the ‘disease.’ In years of low population densities they probably did something else and only felt it worthwhile to return to the trap lines when the hares were again sufficiently numerous. Since lynx were more profitable to trap than hare they would probably have devoted more time to the lynx than the hare. This would result in the phenomenon illustrated by Figures 3.3(b) and (c). Schaffer (1984) has suggested that the lynx–hare data could be evidence of a strange attractor (that is, they exhibit chaotic behaviour) in Nature. The moral of the story is that it is not enough simply to produce a model which exhibits oscillations but rather to provide a proper explanation of the phenomenon which can stand up to ecological and biological scrutiny.

3.2 Complexity and Stability

To get some indication of the effect of complexity on stability we briefly consider the generalised Lotka–Volterra predator–prey system where there are k prey species and k predators, which prey on all the prey species but with different severity. Then in place of (3.1) and (3.2) we have

$$\begin{aligned} \frac{dN_i}{dt} &= N_i \left[a_i - \sum_{j=1}^k b_{ij} P_j \right] \\ & \quad i = 1, \dots, k \\ \frac{dP_i}{dt} &= P_i \left[\sum_{j=1}^k c_{ij} N_j - d_i \right], \end{aligned} \quad (3.10)$$

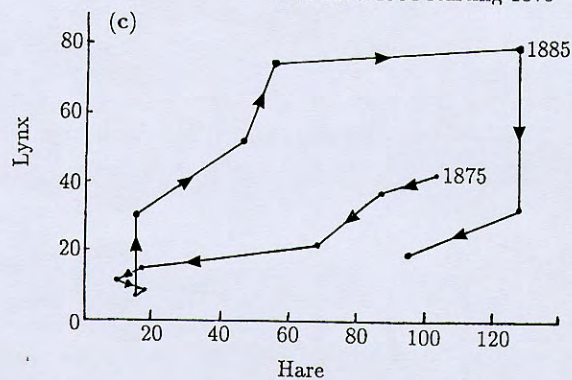
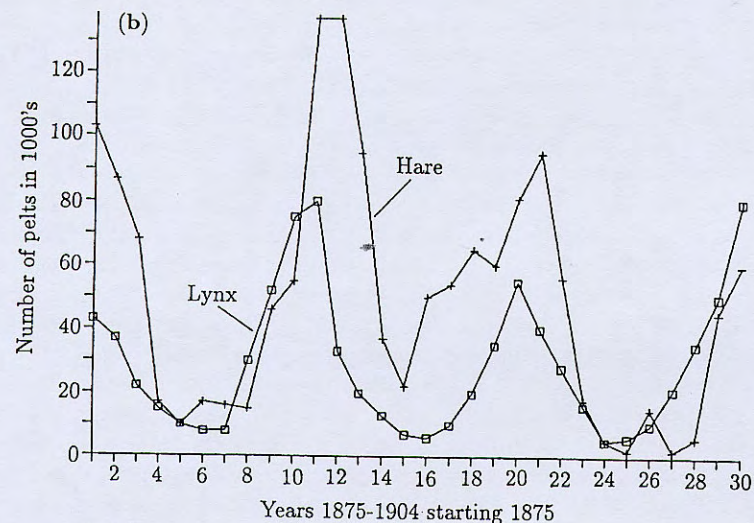
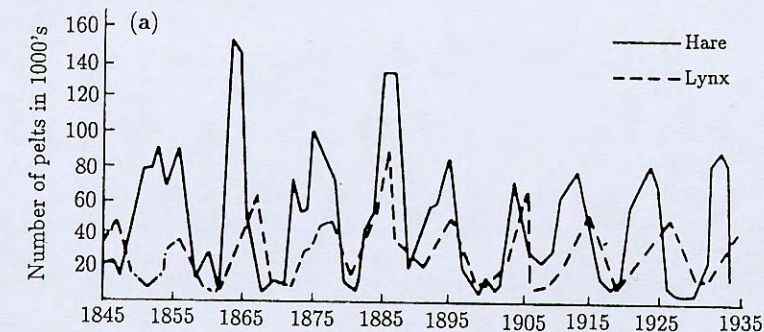


Figure 3.3. (a) Fluctuations in the number of pelts sold by the Hudson Bay Company. (Redrawn from Odum 1953) (b) Detail of the 30-year period starting in 1875, based on the data from Elton and Nicholson (1942). (c) Phase plane plot of the data represented in (b). (After Gilpin 1973)

where all of the a_i , b_{ij} , c_{ij} and d_i are positive constants. The trivial steady state is $N_i = P_i = 0$ for all i , and the community matrix is the diagonal matrix

$$A = \begin{pmatrix} a_1 & & 0 & & \\ & \ddots & & & \\ 0 & & a_k & & 0 \\ \hline & & & -d_1 & 0 \\ 0 & & & & \ddots \\ & & & 0 & & -d_k \end{pmatrix}$$

The $2k$ eigenvalues are thus

$$\lambda_i = a_i > 0, \quad \lambda_{k+i} = -d_i < 0, \quad i = 1, \dots, k$$

so this steady state is unstable since all $\lambda_i > 0$, $i = 1, \dots, k$.

The nontrivial steady state is the column vector solution \mathbf{N}^* , \mathbf{P}^* where

$$\sum_{j=1}^k b_{ij} P_j^* = a_i, \quad \sum_{j=1}^k c_{ij} N_j^* = d_i, \quad i = 1, \dots, k$$

or, in vector notation, with \mathbf{N}^* , \mathbf{P}^* , \mathbf{a} , and \mathbf{d} column vectors,

$$B\mathbf{P}^* = \mathbf{a}, \quad C\mathbf{N}^* = \mathbf{d}, \quad (3.11)$$

where B and C are the $k \times k$ matrices $[b_{ij}]$ and $[c_{ij}]$ respectively.

Equations (3.10) can be written as

$$\frac{d\mathbf{N}}{dt} = \mathbf{N}^T \cdot [\mathbf{a} - B\mathbf{P}], \quad \frac{d\mathbf{P}}{dt} = \mathbf{P}^T \cdot [C\mathbf{N} - \mathbf{d}],$$

where the superscript T denotes the transpose. So, on linearising about $(\mathbf{N}^*, \mathbf{P}^*)$ in (3.11) by setting

$$\mathbf{N} = \mathbf{N}^* + \mathbf{u}, \quad \mathbf{P} = \mathbf{P}^* + \mathbf{v},$$

where $|\mathbf{u}|$, $|\mathbf{v}|$ are small compared with $|\mathbf{N}^*|$ and $|\mathbf{P}^*|$, we get

$$\frac{d\mathbf{u}}{dt} \approx -\mathbf{N}^{*T} \cdot B\mathbf{v}, \quad \frac{d\mathbf{v}}{dt} \approx \mathbf{P}^{*T} \cdot C\mathbf{u}.$$

Then

$$\begin{pmatrix} \frac{d\mathbf{u}}{dt} \\ \frac{d\mathbf{v}}{dt} \end{pmatrix} \approx A \begin{pmatrix} \mathbf{u} \\ \mathbf{v} \end{pmatrix}, \quad A = \begin{pmatrix} 0 & -\mathbf{N}^{*T} \cdot B \\ \mathbf{P}^{*T} \cdot C & 0 \end{pmatrix}, \quad (3.12)$$

where here the community matrix A is a $2k \times 2k$ block matrix with null diagonal blocks. Since the eigenvalues $\lambda_i, i = 1, \dots, 2k$ are solutions of $|A - \lambda I| = 0$ the sum of the roots λ_i satisfies

$$\sum_{i=1}^{2k} \lambda_i = \text{tr}A = 0, \tag{3.13}$$

where $\text{tr}A$ is the trace of A . Since the elements of A are real, the eigenvalues, if complex, occur as complex conjugates. Thus from (3.13) there are two cases: all the eigenvalues are purely imaginary or they are not. If all $\text{Re} \lambda_i = 0$ then the steady state (N^*, P^*) is neutrally stable as in the 2-species case. However if there are λ_i such that $\text{Re} \lambda_i \neq 0$ then, since they occur as complex conjugates, (3.13) implies that at least one exists with $\text{Re} \lambda > 0$ and hence (N^*, P^*) is unstable.

We see from this analysis that complexity in the population interaction web introduces the possibility of instability. If a model by chance resulted in only imaginary eigenvalues (and hence perturbations from the steady state are periodic in time) only a small change in one of the parameters in the community matrix would result in at least one eigenvalue with $\text{Re} \lambda \neq 0$ and hence an unstable steady state. This of course only holds for community matrices such as in (3.12). Even so, we get indications of the fairly general and important result that *complexity usually results in instability rather than stability*.

3.3 Realistic Predator–Prey Models

The Lotka–Volterra model, unrealistic though it is, does suggest that simple predator–prey interactions can result in periodic behaviour of the populations. Reasoning heuristically this is not unexpected since if a prey population increases, it encourages growth of its predator. More predators however consume more prey the population of which starts to decline. With less food around the predator population declines and when it is low enough, this allows the prey population to increase and the whole cycle starts over again. Depending on the detailed system such oscillations can grow or decay or go into a stable *limit cycle* oscillation or even exhibit chaotic behaviour, although in the latter case there must be at least 3 interacting species, or the model has to have some delay terms.

A limit cycle solution is a closed trajectory in the predator–prey space which is not a member of a continuous family of closed trajectories such as the solutions of the Lotka–Volterra model illustrated in Figure 3.1. A stable limit cycle trajectory is such that any small perturbation from the trajectory decays to zero. A schematic example of a limit cycle trajectory in a two-species predator(P)–prey(N) interaction is illustrated in Figure 3.4. Conditions for the existence of such a solution are given in Appendix A.

One of the unrealistic assumptions in the Lotka–Volterra models, (3.1) and (3.2), and generally (3.10), is that the prey growth is unbounded in the absence of predation. In the form we have written the model (3.1) and (3.2) the bracketed terms on the right are the density-dependent per capita growth rates. To be more realistic these growth

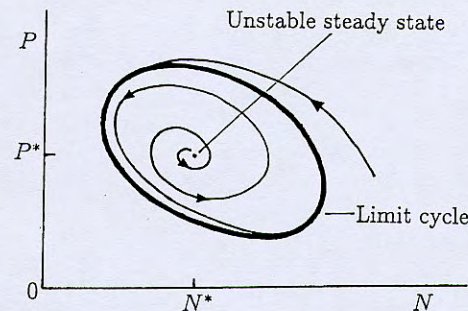


Figure 3.4. Typical closed predator–prey trajectory which implies a limit cycle periodic oscillation. Any perturbation from the limit cycle tends to zero asymptotically with time.

rates should depend on both the prey and predator densities as in

$$\frac{dN}{dt} = NF(N, P), \quad \frac{dP}{dt} = PG(N, P), \tag{3.14}$$

where the forms of F and G depend on the interaction, the species and so on.

As a reasonable first step we might expect the prey to satisfy a logistic growth, say, in the absence of any predators, that is, like (1.2) in Chapter 1, or have some similar growth dynamics which has some maximum carrying capacity. So, for example, a more realistic prey population equation might take the form

$$\frac{dN}{dt} = NF(N, P), \quad F(N, P) = r \left(1 - \frac{N}{K} \right) - PR(N), \tag{3.15}$$

where $R(N)$ is one of the predation terms discussed below and illustrated in Figure 3.5 and K is the constant carrying capacity for the prey when $P \equiv 0$.

