

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

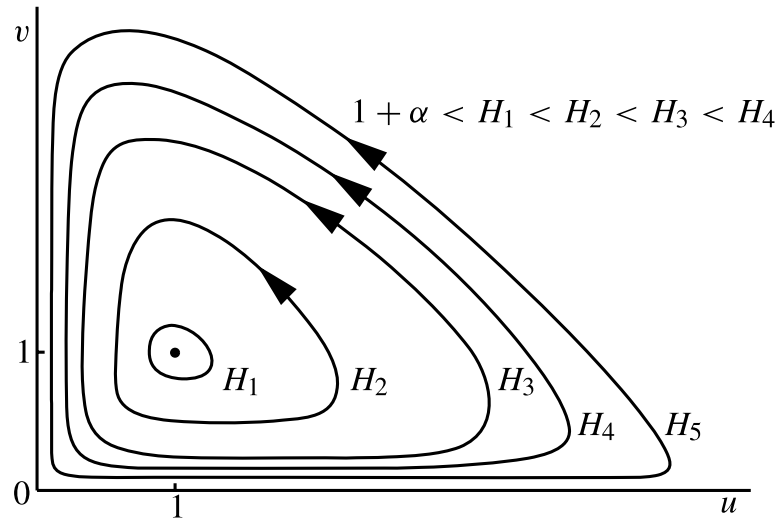


Figure 3.1. Closed (u, v) phase plane trajectories, from (3.6) with various H , for the Lotka–Volterra system (3.4): $H_1 = 2.1$, $H_2 = 2.4$, $H_3 = 3.0$, $H_4 = 4$. The arrows denote the direction of change with increasing time τ .

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

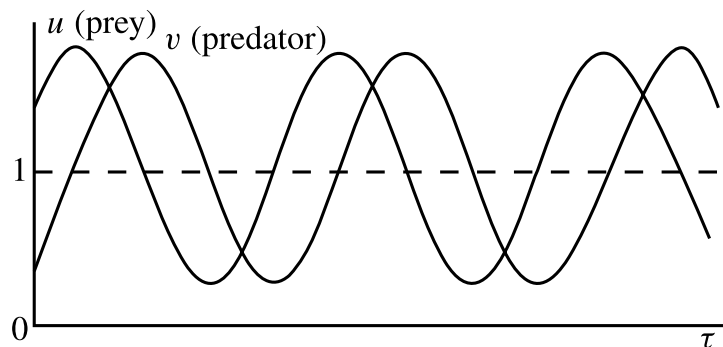


Figure 3.2. Periodic solutions for the prey $u(\tau)$ and the predator $v(\tau)$ for the Lotka–Volterra system (3.4) with $\alpha = 1$ and initial conditions $u(0) = 1.25$, $v(0) = 0.66$.

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

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

$$\frac{dN_i}{dt} = N_i \left[a_i - \sum_{j=1}^k b_{ij} P_j \right] \quad i = 1, \dots, k \quad (3.10)$$

