Devashish Chaudhari - MA21BTECH11005
Roshan Kumar - MA21BTECH11013

Introduction

Aim of the project: To build a mathematical model of an epidemic.

The increasing study of realistic and practically useful mathematical models in population biology, e.g., human population, population of an endangered species, bacterial or viral growth and so on, is a reflection of their use in helping to understand the dynamic processes involved and in making practical predictions.
Ecology, the study of the interrelationship between species and their environment, in areas such as predator–prey and competition interactions, evolution of pesticide resistant strains, multi-species societies, plant–herbivore systems and so on is now an enormous field. The continually expanding list of applications is extensive. There are also highly practical applications of single-species models in the biomedical sciences.

Continuous Population Models for Single Species

The simplest model for a single-species population can be

$$\frac{dN}{dt} = \text{births} - \text{deaths} + \text{migration},$$

Malthusian growth model:

Thomas Malthus proposed this model 1798, where no migration is considered and the birth and death terms are proportional to N.
That is,

$$\frac{dN}{dt} = bN - dN \quad \Rightarrow \quad N(t) = N_0 e^{(b-d)t},$$

where b, d are positive constants and the initial population $N(0) = N_0$. Thus if b > d

the population grows exponentially while if b < d it dies out. This model is pretty unrealistic. (Though the human population has grown exponentially since 1900)

In the long run, such exponential growth does not make sense and there must be a self-limiting process which would operate when the population becomes too large.

Logistic growth model:

The model was proposed by Verhulst between 1838-45.

$$\frac{dN}{dt} = rN(1 - N/K), \tag{1.2}$$

Here r and K are positive constants. In this model, the rate of change of population per capita is $r(1 - N/K)$; that is, it is dependent on N. Here r signifies the linear birth rate and the constant K is the **carrying capacity** of the environment, which is usually determined by the available sustaining resources.

Analysis of equilibrium/steady states:
These are the states where dN/dt = 0. For the above model, this happens at N = 0 and N = K. To check their stability, we use linearization about them,

- N = 0
  To analyze the stability around this equilibrium point, we consider small perturbations away from N=0, represented by N=ϵ, where ϵ is a small positive value.

  Substituting N=ϵ into the logistic growth equation, we get:

  $$dN/dt = r\epsilon(1 - \epsilon/K)$$

  Using a Taylor expansion, retaining terms up to linear order in ϵ:

  $$dN/dt \approx r\epsilon(1 - \epsilon/K)$$
  $$dN/dt \approx r\epsilon - r\epsilon^2/K$$

  As ϵ is small, ϵ^2/K is even smaller, so we can neglect it compared to ϵ. Therefore:

  $$dN/dt \approx r\epsilon$$

This shows that the rate of change of population size is approximately proportional to the perturbation ϵ away from the equilibrium point N=0, with a positive sign indicating that it leads to exponential growth away from the equilibrium point.

Thus, linearization around N=0 suggests instability, as any small perturbation away from N=0 results in exponential growth rather than returning to the equilibrium point.

- N = K
  To analyze the stability around this equilibrium point, we consider small perturbations away from N=K, represented by N=K+ϵ, where ϵ is a small positive value.

  Substituting N=K+ϵ into the logistic growth equation, we get:

$$dN/dt = r(K + \epsilon)(1 - (K + \epsilon)/K)$$

Using a Taylor expansion, retaining terms up to linear order in ϵ:

$$dN/dt \approx r(K + \epsilon)(1 - K/K - \epsilon/K)$$
$$dN/dt \approx r(K + \epsilon)(1 - 1 - \epsilon/K)$$
$$dN/dt \approx r(K + \epsilon)(-\epsilon/K)$$
$$dN/dt \approx - r(K + \epsilon)(\epsilon/K)$$
$$dN/dt \approx - r\epsilon(1 + \epsilon/K)$$