The predation term, which is the functional response of the predator to change in the prey density, generally shows some saturation effect. Instead of a predator response of bNP , as in the Lotka–Volterra model (3.1), we take $PNR(N)$ where $NR(N)$ saturates for N large. Some examples are

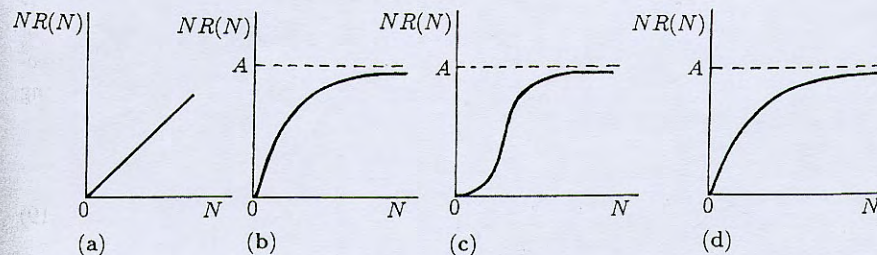


Figure 3.5. Examples of predator response $NR(N)$ to prey density N . (a) $R(N) = A$, the unsaturated Lotka–Volterra type. (b) $R(N) = A/(N + B)$. (c) $R(N) = AN/(N^2 + B^2)$. (d) $R(N) = A(1 - e^{-aN})/N$.

$$R(N) = \frac{A}{N+B}, \quad R(N) = \frac{AN}{N^2+B^2}, \quad R(N) = \frac{A[1-e^{-aN}]}{N}, \quad (3.16)$$

where A , B and a are positive constants; these are illustrated in Figures 3.5(b) to (d). The second of (3.16), illustrated in Figure 3.5(c), is similar to that used in the budworm model in equation (1.6) in Chapter 1. It is also typical of aphid (*Aphidicus zbeckistanicus*) predation. The examples in Figures 3.5(b) and (c) are approximately linear in N for low densities. The saturation for large N is a reflection of the limited predator capability, or perseverance, when the prey is abundant.

The predator population equation, the second of (3.14), should also be made more realistic than simply having $G = -d + cN$ as in the Lotka–Volterra model (3.2). Possible forms are

$$G(N, P) = k \left(1 - \frac{hP}{N}\right), \quad G(N, P) = -d + eR(N), \quad (3.17)$$

where k , h , d and e are positive constants and $R(N)$ is as in (3.16). The first of (3.17) says that the carrying capacity for the predator is directly proportional to the prey density.

The models given by (3.14)–(3.17) are only examples of the many that have been proposed and studied. They are all more realistic than the classical Lotka–Volterra model. Other examples are discussed, for example, in the book by Nisbet and Gurney (1982) and that edited by Levin (1994), to mention but two.

3.4 Analysis of a Predator–Prey Model with Limit Cycle Periodic Behaviour: Parameter Domains of Stability

As an example of how we analyze such realistic 2-species models we consider one of them in detail, namely,

$$\begin{aligned} \frac{dN}{dt} &= N \left[r \left(1 - \frac{N}{K}\right) - \frac{kP}{N+D} \right], \\ \frac{dP}{dt} &= P \left[s \left(1 - \frac{hP}{N}\right) \right], \end{aligned} \quad (3.18)$$

where r , K , k , D , s and h are positive constants, 6 in all. It is, as always, extremely useful to write the system in nondimensional form. Although there is no unique way of doing this it is often a good idea to relate the variables to some key relevant parameter. Here, for example, we express N and P as fractions of the predator-free carrying capacity K . Let us write

$$\begin{aligned} u(\tau) &= \frac{N(t)}{K}, \quad v(\tau) = \frac{hP(t)}{K}, \quad \tau = rt, \\ a &= \frac{k}{hr}, \quad b = \frac{s}{r}, \quad d = \frac{D}{K} \end{aligned} \quad (3.19)$$

and (3.18) become

$$\begin{aligned} \frac{du}{d\tau} &= u - (1-u) - \frac{auv}{u+d} = f(u, v), \\ \frac{dv}{d\tau} &= bv \left(1 - \frac{v}{u}\right) = g(u, v), \end{aligned} \quad (3.20)$$

which have only 3 dimensionless parameters a , b and d . Nondimensionalisation reduces the number of parameters by grouping them in a meaningful way. Dimensionless groupings generally give relative measures of the effect of dimensional parameters. For example, b is the ratio of the linear growth rate of the predator to that of the prey and so $b > 1$ and $b < 1$ have definite ecological meanings; with the latter the prey reproduce faster than the predator.

The equilibrium or steady state populations u^* , v^* are solutions of $du/d\tau = 0$, $dv/d\tau = 0$; namely,

$$f(u^*, v^*) = 0, \quad g(u^*, v^*) = 0$$

which, from the last equations, are

$$u^*(1-u^*) - \frac{au^*v^*}{u^*+d} = 0, \quad bv^* \left(1 - \frac{v^*}{u^*}\right) = 0. \quad (3.21)$$

We are only concerned here with positive solutions, namely, the positive solutions of

$$v^* = u^*, \quad u^{*2} + (a+d-1)u^* - d = 0,$$

of which the only positive one is

$$u^* = \frac{(1-a-d) + \{(1-a-d)^2 + 4d\}^{1/2}}{2}, \quad v^* = u^*. \quad (3.22)$$

We are interested in the stability of the steady states, which are the singular points in the phase plane of (3.20). A linear stability analysis about the steady states is equivalent to the phase plane analysis. For the linear analysis write

$$x(\tau) = u(\tau) - u^*, \quad y(\tau) = v(\tau) - v^* \quad (3.23)$$

which on substituting into (3.20), linearising with $|x|$ and $|y|$ small, and using (3.21), gives

$$\begin{aligned} \begin{pmatrix} dx \\ d\tau \\ dy \\ d\tau \end{pmatrix} &= A \begin{pmatrix} x \\ y \end{pmatrix}, \\ A &= \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{u^*, v^*} = \begin{pmatrix} u^* \left[\frac{au^*}{(u^*+d)^2} - 1 \right] & \frac{-au^*}{u^*+d} \\ b & -b \end{pmatrix}. \end{aligned} \quad (3.24)$$

A, the community matrix, has eigenvalues λ given by

$$|A - \lambda I| = 0 \Rightarrow \lambda^2 - (\text{tr}A)\lambda + \det A = 0. \quad (3.25)$$

For stability we require $\text{Re } \lambda < 0$ and so the necessary and sufficient conditions for linear stability are, from the last equation,

$$\begin{aligned} \text{tr}A < 0 &\Rightarrow u^* \left[\frac{au^*}{(u^* + d)^2} - 1 \right] < b, \\ \det A > 0 &\Rightarrow 1 + \frac{a}{u^* + d} - \frac{au^*}{(u^* + d)^2} > 0. \end{aligned} \quad (3.26)$$

Substituting for u^* from (3.22) gives the stability conditions in terms of the parameters a, b and d , and hence in terms of the original parameters r, K, k, D, s and h in (3.18).

In general there is a domain in the a, b, d space such that, if the parameters lie within it, (u^*, v^*) is stable, that is, $\text{Re } \lambda < 0$, and if they lie outside it the steady state is unstable. The latter requires at least one of (3.26) to be violated. With (3.22) for u^* and using the first of (3.21) and $v^* = u^*$,

$$\begin{aligned} \det A &= \left[1 + \frac{a}{u^* + d} - \frac{au^*}{(u^* + d)^2} \right] bu^* \\ &= \left[1 + \frac{ad}{(u^* + d)^2} \right] bu^* \\ &> 0 \end{aligned} \quad (3.27)$$

for all $a > 0, b > 0, d > 0$ and so the second of (3.26) is always satisfied. The instability domain is thus determined solely by the first inequality of (3.26), namely, $\text{tr} A < 0$ which, with (3.22) for u^* and again using (3.21), becomes

$$b > \left[a - \{(1 - a - d)^2 + 4d\}^{1/2} \right] \frac{[1 + a + d - \{(1 - a - d)^2 + 4d\}^{1/2}]}{2a}. \quad (3.28)$$

This defines a three-dimensional surface in (a, b, d) parameter space.

We are only concerned with a, b , and d positive. The second square bracket in (3.28) is a monotonic decreasing function of d and always positive. The first square bracket is a monotonic decreasing function of d with a maximum at $d = 0$. Thus, from (3.28),

$$b_{d=0} \begin{cases} > 2a - 1 \\ > 1/a \end{cases} \quad \text{if} \quad \begin{cases} 0 < a \leq 1 \\ 1 \leq a \end{cases}$$

and so for $0 < a < 1/2$ and all $d > 0$ the stability condition (3.28) is satisfied with any $b > 0$. That is, the steady state u^*, v^* is linearly stable for all $0 < a < 1/2, b > 0, d > 0$. On the other hand if $a > 1/2$ there is a domain in the (a, b, d) space with $b > 0$ and $d > 0$ where (3.28) is not satisfied and so the first of (3.26) is violated and hence

one of the eigenvalues λ in (3.25) has $\text{Re } \lambda > 0$. This in turn implies the steady state u^*, v^* is unstable to small perturbations. The boundary surface is given by (3.28) and it crosses the $b = 0$ plane at $d = d_m(a)$ given by the positive solution of

$$a = \{(1 - a - d_m)2 + 4d_m\}^{1/2} \Rightarrow d_m(a) = d_{b=0} = (a^2 + 4a)^{1/2} - (1 + a).$$

Thus $d_m(a)$ is a monotonic increasing function of a bounded above by $d = 1$. Note also that $d < a$ for all $a > 1/2$. Figure 3.6 illustrates the stability/instability domains in the (a, b, d) space.

When $\text{Re } \lambda < 0$ the steady state is stable and either both λ 's are real in (3.25), in which case the singular point u^*, v^* in (3.21) is a stable node in the u, v phase plane of (3.20), or the λ 's are complex and the singular point is a stable spiral. When the parameters result in $\text{Re } \lambda > 0$ the singular point is either an unstable node or spiral. In this case we must determine whether or not there is a confined set, or bounding domain, in the (u, v) phase plane so as to use the Poincaré–Bendixson theorem for the existence of a limit cycle oscillation; see Appendix A. In other words we must find a simple closed boundary curve in the positive quadrant of the (u, v) plane such that on it the phase trajectories always point into the enclosed domain. That is, if \mathbf{n} denotes the outward normal to this boundary, we require

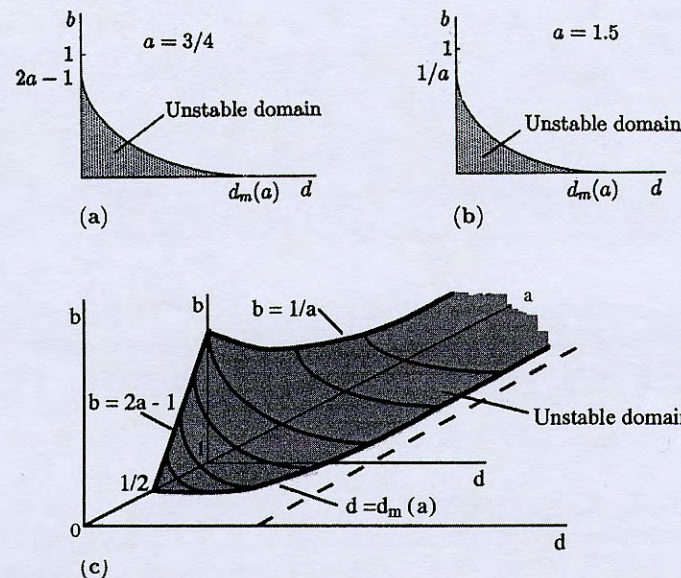


Figure 3.6. Parameter domains (schematic) of stability of the positive steady state for the predator–prey model (3.20). For $a < 1/2$ and all parameter values $b > 0, d > 0$, stability is obtained. For a fixed $a > 1/2$, the domain of instability is finite as in (a) and (b). The three-dimensional bifurcation surface between stability and instability is sketched in (c) with $d_m(a) = (a^2 + 4a)^{1/2} - (1 + a)$. When parameter values are in the unstable domain, limit cycle oscillations occur in the populations.

$$\mathbf{n} \cdot \left(\frac{du}{d\tau}, \frac{dv}{d\tau} \right) < 0$$

for all points on the boundary. If this inequality holds at a point on the boundary it means that the 'velocity' vector $(du/d\tau, dv/d\tau)$ points inwards. Intuitively this means that no solution trajectory can leave the domain if once inside, since, if it did reach the boundary, its 'velocity' points inwards and so the trajectory moves back into the domain.

To find a confined set it is essential and always informative to draw the null clines of the system, that is, the curves in the phase plane where $du/d\tau = 0$ and $dv/d\tau = 0$. From (3.20) these are the curves $f(u, v) = 0$ and $g(u, v) = 0$ which are illustrated in Figure 3.7. The sign of the vector components of $(f(u, v), g(u, v))$ indicate the direction of the vector $(du/d\tau, dv/d\tau)$ and hence the direction of the (u, v) trajectory. So if $f > 0$ in a domain, $du/d\tau > 0$ and u is thus increasing there. On DE, EA, AB and BC , the trajectories clearly point inwards because of the signs of $f(u, v)$ and $g(u, v)$ on them. It can be shown simply but tediously that a line DC exists such that on it $\mathbf{n} \cdot (du/d\tau, dv/d\tau) < 0$; that is, $\mathbf{n} \cdot (f(u, v), g(u, v)) < 0$ where \mathbf{n} is the unit vector perpendicular to DC .