$$\frac{dP_i}{dt} = P_i \left[\sum_{j=1}^k c_{ij} N_j - d_i \right],$$

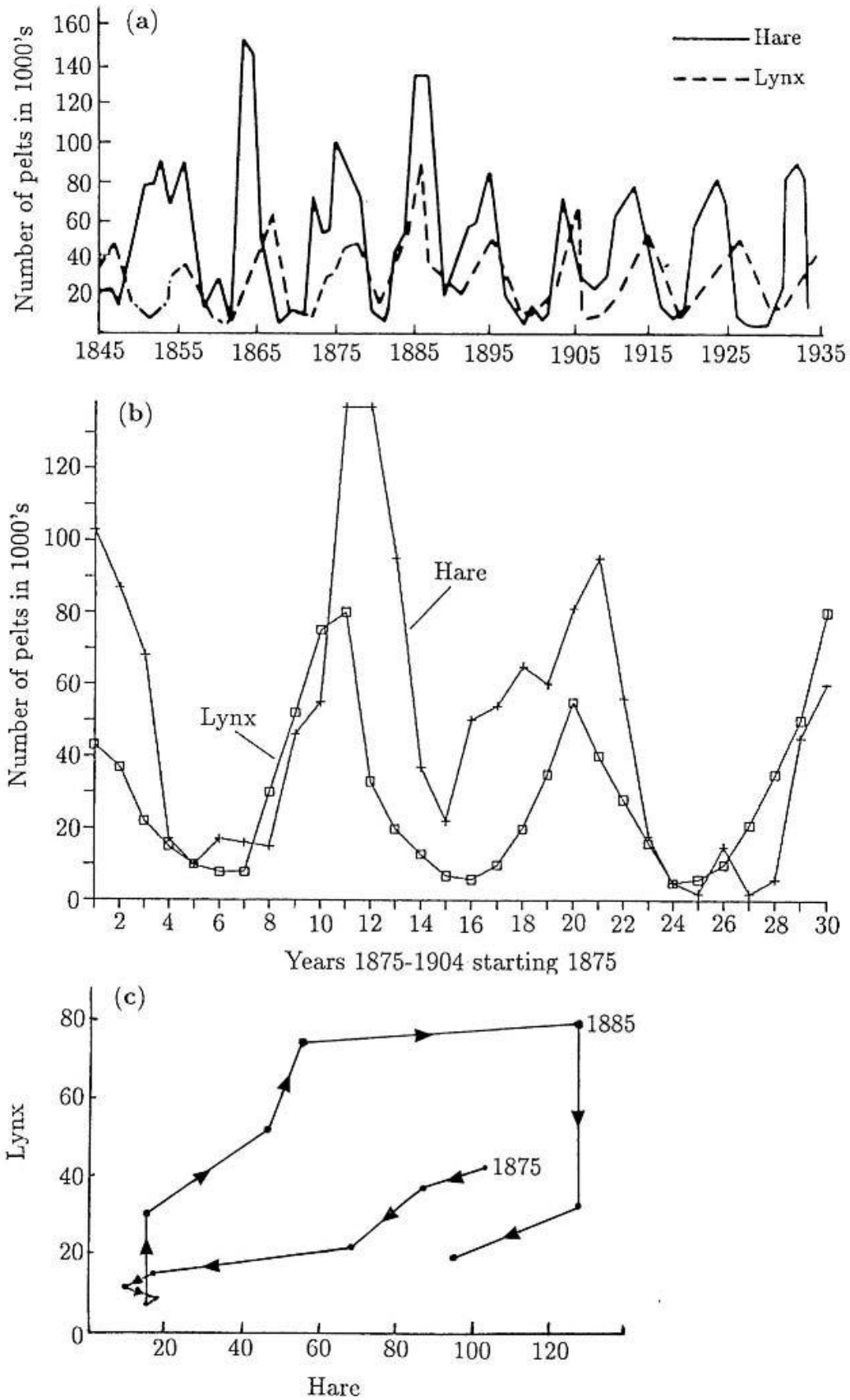


Figure 3.3. (a) Fluctuations in the number of pelts sold by the Hudson Bay Company. (Redrawn from Odum 1953) (b) Detail of the 30-year period starting in 1875, based on the data from Elton and Nicholson (1942). (c) Phase plane plot of the data represented in (b). (After Gilpin 1973)

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

$$A = \left(\begin{array}{cc|cc} a_1 & 0 & & \\ & \ddots & & \\ 0 & & a_k & \\ \hline & & & -d_1 & 0 \\ & 0 & & & \ddots \\ & & & 0 & & -d_k \end{array} \right).$$

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

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

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

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

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 $(\mathbf{N}^*, \mathbf{P}^*)$ 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 $(\mathbf{N}^*, \mathbf{P}^*)$ 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

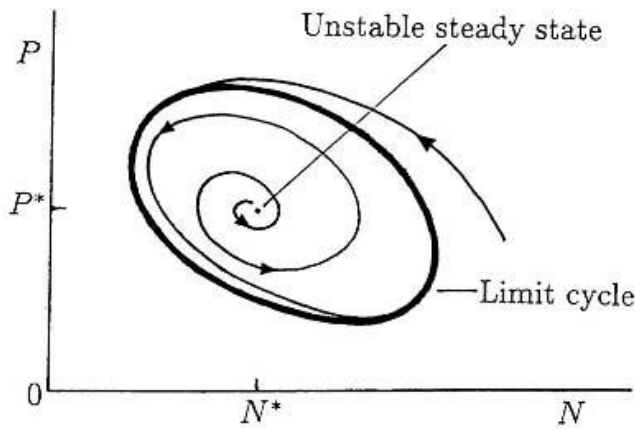


Figure 3.4. Typical closed predator–prey trajectory which implies a limit cycle periodic oscillation. Any perturbation from the limit cycle tends to zero asymptotically with time.