As ϵ is small, ϵ/K is even smaller. So, we can neglect terms of order ϵ/K or higher. This simplifies the expression to:

$$dN/dt \approx - r\epsilon$$

This shows that the rate of change of population size is approximately proportional to the perturbation ϵ away from the equilibrium point N=K, with a negative sign indicating that it acts as a restoring force, pulling the population back towards the equilibrium point.
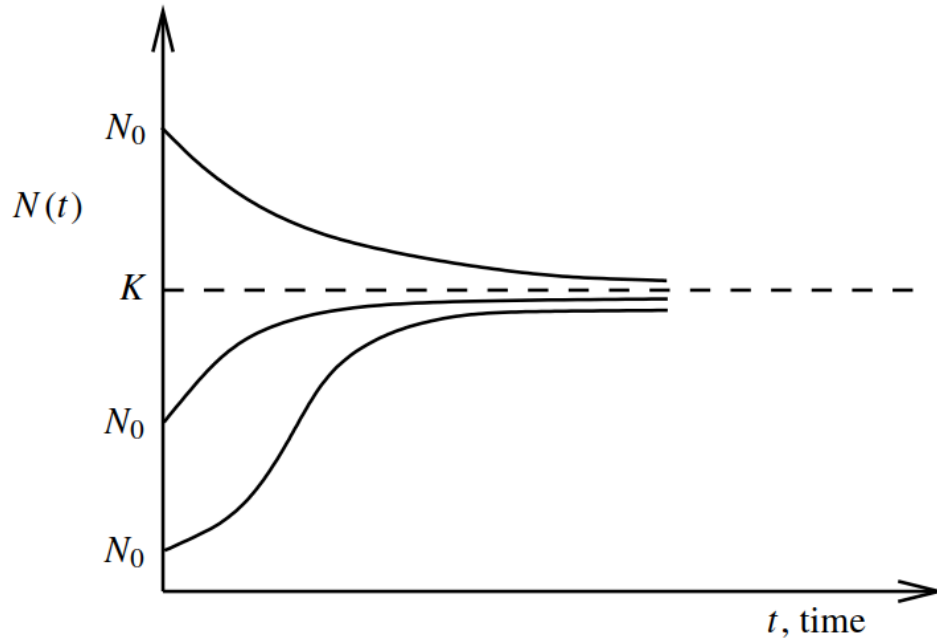
Thus, linearization around N=K suggests stability, as any deviation from this equilibrium point results in a restorative force that pushes the population back towards N=K, ensuring stability over time.

Solution of the logistic growth model is:

$$N(t) = \frac{N_0 K e^{rt}}{\left[K + N_0\left(e^{rt} - 1\right)\right]} \quad \to K \quad \text{as} \quad t \to \infty, \tag{1.3}$$

where $N(0) = N_0$

Plot of the solution:

From the model, we can see that if $N_0 > K$, N(t) should decrease monotonically to K while for $N_0 < K$, it should increase monotonically to K. In the 2nd case, two different nature of the graph are possible, depending on the value of N_0. ($N_0 = K/2$ is a critical point for dN/dt) For $N_0 < K/2$, the curve has a sigmoid nature.

General growth equation:

$$\frac{dN}{dt} = f(N), \tag{1.4}$$

Typically, f(N) is a nonlinear function. Let N* be equilibrium points, i.e., solutions of f(N) = 0. An equilibrium point is stable if f'(N*) < 0, and unstable if f'(N*) > 0. We can confirm this by using linearization around N* as,

$$n(t) \approx N(t) - N^*, \quad |n(t)| \ll 1$$

Then, the equation 1.4 becomes,

$$dN/dt = f(N^* + n) \approx f(N^*) + nf'(N^*) + \cdots$$
$$\approx nf'(N^*)$$
$$\Rightarrow n(t) \propto \exp[f'(N^*)\,t]$$

So n grows or decays accordingly as f'(N*) > 0 or f'(N*) < 0. The timescale of the response of the population to a disturbance is of the order of 1/| f'(N∗) |; it is the time to change the initial disturbance by a factor e.

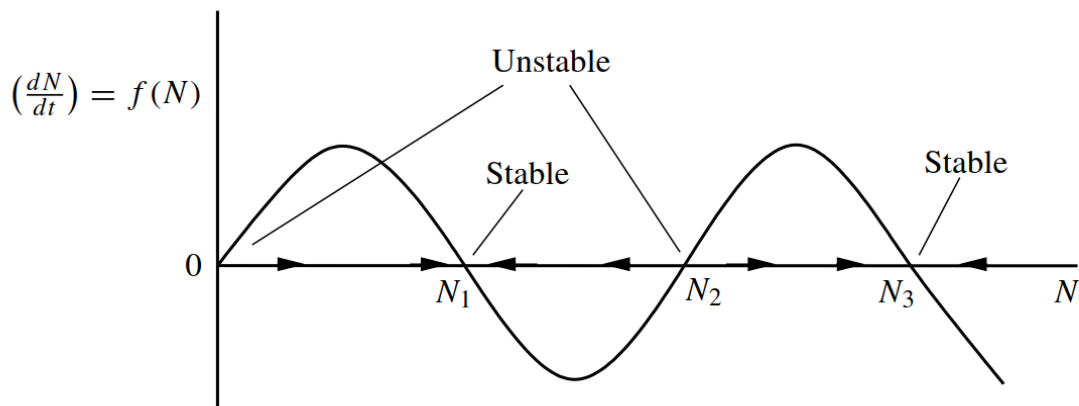Understanding the stability of equilibrium points is much easier graphically. Take for example the below plot,