We now have a confined set appropriate for the Poincaré–Bendixson theorem to apply when (u^*, v^*) is unstable. Hence the solution trajectory tends to a *limit cycle* when the parameters a, b and d lie in the unstable domain in Figure 3.6(c). Basically the Poincaré–Bendixson theorem says that since any trajectory coming out of the unstable steady state (u^*, v^*) cannot cross the confining boundary $ABCDEA$, it must evolve into a closed limit cycle trajectory qualitatively similar to that illustrated in Figure 3.4. With our model (3.20), Figure 3.8(a) illustrates such a closed trajectory with Figure 3.8(b) showing the temporal variation of the populations with time. With the specific parameter values used in Figure 3.8 the steady state is an unstable node in the phase plane; that is, both eigenvalues are real and positive. Any perturbation from the limit cycle decays quickly.

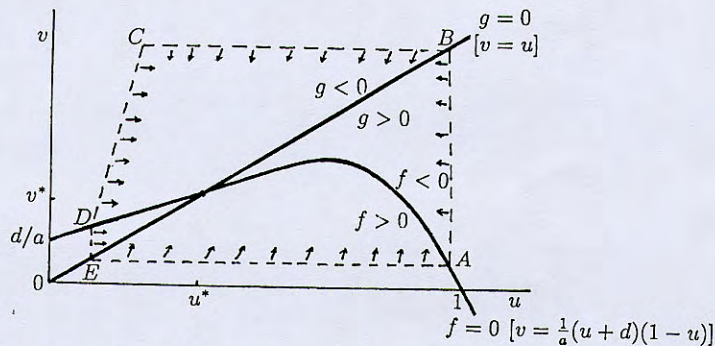


Figure 3.7. Null clines $f(u, v) = 0, g(u, v) = 0$ for the system (3.20); note the signs of f and g on either side of their null clines. $ABCDEA$ is the boundary of the confined set about (u^*, v^*) on which the trajectories all point inwards; that is, $\mathbf{n} \cdot (du/d\tau, dv/d\tau) < 0$ where \mathbf{n} is the unit outward normal on the boundary $ABCDEA$.

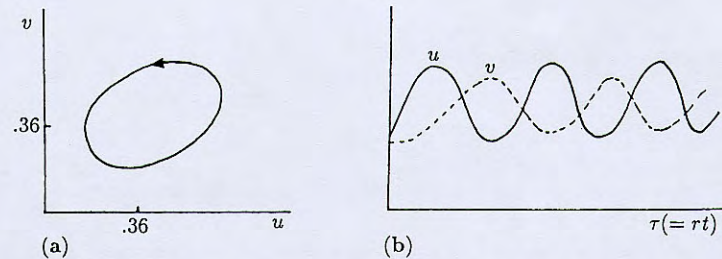


Figure 3.8. (a) Typical phase trajectory limit cycle solution for the predator–prey system (3.20). (b) Corresponding periodic behaviour of the prey (u) and predator (v) populations. Parameter values: $a = 1, b = 5, d = 0.2$, which give the steady state as $u^* = v^* = 0.36$. Relations (3.19) relate the dimensionless to the dimensional parameters.

This model system, like most which admit limit cycle behaviour, exhibits bifurcation properties as the parameters vary, although not with the complexity shown by discrete models as we see in Chapters 2 and 5, nor with delay models such as in Chapter 1. We can see this immediately from Figure 3.6. To be specific, consider a fixed $a > 1/2$ so that a finite domain of instability exists, as illustrated in Figure 3.9, and let us choose a fixed $0 < d < d_m$ corresponding to the line DEF . Suppose b is initially at the value D and is then continuously decreased. On crossing the bifurcation line at E , the steady state becomes unstable and a periodic limit cycle solution appears; that is, the uniform steady state bifurcates into an oscillatory solution. A similar situation occurs along any parameter variation from the stable to the unstable domains in Figure 3.6(c).

The fact that a dimensionless variable passes through a bifurcation value provides useful practical information on equivalent effects of dimensional parameters. For example, from (3.19), $b = s/r$, the ratio of the linear growth rates of the predator and prey. If the steady state is stable, then as the predators' growth rate s decreases there is more likelihood of periodic behaviour since b decreases and, if it decreases enough, we move into the instability regime. On the other hand if r decreases, b increases and so probably reduces the possibility of oscillatory behaviour. In this latter case it is not so clear-cut since, from (3.19), reducing r also increases a , which from Figure 3.6(c) tends to increase the possibility of periodic behaviour. The dimensional bifurcation space is 6-dimensional which is difficult to express graphically; the nondimensionalisation reduces it to a simple 3-dimensional space with (3.19) giving clear equivalent effects of

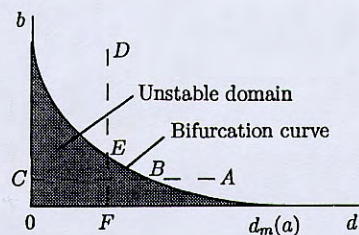


Figure 3.9. Typical stability bifurcation curve for the predator–prey model (3.20). As the point in parameter space crosses the bifurcation curve, the steady state changes stability.

different dimensional parameter changes. For example, doubling the carrying capacity K is exactly equivalent to halving the predator response parameter D . The dimensionless parameters are the important bifurcation ones to determine.

3.5 Competition Models: Principle of Competitive Exclusion

Here two or more species compete for the same limited food source or in some way inhibit each other's growth. For example, competition may be for territory which is directly related to food resources. Some interesting phenomena have been found from the study of practical competition models; see, for example, Hsu et al. (1979). Here we discuss a very simple competition model which demonstrates a fairly general principle which is observed to hold in Nature, namely, that when two species compete for the same limited resources one of the species usually becomes extinct.

Consider the basic 2-species Lotka–Volterra competition model with each species N_1 and N_2 having logistic growth in the absence of the other. Inclusion of logistic growth in the Lotka–Volterra systems makes them much more realistic, but to highlight the principle we consider the simpler model which nevertheless reflects many of the properties of more complicated models, particularly as regards stability. We thus consider

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right], \quad (3.29)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right], \quad (3.30)$$

where $r_1, K_1, r_2, K_2, b_{12}$ and b_{21} are all positive constants and, as before, the r 's are the linear birth rates and the K 's are the carrying capacities. The b_{12} and b_{21} measure the competitive effect of N_2 on N_1 and N_1 on N_2 respectively: they are generally not equal. Note that the competition model (3.29) and (3.30) is not a conservative system like its Lotka–Volterra predator–prey counterpart.

If we nondimensionalise this model by writing

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad (3.31)$$

$$a_{12} = b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2}$$

(3.29) and (3.30) become

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2), \quad (3.32)$$

$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2).$$

The steady states, and phase plane singularities, u_1^*, u_2^* , are solutions of $f_1(u_1, u_2) = f_2(u_1, u_2) = 0$ which, from (3.32), are

$$u_1^* = 0, u_2^* = 0; \quad u_1^* = 1, u_2^* = 0; \quad u_1^* = 0, u_2^* = 1; \quad (3.33)$$

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}}, u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}.$$

The last of these is only of relevance if $u_1^* \geq 0$ and $u_2^* \geq 0$ are finite, in which case $a_{12}a_{21} \neq 1$. The four possibilities are seen immediately on drawing the null clines $f_1 = 0$ and $f_2 = 0$ in the u_1, u_2 phase plane as shown in Figure 3.10. The crucial part of the null clines are, from (3.32), the straight lines

$$1 - u_1 - a_{12}u_2 = 0, \quad 1 - u_2 - a_{21}u_1 = 0.$$

The first of these together with the u_2 -axis is $f_1 = 0$, while the second, together with the u_1 -axis is $f_2 = 0$.

The stability of the steady states is again determined by the community matrix which, for (3.32), is

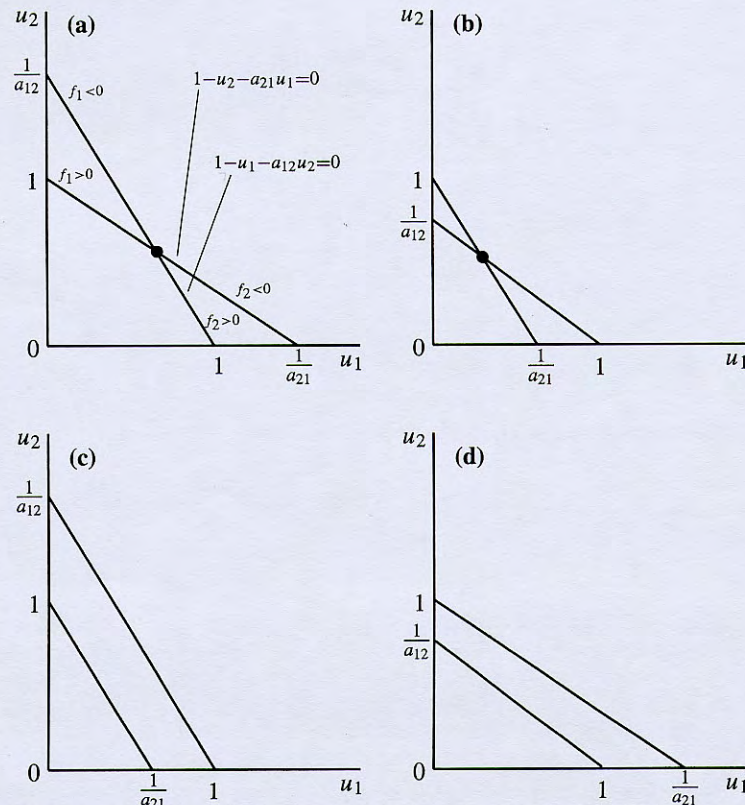


Figure 3.10. The null clines for the competition model (3.32). $f_1 = 0$ is $u_1 = 0$ and $1 - u_1 - a_{12}u_2 = 0$ with $f_2 = 0$ being $u_2 = 0$ and $1 - u_2 - a_{21}u_1 = 0$. The intersection of the two solid lines gives the positive steady state if it exists as in (a) and (b): the relative sizes of a_{12} and a_{21} as compared with 1 for it to exist are obvious from (a) to (d).

$$A = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}_{u_1^*, u_2^*} \quad (3.34)$$

$$= \begin{pmatrix} 1 - 2u_1 - a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1 - 2u_2 - a_{21}u_1) \end{pmatrix}_{u_1^*, u_2^*}$$

The first steady state in (3.33), that is, $(0, 0)$, is unstable since the eigenvalues λ of its community matrix, given from (3.34) by

$$|A - \lambda I| = \begin{vmatrix} 1 - \lambda & 0 \\ 0 & \rho - \lambda \end{vmatrix} = 0 \Rightarrow \lambda_1 = 1, \lambda_2 = \rho,$$

are positive. For the second of (3.33), namely, $(1, 0)$, (3.34) gives

$$|A - \lambda I| = \begin{vmatrix} -1 - \lambda & -a_{12} \\ 0 & \rho(1 - a_{21}) - \lambda \end{vmatrix} = 0 \Rightarrow \lambda_1 = -1, \lambda_2 = \rho(1 - a_{21})$$

and so

$$u_1^* = 1, u_2^* = 0 \text{ is } \begin{cases} \text{stable} & \text{if } \begin{cases} a_{21} > 1 \\ a_{21} < 1 \end{cases} \end{cases} \quad (3.35)$$

Similarly, for the third steady state, $(0, 1)$, the eigenvalues are $\lambda = -\rho, \lambda_2 = (1 - a_{12})$ and so

$$u_1^* = 0, u_2^* = 1 \text{ is } \begin{cases} \text{stable} & \text{if } \begin{cases} a_{12} > 1 \\ a_{12} < 1 \end{cases} \end{cases} \quad (3.36)$$

Finally for the last steady state in (3.33), when it exists in the positive quadrant, the matrix A from (3.34) is

$$A = (1 - a_{12}a_{21})^{-1} \begin{pmatrix} a_{12} - 1 & a_{12}(a_{12} - 1) \\ \rho a_{21}(a_{21} - 1) & \rho(a_{21} - 1) \end{pmatrix}$$

which has eigenvalues

$$\lambda_{1,2} = [2(1 - a_{12}a_{21})]^{-1} [(a_{12} - 1) + \rho(a_{21} - 1) \pm \{[(a_{12} - 1) + \rho(a_{21} - 1)]^2 - 4\rho(1 - a_{12}a_{21})(a_{12} - 1)(a_{21} - 1)\}^{1/2}]. \quad (3.37)$$

The sign of λ , or $\text{Re } \lambda$ if complex, and hence the stability of the steady state, depends on the size of ρ, a_{12} and a_{21} . There are several cases we have to consider, all of which have ecological implications which we come to below.