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

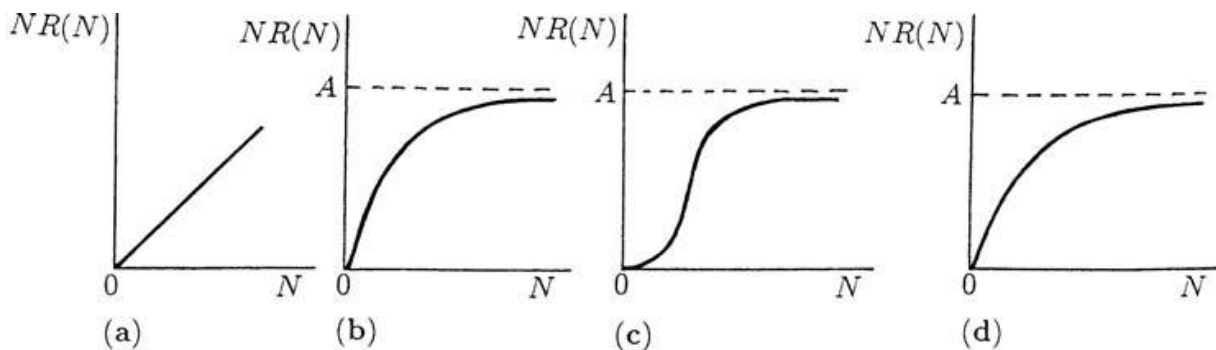


Figure 3.5. Examples of predator response $NR(N)$ to prey density N . (a) $R(N) = A$, the unsaturated Lotka–Volterra type. (b) $R(N) = A/(N + B)$. (c) $R(N) = AN/(N^2 + B^2)$. (d) $R(N) = A(1 - e^{-aN})/N$.

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

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

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

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

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

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

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

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

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

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

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

A , the community matrix, has eigenvalues λ given by

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

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

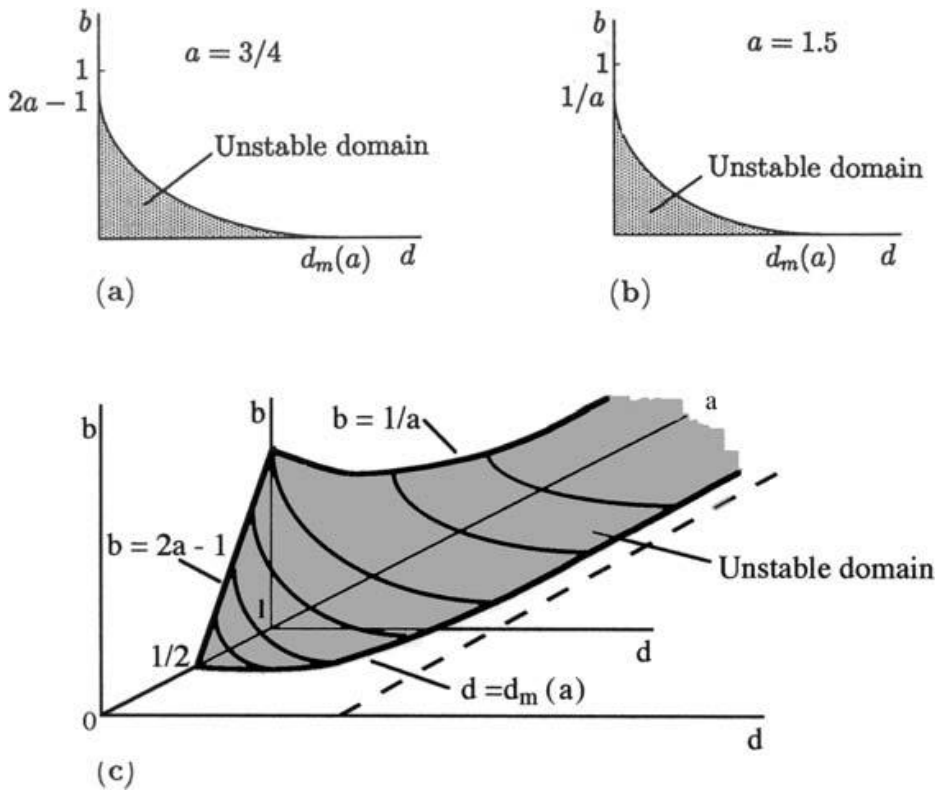


Figure 3.6. Parameter domains (schematic) of stability of the positive steady state for the predator–prey model (3.20). For $a < 1/2$ and all parameter values $b > 0, d > 0$, stability is obtained. For a fixed $a > 1/2$, the domain of instability is finite as in (a) and (b). The three-dimensional bifurcation 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.