Before discussing the various cases note that there is a confined set on the boundary of which the vector of the derivatives, $(du_1/d\tau, du_2/d\tau)$, points along it or inwards: here it is a rectangular box in the (u_1, u_2) plane. From (3.32) this condition holds on the u_1 - and u_2 -axes. Outer edges of the rectangle are, for example, the lines $u_1 = U_1$ where $1 - U_1 - a_{12}u_2 < 0$ and $u_2 = U_2$ where $1 - U_2 - a_{21}u_1 < 0$. Any $U_1 > 1, U_2 > 1$ suffice. So the system is always globally stable.

The various cases are: (i) $a_{12} < 1, a_{21} < 1$, (ii) $a_{12} > 1, a_{21} > 1$, (iii) $a_{12} < 1, a_{21} > 1$, (iv) $a_{12} > 1, a_{21} < 1$. All of these are analyzed in a similar way. Figures 3.10(a) to (d) and Figures 3.11(a) to (d) relate to these cases (i) to (iv) respectively. By way of example, we consider just one of them, namely, (ii). The analysis of the other cases is left as an exercise. The results are encapsulated in Figure 3.11. The arrows in-

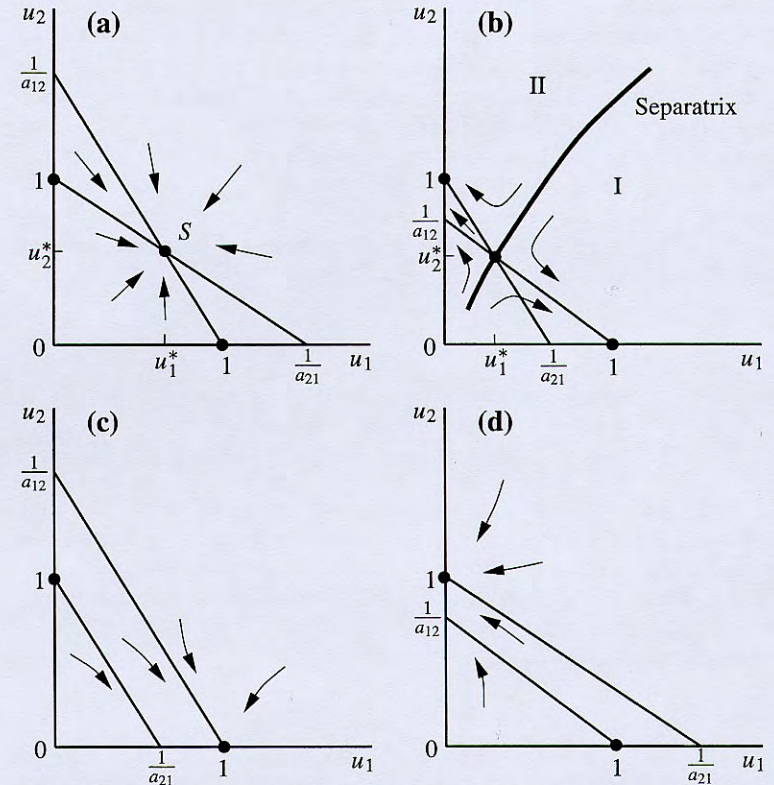


Figure 3.11. Schematic phase trajectories near the steady states for the dynamic behaviour of competing populations satisfying the model (3.32) for the various cases. (a) $a_{12} < 1, a_{21} < 1$. Only the positive steady state S is stable and all trajectories tend to it. (b) $a_{12} > 1, a_{21} > 1$. Here, $(1, 0)$ and $(0, 1)$ are stable steady states, each of which has a domain of attraction separated by a separatrix which passes through (u_1^*, u_2^*) . (c) $a_{12} < 1, a_{21} > 1$. Only one stable steady state exists, $u_1^* = 1, u_2^* = 0$ with the whole positive quadrant its domain of attraction. (d) $a_{12} > 1, a_{21} < 1$. The only stable steady state is $u_1^* = 0, u_2^* = 1$ with the positive quadrant as its domain of attraction. Cases (b) to (d) illustrate the competitive exclusion principle whereby 2 species competing for the same limited resource cannot in general coexist.

dicates the direction of the phase trajectories. The qualitative behaviour of the phase trajectories is given by the signs of $du_1/d\tau$, namely, $f_1(u_1, u_2)$, and $du_2/d\tau$ which is $f_2(u_1, u_2)$, on either side of the null clines.

Case $a_{12} > 1, a_{21} > 1$. This corresponds to Figure 3.10(b). From (3.35) and (3.36), $(1, 0)$ and $(0, 1)$ are stable. Since $1 - a_{12}a_{21} < 0$, (u_1^*, u_2^*) , the fourth steady state in (3.33), lies in the positive quadrant and from (3.37) its eigenvalues are such that $\lambda_2 < 0 < \lambda_1$ and so it is unstable to small perturbations: it is a saddle point. In this case, then, the phase trajectories can tend to either one of the two steady states, as illustrated in Figure 3.11(b). Each steady state has a *domain of attraction*. There is a line, a *separatrix*, which divides the positive quadrant into 2 nonoverlapping regions I and II as in Figure 3.11(b). The separatrix passes through the steady state (u_1^*, u_2^*) : it is one of the saddle point trajectories in fact.

Now consider some of the ecological implications of these results. In case (i) where $a_{12} < 1$ and $a_{21} < 1$ there is a stable steady state where both species can exist as in Figure 3.10(a). In terms of the original parameters from (3.31) this corresponds to $b_{12}K_2/K_1 < 1$ and $b_{21}K_1/K_2 < 1$. For example, if K_1 and K_2 are approximately the same and the interspecific competition, as measured by b_{12} and b_{21} , is not too strong, these conditions say that the two species simply adjust to a lower population size than if there were no competition. In other words, the competition is not aggressive. On the other hand if the b_{12} and b_{21} are about the same and the K_1 and K_2 are different, it is not easy to tell what will happen until we form and compare the *dimensionless* groupings a_{12} and a_{21} .

In case (ii), where $a_{12} > 1$ and $a_{21} > 1$, if the K 's are about equal, then the b_{12} and b_{21} are not small. The analysis then says that the competition is such that all three nontrivial steady states can exist, but, from (3.35) to (3.37), only $(1, 0)$ and $(0, 1)$ are stable, as in Figure 3.11(b). It can be a delicate matter which ultimately wins out. It depends crucially on the starting advantage each species has. If the initial conditions lie in domain I then eventually species 2 will die out, $u_2 \rightarrow 0$ and $u_1 \rightarrow 1$; that is, $N_1 \rightarrow K_1$ the carrying capacity of the environment for N_1 . Thus competition here has eliminated N_2 . On the other hand if N_2 has an initial size advantage so that u_1 and u_2 start in region II then $u_1 \rightarrow 0$ and $u_2 \rightarrow 1$ in which case the N_1 -species becomes extinct and $N_2 \rightarrow K_2$, its environmental carrying capacity. We expect extinction of one species even if the initial populations are close to the separatrix and in fact if they lie on it, since the ever present random fluctuations will inevitably cause one of $u_i, i = 1, 2$ to tend to zero.

Cases (iii) and (iv) in which the *interspecific* competition of one species is much stronger than the other, or the carrying capacities are sufficiently different so that $a_{12} = b_{12}K_2/K_1 < 1$ and $a_{21} = b_{21}K_1/K_2 > 1$ or alternatively $a_{12} > 1$ and $a_{21} < 1$, are quite definite in the ultimate result. In case (iii), as in Figure 3.11(c), the stronger dimensionless interspecific competition of the u_1 -species dominates and the other species, u_2 , dies out. In case (iv) it is the other way round and species u_1 becomes extinct.

Although all cases do not result in species elimination, those in (iii) and (iv) always do and in (ii) it is inevitable due to natural fluctuations in the population levels. This work led to the *principle of competitive exclusion* which was mentioned above. Note that the conditions for this to hold depend on the *dimensionless* parameter groupings a_{12} and a_{21} : the growth rate ratio parameter ρ does not affect the gross stability results, just

the dynamics of the system. Since $a_{12} = b_{12}K_2/K_1$, $a_{21} = b_{21}K_1/K_2$ the conditions for competitive exclusion depend critically on the interplay between competition and the carrying capacities as well as the initial conditions in case (ii).

Suppose, for example, we have 2 species comprised of large animals and small animals, with both competing for the same grass in a fixed area. Suppose also that they are equally competitive with $b_{12} = b_{21}$. With N_1 the large animals and N_2 the small, $K_1 < K_2$ and so $a_{12} = b_{12}K_2/K_1 < b_{21}K_2/K_1 = a_{21}$. As an example if $b_{12} = 1 = b_{21}$, $a_{12} < 1$ and $a_{21} > 1$ then in this case $N_1 \rightarrow 0$ and $N_2 \rightarrow K_2$; that is, the large animals become extinct.

The situation in which $a_{12} = 1 = a_{21}$ is special and, with the usual stochastic variability in nature, is unlikely in the real world to hold exactly. In this case the competitive exclusion of one or the other of the species also occurs.

The importance of species competition in Nature is obvious. We have discussed only one particularly simple model but again the method of analysis is quite general. A review and introductory article by Pianka (1981) deals with some practical aspects of competition as does the book of lectures by Waltman (1984). A slightly simpler competition model (see Exercise 2) was applied by Flores (1998) to the extinction of Neanderthal man by Early Modern man. Flores' model is based on a slightly different mortality rate of the two species and he shows that coexistence is not possible. He estimates the relevant parameter from independent sources and his extinction period is in line with the accepted palaeontological data of 5000 to 10,000 years. In Chapters 1 and 14, Volume II we discuss some practical cases of spatial competition associated with squirrels, wolf-deer survival and the release of genetically engineered organisms.

3.6 Mutualism or Symbiosis

There are many examples where the interaction of two or more species is to the advantage of all. Mutualism or symbiosis often plays the crucial role in promoting and even maintaining such species: plant and seed dispersal is one example. Even if survival is not at stake the mutual advantage of mutualism or symbiosis can be very important. As a topic of theoretical ecology, even for two species, this area has not been as widely studied as the others even though its importance is comparable to that of predator-prey and competition interactions. This is in part due to the fact that simple models in the Lotka-Volterra vein give silly results. The simplest mutualism model equivalent to the classical Lotka-Volterra predator-prey one is

$$\frac{dN_1}{dt} = r_1N_1 + a_1N_1N_2, \quad \frac{dN_2}{dt} = r_2N_2 + a_2N_2N_1,$$

where r_1, r_2, a_1 and a_2 are all positive constants. Since $dN_1/dt > 0$ and $dN_2/dt > 0$, N_1 and N_2 simply grow unboundedly in, as May (1981) so aptly put it, 'an orgy of mutual benefaction.'

Realistic models must at least show a mutual benefit to both species, or as many as are involved, and have some positive steady state or limit cycle type oscillation.

Some models which do this are described by Whittaker (1975). A practical example is discussed by May (1975).

As a first step in producing a reasonable 2-species model we incorporate limited carrying capacities for both species and consider

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2} \right), \end{aligned} \quad (3.38)$$

where $r_1, r_2, K_1, K_2, b_{12}$ and b_{21} are all positive constants. If we use the same nondimensionalisation as in the competition model (the signs preceding the b 's are negative there), namely, (3.31), we get

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2), \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2), \end{aligned} \quad (3.39)$$

where

$$\begin{aligned} u_1 &= \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \\ a_{12} &= b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2}. \end{aligned} \quad (3.40)$$

Analysing the model in the usual way we start with the steady states (u_1^*, u_2^*) which from (3.39) are

$$\begin{aligned} (0, 0), \quad (1, 0), \quad (0, 1), \\ \left(\frac{1 + a_{12}}{\delta}, \frac{1 + a_{21}}{\delta} \right), \quad \text{positive if } \delta = 1 - a_{12}a_{21} > 0. \end{aligned} \quad (3.41)$$

After calculating the community matrix for (3.39) and evaluating the eigenvalues λ for each of (3.41) it is straightforward to show that $(0, 0)$, $(1, 0)$ and $(0, 1)$ are all unstable: $(0, 0)$ is an unstable node and $(1, 0)$ and $(0, 1)$ are saddle point equilibria. If $1 - a_{12}a_{21} < 0$ there are only three steady states, the first three in (3.41), and so the populations become unbounded. We see this by drawing the null clines in the phase plane for (3.39), namely, $f_1 = 0$, $f_2 = 0$, and noting that the phase trajectories move off to infinity in a domain in which $u_1 \rightarrow \infty$ and $u_2 \rightarrow \infty$ as in Figure 3.12(a).

When $1 - a_{12}a_{21} > 0$, the fourth steady state in (3.41) exists in the positive quadrant. Evaluation of the eigenvalues of the community matrix shows it to be a stable equilibrium: it is a node singularity in the phase plane. This case is illustrated in Figure 3.12(b). Here all the trajectories in the positive quadrant tend to $u_1^* > 1$ and $u_2^* > 1$; that is, $N_1 > K_1$ and $N_2 > K_2$ and so each species has increased its steady state population from its maximum value in isolation.

This model has certain drawbacks. One is the sensitivity between unbounded growth and a finite positive steady state. It depends on the inequality $a_{12}a_{21} < 1$, which from

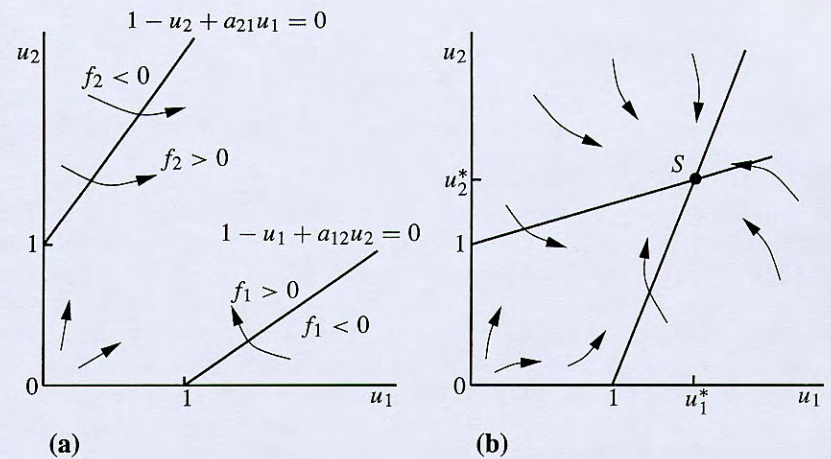


Figure 3.12. Phase trajectories for the mutualism model for two species with limited carrying capacities given by the dimensionless system (3.39). (a) $a_{12}a_{21} > 1$: unbounded growth occurs with $u_1 \rightarrow \infty$ and $u_2 \rightarrow \infty$ in the domain bounded by the null clines—the solid lines. (b) $a_{12}a_{21} < 1$: all trajectories tend to a positive steady state S with $u_1^* > 1$, $u_2^* > 1$ which shows the initial benefit that accrues since the carrying capacity for each species is greater than if no interaction were present.

(3.40) in terms of the original parameters in (3.38) is $b_{12}b_{21} < 1$: the b 's are dimensionless. So if symbiosis of either species is too large, this last condition is violated and both populations grow unboundedly.

3.7 General Models and Some General and Cautionary Remarks

All of the models we have discussed in this chapter result in systems of nonlinear differential equations of the form

$$\frac{dN_i}{dt} = N_i F_i(N_1, N_2, \dots, N_n), \quad i = 1, 2, \dots, \quad (3.42)$$

which emphasises the fact that the vector of populations \mathbf{N} has $\mathbf{N} = 0$ as a steady state. The two-species version is sometimes referred to as the Kolmogorov model or as the *Kolmogorov equations*.

Although we have mainly considered 2-species interactions in this chapter, in nature, and in the sea in particular, there are many species or *trophic levels* where energy, in the form of food, flows from one species to another. That is, there is a flow from one trophic level to another. The mass of the total number of individuals in a species is often referred to as its *biomass*, here the population times the unit mass. The ultimate source of energy is the sun, and in the sea, for example, the trophic web runs through plankton, fish, sharks up to whales and finally man, with the myriad of species in between. The species on one trophic level may predate several species below it. In general, models involve interaction between several species.

Multi-species models are of the form

$$\frac{d\mathbf{u}}{dt} = \mathbf{f}(\mathbf{u}) \quad \text{or} \quad \frac{du_i}{dt} = f_i(u_1, \dots, u_n), \quad i = 1, \dots, n, \quad (3.43)$$

where $\mathbf{u}(t)$ is the n -dimensional vector of population densities and $\mathbf{f}(\mathbf{u})$ describes the nonlinear interaction between the species. The function $\mathbf{f}(\mathbf{u})$ involves parameters which characterise the various growth and interaction features of the system under investigation, with $f_i(u_1, \dots, u_n)$ specifying the overall rate of growth for the i th species. The stability of the steady states is determined in exactly the same way as before by linearising about the steady states \mathbf{u}^* , where $\mathbf{f}(\mathbf{u}^*) = 0$ and examining the eigenvalues λ of the community or stability matrix

$$A = (a_{ij}) = \left(\frac{\partial f_i}{\partial u_j} \right)_{\mathbf{u}=\mathbf{u}^*}. \quad (3.44)$$

The necessary and sufficient conditions for the eigenvalues λ , solutions of polynomial $|A - \lambda I| = 0$, to have $\text{Re } \lambda > 0$ are given by the Routh–Hurwitz conditions which are listed in Appendix B.

If a steady state is unstable then the solution \mathbf{u} may grow unboundedly or evolve into another steady state or into a stable oscillatory pattern like a limit cycle. For 2-species models the theory of such equations is essentially complete: they are phase plane systems and a brief review of their analysis is given in Appendix A. For three or more interacting species considerably less general theory exists. Some results, at least for solutions near the steady state when it becomes unstable, can often be found using *Hopf bifurcation theory*; see, for example, the book by Strogatz (1994) for a good pedagogical discussion of Hopf bifurcation. At its simplest this theory says that if a parameter of the system, p say, has a critical value p_c such that for $p < p_c$ the eigenvalue with the largest $\text{Re } \lambda < 0$, and for $p = p_c$ $\text{Re } \lambda = 0$, $\text{Im } \lambda \neq 0$ and for $p > p_c$ $\text{Re } \lambda > 0$, $\text{Im } \lambda \neq 0$ then for $p - p_c > 0$ and small, the solution \mathbf{u} will exhibit small amplitude limit cycle behaviour around \mathbf{u}^* . Smith (1993) has developed a new approach to the study of 3 (and higher) competitive or cooperative species. His approach lets you apply the Poincaré–Bendixson theorem to three-species systems by relating the flows to topologically equivalent flows in two dimensions.

The community matrix A , defined by (3.44), which is so crucial in determining the linear stability of the steady states, has direct biological significance. The elements a_{ij} measure the effect of the j -species on the i -species near equilibrium. For example, if U_i is the perturbation from the steady state u_i^* , the equation for U_i is

$$\frac{dU_i}{dt} = \sum_{j=1}^n a_{ij} U_j \quad (3.45)$$

and so $a_{ij} U_j$ is the effect of the species U_j on the growth of U_i . If $a_{ij} > 0$ then U_j directly enhances U_i 's growth while if $a_{ij} < 0$ it diminishes it. If $a_{ij} > 0$ and $a_{ji} > 0$ then U_i and U_j enhance each other's growth and so they are in a symbiotic interaction. If $a_{ij} < 0$ and $a_{ji} < 0$ then they are in competition. May (1975) gives a survey of some

generalised models and, in his discussion on stability versus complexity, gives some results for stability based on properties of the community matrix.

There has been a considerable amount of study of systems where the community matrix has diagonal symmetry or antisymmetry or has other rather special properties, where general results can be given about the eigenvalues and hence the stability of the steady states. This has had very limited practical value since models of real situations do not have such simple properties. The stochastic element in assessing parameters mitigates against even approximations by such models. However, just as the classical Lotka–Volterra system is not relevant to the real world, these special models have often made people ask the right questions. Even so, a preoccupation with such models or their generalizations must be avoided if the basic aim is to understand the real world.

An important class of models which we have not discussed is interaction models with delay. If the species exhibit different or distributed delays, such models open up a veritable Pandora's box of solution behaviour which to a large extent is still relatively unexplored.

If we consider three or more species, aperiodic behaviour can arise. Lorenz (1963) first demonstrated this with the model system

$$\frac{du}{dt} = a(v - u), \quad \frac{dv}{dt} = -uw + bu - v, \quad \frac{dw}{dt} = uv - cw,$$

where a , b and c are positive parameters. (The equations arose in a fluid flow model.) As the parameters are varied the solutions exhibit period doubling and eventually chaos or aperiodicity. Many authors have considered such systems. For example, Rössler (1976a,b, 1979, 1983), Sparrow (1982, 1986) and Strogatz (1994) have made a particular study of such systems and discovered several other basic examples which show similar properties; see also the book edited by Holden (1986). It would be surprising if certain population interaction models of three or more species did not display similar properties. Competition models of three or more species produce some unexpected results.

Evidence for chaos (even complex oscillations) in wild populations is difficult to find as well as difficult to verify unequivocally. It has been suggested therefore that evolution tends to preserve populations from such chaotic behaviour. Possible chaotic population dynamics which results from natural selection has been investigated in an interesting article by Ferrière and Gatto (1993). From their results they hypothesize that evolution might support considerably more chaotic population dynamics than believed up to now. Controversially they suggest that chaos is possibly optimal in population dynamics. They suggest, in fact, that chaos could be an optimal behaviour for various biological systems. This conclusion is in line with the views expressed by Schaffer and Kot (1986) with regard to epidemics.

Notwithstanding the above, evolutionary development of complex population interactions seems to have generally produced reasonably stable systems. From our study of interaction models up to now we know that a system can be driven unstable if certain parameters are changed appropriately, that is, pass through bifurcation values. It should therefore be a matter of considerable scientific study before any system is altered by external manipulation. The use of models to study the effect of artificially interfering in such trophic webs is essential and can be extremely illuminating. Had this been done it

is likely that the following catastrophe would have been avoided. Although the use of realistic dynamic models cannot give the complete answer, in the form of predictions which might result from introducing another species or eradicating one in the chain, they can certainly point to various danger signs that must be seriously considered. By the same arguments it is essential that not too much credence be put on models since the interactions can often be extremely complicated and the modeller might simply not construct a sufficiently good model. To conclude this section we describe a major ecological catastrophe which came from one such attempt to manipulate a complex trophic web in East Africa.

Lake Victoria and the Nile Perch Catastrophe 1960

In 1960, the Nile perch (*Lates niloticus*) was introduced into Lake Victoria, the largest lake in East Africa. The lake is bordered by Kenya, Tanzania and Uganda and it was used to support hundreds of small fishing communities along the shore. It was thought that the introduction of this large carnivorous species, which can weigh up to 100 Kg or more, would provide a high-yielding and valuable source of protein. Its introduction was supported at the time by the United Nations Food and Agriculture Organisation. There were dissenting views from some scientists but these were ignored.

The presence of the large carnivorous perch over the past 35 years has essentially wiped out the several hundred smaller cichlid fish in the lake; many of these provided the main basis of the fishing communities' economy on the lake's shore. Markets were flooded with perch. It was estimated that in 1984 the overall productivity of the lake was reduced by about 80% of its pre-1960 level.

Within the lake, the unplanned introduction of such a major, new and unsuitable species was a mistake of horrifying dimensions and caused an ecological disaster. There are, however, other knock-on effects outside the lake over and above the economic catastrophe which engulfed the shore communities: these effects should certainly have been anticipated. For example, the large perch are oily and cannot be dried in the sun but have to be preserved by smoking. This resulted in major felling of valuable trees to provide fuel.

Even more serious is the fact that many of the cichlid species, which have all but disappeared and which used to flourish in the lake, helped to control the level of a particular snail which lives in and around the lake.