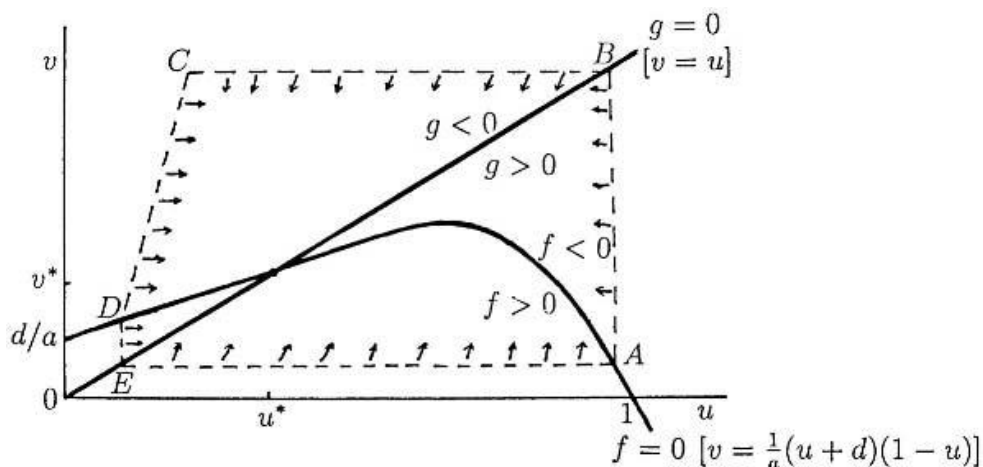


Figure 3.7. Null clines $f(u, v) = 0, g(u, v) = 0$ for the system (3.20); note the signs of f and g on either side of their null clines. $ABCDEA$ is the boundary of the confined set about (u^*, v^*) on which the trajectories all point inwards; that is, $\mathbf{n} \cdot (du/d\tau, dv/d\tau) < 0$ where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

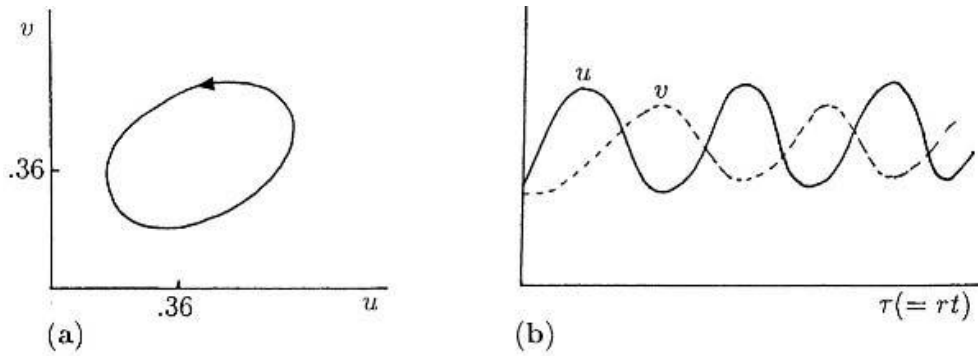


Figure 3.8. (a) Typical phase trajectory limit cycle solution for the predator–prey system (3.20). (b) Corresponding periodic behaviour of the prey (u) and predator (v) populations. Parameter values: $a = 1, b = 5, d = 0.2$, which give the steady state as $u^* = v^* = 0.36$. Relations (3.19) relate the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

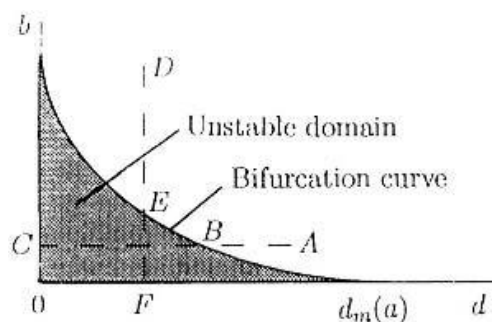


Figure 3.9. Typical stability bifurcation curve for the predator–prey model (3.20). As the point in parameter space crosses the bifurcation curve, the steady state changes stability.