These freshwater snails, which live in many of the major reservoirs of large dams, are an essential link in the cycle of the parasitic disease called schistosomiasis (also known as bilharzia), a disease which is considered to rank second only to malaria in importance. It is a disease which is not attacked by the body's immune system and is invariably fatal to humans if not treated. Since the best mathematical biology is usually carried out within a truly interdisciplinary environment, it is often the case that in trying to make a model certain questions and answers are elicited from the ecologists, which in turn initiate other related questions not directly connected with the model. These knock-on effects would have been important examples. In spite of the disaster caused by this introduction of an unsuitable species into such a delicate and complex trophic web there were (in 1987) plans to introduce Nile perch into other large lakes in the region, such as Lake Malawi.

Schistosomiasis¹ is a particularly nasty disease which affects more than 200 million people in 74 countries. In Egypt, for example, it is linked to cancer and is the primary cause of death among men between 20 and 44 years old. The snails shed parasites, called (schistosome) cercariae, into the water: a single snail releases cercariae at a rate of up to 3000 a day. These penetrate the human skin (when wading or swimming in infected waters), migrate to the lung, liver, the bladder and elsewhere. After about five weeks the worms mate and lay eggs at a rate of about 300 a day, about half of which are eventually excreted. Those not secreted tend to lodge mainly in the liver. The eggs cause the damage since they are recognised as a foreign invader and the immune system forms scar tissue in a capsule which contains the egg. Chronic infection causes more capsules and scar tissue leading to high blood pressure. The body tries to cope by making new fragile and leaky blood vessels; eventually the patients in effect bleed to death. The excreted eggs, on reaching the freshwater, hatch to become miracidia which then pass into the snail and undergo asexual reproduction to produce cercariae thereby completing the cycle. One of the interesting ideas to treat the disease is to try to get the immune system to attack the eggs without forming these capsules.

Lately (1990's) yet another catastrophe struck Lake Victoria in which water hyacinths (*Eichhorria crassipes*) are ringing the lake with a wide thick mat which is destroying fish breeding grounds, clogging hydroelectric plants and more. About 80% of Uganda's coastline is now infected. Although it is partially controlled in its native Brazil with a predator (a rust fungus) there is some hesitancy in using an introduced predator. However, this and chemical herbicides are being seriously mooted.

3.8 Threshold Phenomena

With the exception of the Lotka-Volterra predator-prey model, the 2-species models, which we have considered or referred to in this chapter, have either had stable steady states where small perturbations die out, or unstable steady states where perturbations from them grow unboundedly or result in limit cycle periodic solutions. There is an interesting group of models which have a nonzero stable state such that if the perturbation from it is sufficiently large or of the right kind, the population densities undergo

¹ An interesting speculation arose from a dinner discussion in Corpus Christi College, Oxford one evening concerning this disease, which I was working on at the time. Others in the discussion included an ancient historian and an archaeologist who asked me to describe some of the symptoms of schistosomiasis. I briefly described them and how it manifested itself. When a male has the disease from early childhood he begins to pass blood in his urine around the age of 11 or so, roughly the time that girls start to menstruate in warm climates. Infected males (and females) eventually die (if untreated) in their twenties or thirties. The ancient historian then noted that in ancient Egypt it was believed that both males and females had 'periods,' starting about the same age. Schistosomiasis was endemic in ancient Egypt (and is still highly prevalent today—the Aswan Dam made the problem worse!). He went on to add that if a boy did not 'menstruate' he was clearly singled out by the gods and was destined to become a priest. The archaeologist then pointed out that it was interesting that most of the Egyptian mummies were of young people and that the mummies of older people were primarily priests. One can speculate that the reason the priests as young boys did not develop the disease is that they had some natural immunity and offers an explanation as to why priests frequently lived considerably longer than the average life span in ancient Egypt. A touch fanciful perhaps but it is not totally outside the possibility of reality and gives justification for a truly interdisciplinary society!

large variations before returning to the steady state. Such models are said to exhibit a threshold effect. We study one such group of models here.

Consider the model predator-prey system

$$\frac{dN}{dt} = N[F(N) - P] = f(N, P), \tag{3.46}$$

$$\frac{dP}{dt} = P[N - G(P)] = g(N, P), \tag{3.47}$$

where for convenience all the parameters have been incorporated in the F and G by a suitable rescaling: the $F(N)$ and $G(P)$ are qualitatively as illustrated in Figure 3.13. The specific form of $F(N)$ demonstrates the *Allee effect* which means that the per capita growth rate of the prey initially increases with prey density but reaches a maximum at some N_m and then decreases for larger prey densities.

The steady states N^*, P^* from (3.46) and (3.47) are $N^* = 0 = P^*$ and the non-negative solutions of

$$P^* = F(N^*), \quad N^* = G(P^*). \tag{3.48}$$

As usual, it is again helpful to draw the null clines $f = 0, g = 0$ which are sketched in Figure 3.14. Depending on the various parameters in $F(N)$ and $G(P)$, the steady state can be typically at S or at S' . To be specific we consider the case where $N^* > N_m$; that is, the steady state is at S in Figure 3.14.

From (3.46) and (3.47) the community matrix A for the zero steady state $N^* = 0, P^* = 0$ is

$$A = \left(\begin{array}{cc} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial P} \\ \frac{\partial g}{\partial N} & \frac{\partial g}{\partial P} \end{array} \right)_{N=0=P} = \left(\begin{array}{cc} F(0) & 0 \\ 0 & -G(0) \end{array} \right).$$

The eigenvalues are $\lambda = F(0) > 0$ and $\lambda = -G(0) < 0$. So, with the $F(N)$ and $G(N)$ in Figure 3.13, $(0, 0)$ is unstable: it is a saddle point singularity in the (N, P) phase plane.

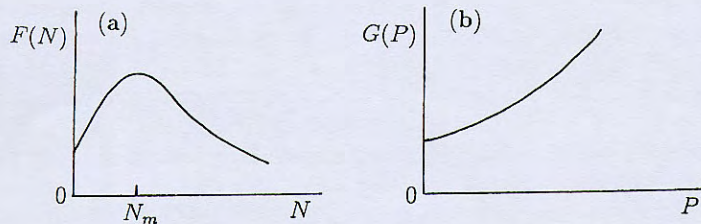


Figure 3.13. (a) Qualitative form of the prey's per capita growth rate $F(N)$ in (3.46) which exhibits the Allee effect. (b) Predators' per capita mortality rate.

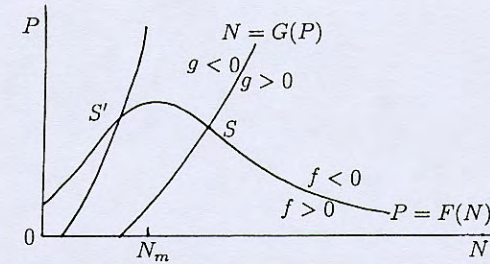


Figure 3.14. Null clines $N = 0, P = 0, N = G(P), P = F(N)$ for the predator-prey system (3.46) and (3.47): $f = N[F(N) - P], g = P[N - G(P)]$. S and S' are possible stable steady states.

For the positive steady state (N^*, P^*) the community matrix is, from (3.46)–(3.48),

$$A = \left(\begin{array}{cc} N^*F'(N^*) & -N^* \\ P^* & -P^*G'(P^*) \end{array} \right),$$

where the prime denotes differentiation and, from Figure 3.14, $G'(P^*) > 0$ and $F'(N^*) < 0$ when (N^*, P^*) is at S and $G'(P^*) > 0$ and $F'(N^*) > 0$ when at S' . The eigenvalues λ are solutions of

$$|A - \lambda I| = 0 \Rightarrow \lambda^2 - (\text{tr}A)\lambda + \det A = 0, \tag{3.49}$$

where

$$\begin{aligned} \text{tr} A &= N^*F'(N^*) - P^*G'(P^*) \\ \det A &= N^*P^*[1 - F'(N^*)G'(P^*)]. \end{aligned} \tag{3.50}$$

When the steady state is at S in Figure 3.14, $\text{tr}A < 0$ and $\det A > 0$ and so it is stable to small perturbations for all $F(N)$ and $G(P)$ since $\text{Re} \lambda < 0$ from (3.49). If the steady state is at S' , $\text{tr}A$ and $\det A$ can be positive or negative since now $F'(N^*) > 0$. Thus S' may be stable or unstable depending on the particular $F(N)$ and $G(P)$. If it is unstable then a limit cycle solution results since there is a confined set for the system; refer to Section 3.4 for a worked example of a qualitatively similar problem and Figure 3.8 which illustrates such a solution behaviour.

The case of interest here is when the steady state is at S and is thus always stable. Suppose we perturb the system to the point X in the phase plane as in Figure 3.15(a). Since here $f < 0$ and $g < 0$, equations (3.46) and (3.47) imply that $dN/dt < 0$ and $dP/dt < 0$ and so the trajectory starts to move qualitatively as on the trajectory shown in Figure 3.15(a): it eventually returns to S but only after a large excursion in the phase plane. The path is qualitatively indicated by the signs of f and g and hence of dN/dt and dP/dt . If the perturbation takes (N, P) to Y then a similar behaviour occurs. If, however, the perturbation is to Z then the perturbation remains close to S . Figures 3.15(b) and (c) illustrate a typical temporal behaviour of N and P .

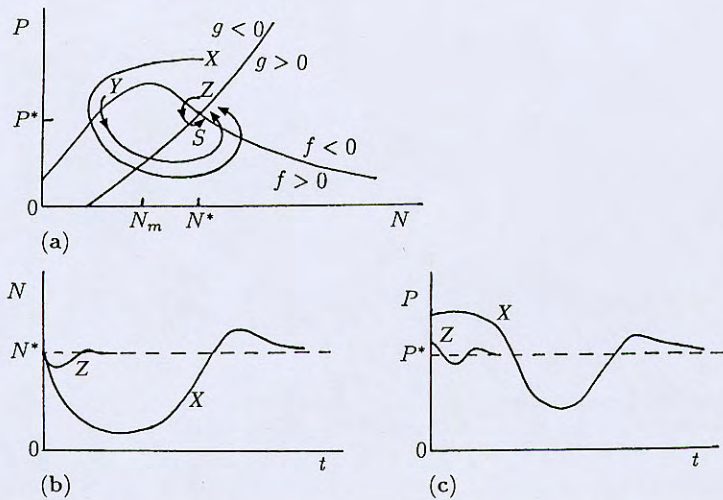


Figure 3.15. (a) Null clines for the predator–prey threshold model (3.46) and (3.47). The steady state S is always stable. A perturbation to X results in a large excursion in phase space before returning to S . A perturbation to Z is under the threshold and hence returns to S without a large excursion. (b) and (c) Schematic time evolution of the solutions illustrating the effect of a perturbation to X and to Z as in (a).

There is clearly a rough threshold perturbation below which the perturbation always remains close to the steady state and above which it does not, even though the solution ultimately returns to the steady state. The threshold perturbation is more a threshold curve or rather domain and is such that if the perturbation results in the trajectory getting past the maximum N_m in Figure 3.15(a) then the trajectories are typically like those from X and Y . If the trajectory crosses $f = 0$ at $N > N_m$ then no large perturbation occurs. The reason that such a threshold property exists is a consequence of the form of the null cline $f = 0$ which has a maximum as shown; in this case this is a consequence of the Allee effect in the dynamics of the model (3.46). With the problems we have discussed earlier in this chapter it might appear from looking at the temporal behaviour of the population that we were dealing with an unstable situation. The necessity for a careful drawing of the null clines is clear. The definition of a threshold at this stage is rather imprecise. We show later in Chapter 1, Volume II that if one of the species is allowed to disperse spatially, for example, by diffusion, then threshold travelling waves are possible. These have important biological consequences. In this context the concept of a threshold can be made precise. This threshold behaviour arises in an important way later in the book in biochemical contexts which are formally similar since the equations for reaction kinetics are mathematically of the same type as those for the dynamics of interacting populations such as we have discussed here.

A final remark on the problem of modelling interacting populations is that there can be no ‘correct’ model for a given situation since many models can give qualitatively similar behaviour. Getting the right qualitative characteristics is only the first step and

must not be considered justification for a model. This important caveat for all models will be repeated with regularity throughout the book. What helps to make a model a good one is the plausibility of the growth dynamics based on observation, real facts and whether or not a reasonable assessment of the various parameters is possible and, finally, whether predictions based on the model are borne out by subsequent experiment and observation.

3.9 Discrete Growth Models for Interacting Populations

We now consider two interacting species, each with nonoverlapping generations, which affect each other’s population dynamics. As in the continuous growth models, there are the same main types of interaction, namely, predator–prey, competition and mutualism. In a predator–prey situation the growth rate of one is enhanced at the expense of the other whereas in competition the growth rates of both are decreased while in mutualism they are both increased. These topics have been widely studied but nowhere near to the same extent as for continuous models for which, in the case of two species, there is a complete mathematical treatment of the equations. The book by Hassel (1978) deals with predator–prey models. Beddington et al. (1975) present some results on the dynamic complexity of coupled predator–prey systems. The book by Gumowski and Mira (1980) is more mathematical, dealing generally with the mathematics of coupled systems but also including some interesting numerically computed results; see also the introductory article by Lauwerier (1986). The review article by May (1986) is apposite to the material here and that in the previous chapters, the central issue of which is how populations regulate. He also discusses, for example, the problems associated with unpredictable environmental factors superimposed on deterministic models and various practical aspects of resource management. In view of the complexity of solution behaviour with single-species discrete models it is not surprising that even more complex behaviour is possible with coupled discrete systems. Even though we expect complex behaviour it is hard not to be overwhelmed by the astonishing solution diversity when we see the baroque patterns that can be generated as has been so beautifully demonstrated by Peitgen and Richter (1986). Their book is devoted in large part to the numerically generated solutions of discrete systems. They show, in striking colour, a wide spectrum of patterns which can arise, for example, with a system of only two coupled equations; the dynamics need not be very complicated. They also show, among other things, how the solutions relate to fractal generation (see, for example, Mandelbrot 1982), Julia sets, Hubbard trees and other exotica. Most of the text is a technical but easily readable discussion of the main topics of current interest in dynamical systems. In Chapter 14 we give a brief introduction to fractals.

Here we are concerned with predator–prey models. An important aspect of evolution by natural selection is the favouring of efficient predators and cleverly elusive prey. Within the general class, we have in mind primarily insect predator–prey systems, since as well as the availability of a substantial body of experimental data, insects often have life cycles which can be modelled by two-species discrete models.

We consider the interaction for the prey (N) and the predator (P) to be governed by the discrete time (t) system of coupled equations

$$N_{t+1} = rN_t f(N_t, P_t), \quad (3.51)$$

$$P_{t+1} = N_t g(N_t, P_t), \quad (3.52)$$

where $r > 0$ is the net linear rate of increase of the prey and f and g are functions which relate the predator-influenced reproductive efficiency of the prey and the searching efficiency of the predator respectively. The techniques we discuss are, of course, applicable to other population interactions. The theory discussed in the following chapter is different in that the interaction is overlapping. The techniques for it have similarities but with some fundamental differences. The crucial difference, however, is that the 'species' in Chapter 5 are marital states.

3.10 Predator-Prey Models: Detailed Analysis

We first consider a simple model in which predators simply search over a constant area and have unlimited capacity for consuming the prey. This is reflected in the system

$$\begin{aligned} N_{t+1} &= rN_t \exp[-aP_t], \\ P_{t+1} &= N_t \{1 - \exp[-aP_t]\}. \end{aligned} \quad a > 0 \quad (3.53)$$

Perhaps it should be mentioned here that it is always informative to try and get an intuitive impression of how the interaction affects each species by looking at the qualitative behaviour indicated by the equations. With this system, for example, try and decide what the outcome of the stability analysis will be. In general if the result is not what you anticipated such a preliminary qualitative impression can often help in modifying the model to make it more realistic.

The equilibrium values N^* , P^* of (3.53) are given by

$$\begin{aligned} N^* &= 0, \quad P^* = 0 \\ \text{or } 1 &= r \exp[-aP^*], \quad P^* = N^*(1 - \exp[-aP^*]) \end{aligned}$$

and so positive steady state populations are

$$P^* = \frac{1}{a} \ln r, \quad N^* = \frac{r}{a(r-1)} \ln r, \quad r > 1. \quad (3.54)$$

The linear stability of the equilibria can be determined in the usual way by writing

$$N_t = N^* + n_t, \quad P_t = P^* + p_t, \quad \left| \frac{n_t}{N^*} \right| \ll 1, \quad \left| \frac{p_t}{P^*} \right| \ll 1, \quad (3.55)$$

substituting into (3.53) and retaining only linear terms. For the steady state (0, 0) the analysis is particularly simple since

$$n_{t+1} = rn_t, \quad p_{t+1} = 0,$$

and so it is stable for $r < 1$ since $N_t \rightarrow 0$ as $t \rightarrow \infty$ and unstable for $r > 1$, that is, the range of r when the positive steady state (3.54) exists. For this positive steady state we have the linear system of equations

$$n_{t+1} = n_t - N^* a p_t, \quad p_{t+1} = n_t \left(1 - \frac{1}{r}\right) + \frac{N^* a}{r} p_t, \quad (3.56)$$

where we have used the relation $1 = r \exp[-aP^*]$ which defines P^* .

A straightforward way to solve (3.56) is to iterate the first equation and then use the second to get a single equation for n_t . That is,

$$\begin{aligned} n_{t+2} &= n_{t+1} - N^* a p_{t+1} \\ &= n_{t+1} - N^* a \left[n_t \left(1 - \frac{1}{r}\right) + \frac{N^* a}{r} p_t \right] \\ &= n_{t+1} - N^* a \left[n_t \left(1 - \frac{1}{r}\right) + \frac{1}{r} (n_t - n_{t+1}) \right] \end{aligned}$$

and so

$$n_{t+2} - \left(1 + \frac{N^* a}{r}\right) n_{t+1} + N^* a n_t = 0. \quad (3.57)$$

We now look for solutions in the form

$$n_t = Ax^t \Rightarrow x^2 - \left(1 + \frac{N^* a}{r}\right) x + N^* a = 0.$$

With N^* from (3.54) the characteristic polynomial is thus

$$x^2 - \left\{1 + \frac{1}{r-1} \ln r\right\} x + \frac{r}{r-1} \ln r = 0, \quad r > 1 \quad (3.58)$$

of which the two solutions x_1 and x_2 are

$$x_1, x_2 = \frac{1}{2} \left\{ \left[1 + \frac{\ln r}{r-1}\right] \pm \left[\left[1 + \frac{\ln r}{r-1}\right]^2 - 4 \frac{r \ln r}{r-1} \right]^{1/2} \right\}. \quad (3.59)$$

Thus

$$n_t = A_1 x^t + A_2 x^t, \quad (3.60)$$

where A_1, A_2 are arbitrary constants. With this, or by a similar analysis, we then get p_t as

$$p_t = B_1 x^t + B_2 x^t, \quad (3.61)$$

where B_1 and B_2 are arbitrary constants.

A more elegant, and easy to generalise, way to find x_1 and x_2 is to write the linear perturbation system (3.56) in matrix form

$$\begin{pmatrix} n_{t+1} \\ p_{t+1} \end{pmatrix} = A \begin{pmatrix} n_t \\ p_t \end{pmatrix}, \quad A = \begin{pmatrix} 1 & -N^*a \\ 1 - \frac{1}{r} & \frac{N^*a}{r} \end{pmatrix} \quad (3.62)$$

and look for solutions in the form

$$\begin{pmatrix} n_t \\ p_t \end{pmatrix} = B \begin{pmatrix} 1 \\ 1 \end{pmatrix} x^t,$$

where B is an arbitrary constant 2×2 matrix. Substituting this into (3.62) gives

$$B \begin{pmatrix} x^{t+1} \\ x^{t+1} \end{pmatrix} = AB \begin{pmatrix} x^t \\ x^t \end{pmatrix} \Rightarrow xB \begin{pmatrix} x^t \\ x^t \end{pmatrix} = AB \begin{pmatrix} x^t \\ x^t \end{pmatrix}$$

which has a nontrivial solution $B \begin{pmatrix} x^t \\ x^t \end{pmatrix}$ if

$$|A - xI| = 0 \Rightarrow \begin{vmatrix} 1-x & -N^*a \\ 1-\frac{1}{r} & \frac{N^*a}{r}-x \end{vmatrix} = 0$$

which again gives the quadratic characteristics equation (3.58). The solutions x_1 and x_2 are simply the eigenvalues of the matrix A in (3.62). This matrix approach is the discrete equation analogue of the one we used for the continuous interacting population models. The generalization to higher-order discrete model systems is clear.

The stability of the steady state (N^*, P^*) is determined by the magnitude of $|x_1|$ and $|x_2|$. If either of $|x_1| > 1$ or $|x_2| > 1$ then n_t and p_t become unbounded as $t \rightarrow \infty$ and hence (N^*, P^*) is unstable since perturbations from it grow with time. A little algebra shows that in (3.59),

$$\left[1 + \frac{\ln r}{r-1} \right]^2 - \frac{4r \ln r}{r-1} < 0 \quad \text{for } r > 1$$

and so the roots x_1 and x_2 are complex conjugates. The product of the roots, from (3.58), or (3.59), is

$$x_1 x_2 = |x_1|^2 = (r \ln r)/(r-1) > 1, \quad \text{for all } r > 1, \Rightarrow |x_1| > 1.$$

(An easy way to see that $(r \ln r)/(r-1) > 1$ for all $r > 1$ is to consider the graphs of $\ln r$ and $(r-1)/r$ for $r > 1$ and note that $d(\ln r)/dr > d[(r-1)/r]/dr$ for all $r > 1$.) Thus the solutions (n_t, p_t) from (3.60) and (3.61) become unbounded as $t \rightarrow \infty$ and so the positive equilibrium (N^*, P^*) in (3.54) is unstable, and by growing oscillations since x_1 and x_2 are complex. Numerical solutions of the system (3.53) indicate that the system is unstable to finite perturbations as well: the solutions grow unboundedly. Thus this simple model is just too simple for any practical applications except possibly under contrived laboratory conditions and then only for a limited time.

Density-Dependent Predator-Prey Model

Let us reexamine the underlying assumptions in the simple initial model (3.53). The form of the equations implies that the number of encounters a predator has with a prey increases unboundedly with the prey density: this seems rather unrealistic. It is more likely that there is a limit to the predators' appetite. Another way of looking at this equation as it stands, and which is formally the same, is that if there were no predators $P_t = 0$ and then N_t would grow unboundedly, if $r > 1$, and become extinct if $0 < r < 1$: it is the simple Malthusian model (2.2). It is reasonable to modify the N_t equation (3.53) to incorporate some saturation of the prey population or, in terms of predator encounters, a prey-limiting model. We thus take as a more realistic model

$$\begin{aligned} N_{t+1} &= N_t \exp \left[r \left(1 - \frac{N_t}{K} \right) - a P_t \right], \\ P_{t+1} &= N_t \{ 1 - \exp[-a P_t] \}. \end{aligned} \quad (3.63)$$

Now with $P_t = 0$ this reduces to the single-species model (2.8) in Section 2.1. There is a stable positive equilibrium $N^* = K$ for $0 < r < 2$ and oscillatory and periodic solutions for $r > 2$. We can reasonably expect a similar bifurcation behaviour here, although probably not with a first bifurcation at $r = 2$ and certainly not the same values for r with higher bifurcations. This model has been studied in detail by Beddington et al. (1975).

The nontrivial steady states of (3.63) are solutions of

$$1 = \exp \left[r \left(1 - \frac{N^*}{K} \right) - a P^* \right], \quad P^* = N^* (1 - \exp[-a P^*]). \quad (3.64)$$

The first of these gives

$$P^* = \frac{r}{a} \left(1 - \frac{N^*}{K} \right) \quad (3.65)$$

which on substituting into the second gives N^* as solutions of the transcendental equation

$$\frac{r \left(1 - \frac{N^*}{K} \right)}{a N^*} = 1 - \exp \left[-r \left(1 - \frac{N^*}{K} \right) \right]. \quad (3.66)$$

Clearly $N^* = K, P^* = 0$ is a solution. If we plot the left- and right-hand sides of (3.66) against N^* as in Figure 3.16 we see there is another equilibrium $0 < N_E^* < K$, the other intersection of the curves: it depends on r, a and K . With N_E^* determined, (3.65) then gives P_E^* .

The linear stability of this equilibrium can be treated in exactly the same way as before with the eigenvalues x again being given by the eigenvalues of the matrix of the linearised system. It has to be done numerically. It can be shown that for some $r > 0$ the equilibrium is stable and that it bifurcates for larger r . Beddington et al.

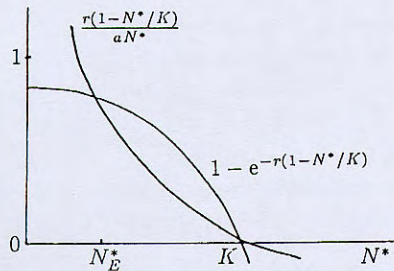


Figure 3.16. Graphical solution for the positive equilibrium N_E^* of the model system (3.63).

(1975) determine the stability boundaries in the $r, N_E^*/K$ parameter space where there is a bifurcation from stability to instability and where the solutions exhibit periodic and ultimately chaotic behaviour. The stability analysis of realistic two-species models often has to be carried out numerically. For three-species and higher, the Jury conditions (see Appendix B) can be used to determine the conditions which the coefficients must satisfy so that the linear solutions x satisfy $|x| < 1$. For higher-order systems, however, they are of little use except within a numerical scheme.

Biological Pest Control: General Remarks

The use of natural predators for pest control is to inhibit any large pest increase by a corresponding increase in the predator population. The aim is to keep both populations at acceptably low levels. The aim is *not* to eradicate the pest, only to control its population. Although many model systems of real predators and real pests are reasonably robust from a stability point of view, some can be extremely sensitive. This is why the analysis of realistic models is so important. When the parameters for a model are taken from observations it is fortunate that many result in either steady state equilibria or simple periodic behaviour: chaotic behaviour is much less common. Thus effective parameter manipulation is more predictable in a substantial number of practical situations.

There are many notable successes of biological pest control particularly with long-standing crops such as fruit and forest crops and so on, where there is a continuous predator-prey interaction. With the major ecological changes caused by harvesting in perennial crops it has been less successful. The successes have mainly been of the predator-prey variety where the predator is a parasite. This can be extremely important in many human diseases. Kot (2001) gives a full discussion of the dynamics of harvesting models, including the important aspect of optimal control.

In the models we have analysed we have concentrated particularly on the model building aspects, the study of stability in relation to parameter ranges and the existence of either steady states or periodic behaviour. What we have not discussed is the influence of initial conditions. Although not generally the case, they can be important. One such example is the control of the red spider mite which is a glass-house tomato plant pest where the initial predator-prey ratio is crucial. We should expect initial data to be important particularly in those cases where the oscillations show outbreak, crashback and slow recovery. The crashback to low levels may bring the species close enough to

extinction to actually cause it. There are several books on biological pest control; see, for example, DeBach (1974) and Huffaker (1971).

A moderately new and, in effect, virgin territory is the study of coupled systems where the time-steps for the predator and prey are not equal. This clearly occurs in the real world. With the wealth of interesting and unexpected behaviour displayed by the models in this chapter and Chapter 2, it would be surprising if different time-step models did not produce equally unexpected solution behaviour.

Exercises

- 1 In the competition model for two species with populations N_1 and N_2

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right),$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - b_{21} \frac{N_1}{K_2} \right),$$

where only one species, N_1 , has limited carrying capacity. Nondimensionalise the system and determine the steady states. Investigate their stability and sketch the phase plane trajectories. Show that irrespective of the size of the parameters the principle of competitive exclusion holds. Briefly describe under what ecological circumstances the species N_2 becomes extinct.

- 2 Flores (1998) proposed the following model for competition between Neanderthal man (N) and Early Modern man (E).

$$\frac{dN}{dt} = N [A - D(N + E) - B], \quad \frac{dE}{dt} = E [A - D(N + E) - sB],$$

where A, B, D are positive constants and $s < 1$ is a measure of the difference in mortality of the two species. Nondimensionalise the system and describe the meaning of any dimensionless parameters. Show that the populations N and C are related by

$$N(t) \propto C(T) \exp[-B(1-s)t].$$

Hence give the order of magnitude of the time for Neanderthal extinction.

If the lifetime of an individual is roughly 30 to 40 years and the time to extinction is (from the palaeontological data) 5000 to 10,000 years, determine the range of the mortality difference parameter s . [An independent estimate (Flores 1998) is of $s = 0.995$.]

Construct a competition model for this situation using the model system in Section 3.5 with equal carrying capacities and linear birth rates in the absence of competition but with slightly different competition efficiencies. Determine the conditions under which Neanderthal man will become extinct and the conditions under which the two species could coexist.

- 3 Determine the kind of interactive behaviour between two species with populations N_1 and N_2 that is implied by the model

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left[1 - \frac{N_1}{K_1 + b_{12} N_2} \right], \\ \frac{dN_2}{dt} &= r_2 N_2 \left[1 - \frac{N_2}{K_2 + b_{21} N_1} \right].\end{aligned}$$

Draw the null clines and determine the steady states and their stability. Briefly describe the ecological implications of the results of the analysis.

- 4 A predator-prey model for herbivore (H)-plankton (P) interaction is

$$\frac{dP}{dt} = rP \left[(K - P) - \frac{BH}{C + P} \right], \quad \frac{dH}{dt} = DH \left[\frac{P}{C + P} - AH \right],$$

where r, K, A, B, C and H are positive constants. Briefly explain the ecological assumptions in the model. Nondimensionalise the system so that it can be written in the form

$$\frac{dp}{d\tau} = p \left[(k - p) - \frac{h}{1 + p} \right], \quad \frac{dh}{d\tau} = dh \left[\frac{p}{1 + p} - ah \right].$$

Sketch the null clines and note any qualitative changes as the parameter k varies. Hence, or otherwise, demonstrate that a positive steady state (p_0, h_0) exists for all $a > 0, k > 0$.

By considering the community matrix determine the signs of the partial derivatives of the right-hand sides of the equation system evaluated at (p_0, h_0) for this steady state to be stable. By noting the signs of $dp/d\tau$ and $dh/d\tau$ relative to the null clines in the p, h phase plane, show that (i) for $k < 1$ the positive steady state is stable and (ii) that for $k > 1$, and small enough a , the positive steady state may be stable or unstable. Hence show that in the a, k parameter plane a necessary condition for a periodic solution to exist is that a, k lie in the domain bounded by $a = 0$ and $a = 4(k - 1)/(k + 1)^3$. Hence show that if $a < 4/27$ there is a window of values of k where periodic solutions are possible. Under what conditions can the system exhibit a threshold phenomenon?

- 5 The interaction between two populations with densities N_1 and N_2 is modelled by

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1 \left(1 - \frac{N_1}{K} \right) - aN_1 N_2 (1 - \exp[-bN_1]), \\ \frac{dN_2}{dt} &= -dN_2 + N_2 e(1 - \exp[-bN_1]),\end{aligned}$$

where a, b, d, e, r and K are positive constants. What type of interaction exists between N_1 and N_2 ? What do the various terms imply ecologically?

Nondimensionalise the system by writing

$$u = \frac{N_1}{K}, \quad v = \frac{aN_2}{r}, \quad \tau = rt, \quad \alpha = \frac{e}{r}, \quad \delta = \frac{d}{r}, \quad \beta = bK.$$

Determine the nonnegative equilibria and note any parameter restrictions. Discuss the linear stability of the equilibria. Show that a nonzero N_2 -population can exist if $\beta > \beta_c = -\ln(1 - \delta/\alpha)$. Briefly describe the bifurcation behaviour as β increases with $0 < \delta/\alpha < 1$.

- 6 The sterile insect release method (SIRM) for pest control releases a number of sterile insects into a population. If a population n of sterile insects is maintained in a population, a possible simple model for the population of fertile insects $N(t)$ is

$$\frac{dN}{dt} = \left[\frac{aN}{N+n} - b \right] N - kN(N+n),$$

where $a > b > 0$ and $k > 0$ are constant parameters. Briefly discuss the assumptions which lie behind the model.

Determine the critical number of sterile insects n_c which would eradicate the pests and show that this is less than a quarter of the environmental carrying capacity.

Suppose that a single release of sterile insects is made and that the sterile insects have the same death rate as fertile insects. Write down the appropriate model system for $N(t)$ and $n(t)$ and show that it is not possible to eradicate the insect pests with a single release of sterile insects.

If a fraction γ of the insects born are sterile, a suggested model is

$$\frac{dN}{dt} = \left[\frac{aN}{N+n} - b \right] N - kN(N+n), \quad \frac{dn}{dt} = \gamma N - bn.$$

Determine the condition on γ for eradication of the pest and briefly discuss the realism of the result.

- 7 A general form for models for insect predator (P)-prey (N), or insect parasitism is

$$N_{t+1} = rN_t f(N_t, P_t), \quad P_{t+1} = N_t [1 - f(N_t, P_t)],$$

where f is a nonlinear function which incorporates assumptions about predator searching, and $r > 0$ is the rate of increase of prey population. The scaling is such that $0 < f < 1$. Here f is an increasing function as N_t increases, and a decreasing function as P_t increases. Does this model make sense ecologically?

Show that a positive equilibrium state (N^*, P^*) can exist and give any conditions on r required. Show that the linear stability of the steady state is ensured if the roots of

$$x^2 - \left[1 + rN^* \frac{\partial f}{\partial N_t} - N^* \frac{\partial f}{\partial P_t} \right] x - rN^* \frac{\partial f}{\partial P_t} = 0$$

have magnitudes less than 1, where $\partial f/\partial N_t$ and $\partial f/\partial P_t$ are evaluated at (N^*, P^*) , and hence determine the conditions for linear stability.

- 8 A model for the regulation of a host population by a microparasite population u_t which was proposed and studied by May (1985) is, in dimensionless form,

$$1 - I_t = \exp[-I_t u_t], \quad u_{t+1} = \lambda u_t (1 - I_t),$$

where $\lambda > 0$ and I_t denotes the fraction of the host population which has been infected by the time the epidemic has run its course. The assumption in this specific form is that the parasite epidemic has spread through each generation before the next population change. [This is why the host population equation does *not* involve I_{t+1} .] Determine the steady states and note any restrictions on λ for a positive steady state to exist for both the host and microparasite populations. Investigate the linear stability of the positive steady state. Show that it is *always* unstable and that the instability arises via a pitchfork bifurcation.

[May (1985) studies this model in depth and shows that the positive steady state and *all* periodic solutions are unstable; that is, the model only exhibits chaotic behaviour without going through the usual period doubling. He also discusses the epidemiological implications of such a simple, yet surprising, system.]

4. Temperature-Dependent Sex Determination (TSD): Crocodilian Survivorship

4.1 Biological Introduction and Historical Asides on the Crocodilia

It is a fascinating subject why some species become extinct and others do not. Why, for example, have the three families of crocodilia (alligators, crocodiles and gavials) not become extinct during the past 100 million or so years? They have survived essentially unchanged for around 63 million years after the dinosaurs became extinct and clearly have great survival powers. As pointed out by Benton (1997), however, those that have survived are only a small group of around the 150 fossil genera of crocodilians that have been documented. Crocodiles and alligators were around in the later part of the Cretaceous (63 to 135 million years ago). As several have noted, such as Benton (1997), they were very much more widespread than they are now, with fossils found as far north as Sweden and Canada. Colbert and Morales (1991) point out that the late Cretaceous was the peak of their evolution with the largest genus being the *Deinosuchus* with the most impressive jaws of any reptiles of the period: one fossil had a skull 6 feet in length which suggests it must have had a total length of 40 to 50 feet—certainly a predator to take notice of. Carroll (1988) suggests that the decline of the genera was probably due to climatic deterioration from around the beginning of the Cenozoic (63 million years ago) era. In spite of the massive extinctions, the families that have survived are rightly viewed as living fossils. Meyer (1984) gives a general overview of them while Pooley and Gans (1976) focus on the Nile crocodile and describe, among other things, its unique biology and social behaviour which have contributed so much to its long survival.

Over the millennia the crocodilia have been vilified like no other animal and the wildest stories associated with them abound. The description of Leviathan in the Old Testament (Job 41:1–34) is just a start. It is clearly the prototype dragon. It was regularly used to scare children in the 19th century and no doubt earlier. One example is in the *Sunday School Advocate* (Volume XVII, January 22, 1888) where it is described as

‘This hideous monster. . . it is an ugly creature—a huge river dragon . . .’

The article concludes:

‘But though this scaly monster does not haunt the rivers of the North, yet there is another great dragon ever prowling. . . It is more terrible than the alligator. . . The name of this monster is Sin!’