Figure 1.3. Population dynamics model $dN/dt = f(n)$ with several steady states. The gradient $f'(N)$ at the steady state, that is, where $f(N) = 0$, determines the linear stability.

Wherever the curve intersects the X-axis is an equilibrium point. The sign of the slope of the curve tells us about the stability.
Also, the points are stable only as long as the perturbations are below a threshold. For example, here N1 and N3 are stable steady states. If the perturbation from N1 is more than N2-N1 on the right side, then N(t) would converge to N3 instead of returning to N1.

Insect Outbreak Model: Spruce Budworm

This model was given by Ludwig in 1978, trying to model the population of Budworms in Canada. They have a predator in the form of birds, so this model also keeps that in consideration.

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B}\right) - p(N).$$

The 1st term is basically the same as the logistic growth model, the p(N) term refers to the predation of the worms.

The qualitative form of p(N) is important and is illustrated in Figure 1.4. Predation usually saturates for large enough N. There is an approximate **threshold value Nc**, below which the predation is small, while above it the predation is close to its saturation value: such a functional form is like a switch with Nc being the critical switch value. For small population densities N, the birds tend to seek food elsewhere and so the predation term p(N) drops more rapidly, as N → 0, than a linear rate proportional to N.

We will focus on the form suggested by Ludwig.

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B}\right) - \frac{BN^2}{A^2 + N^2}. \tag{1.6}$$

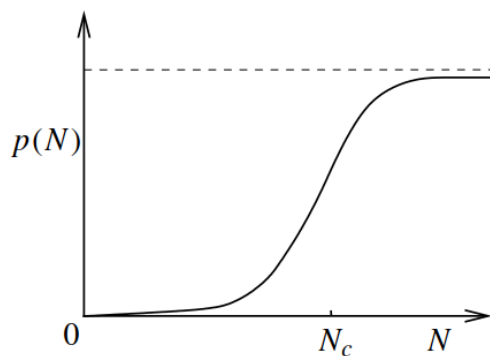A, B are positive constants. A is a measure of Nc.

Figure 1.4. Typical functional form of the predation in the spruce budworm model; note the sigmoid character. The population value N_c is an approximate threshold value. For $N < N_c$ predation is small, while for $N > N_c$, it is 'switched on.'

Nondimensionalization

We use this in the analysis of a model, to free it from uncertainty of units and to reduce the number of relevant parameters to dimensionless groupings which determine the dynamics.

For any model, there are usually several different nondimensionalisations possible. The dimensionless groupings depend on the aspects we want to investigate.

We apply nondimensionalization in insect outbreak model as following,

$$u = \frac{N}{A}, \quad r = \frac{Ar_B}{B}, \quad q = \frac{K_B}{A}, \quad \tau = \frac{Bt}{A} \qquad (1.7)$$

which on substituting into (1.6) becomes

$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2} = f(u; r, q), \qquad (1.8)$$

Analyzing the steady states (the equilibrium points):

$$f(u; r, q) = 0 \quad \Rightarrow \quad ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2} = 0. \qquad (1.9)$$

One solution is u = 0, the other solutions satisfy

$$r\left(1 - \frac{u}{q}\right) = \frac{u}{1+u^2}. \qquad (1.10)$$

This is a cubic in u. (Note- we are focusing on u because it signifies N) For some fixed q, there can be either one or three solutions depending on the value of r (same for fixed r, varying q).

We can see that f'(u=0) > 0, so u = 0 is unstable. If there is only one other root, call u1, then it will be stable. If there are three more roots, call u1, u2, u3, then u1, u3 will be stable and u2 will be unstable steady states.
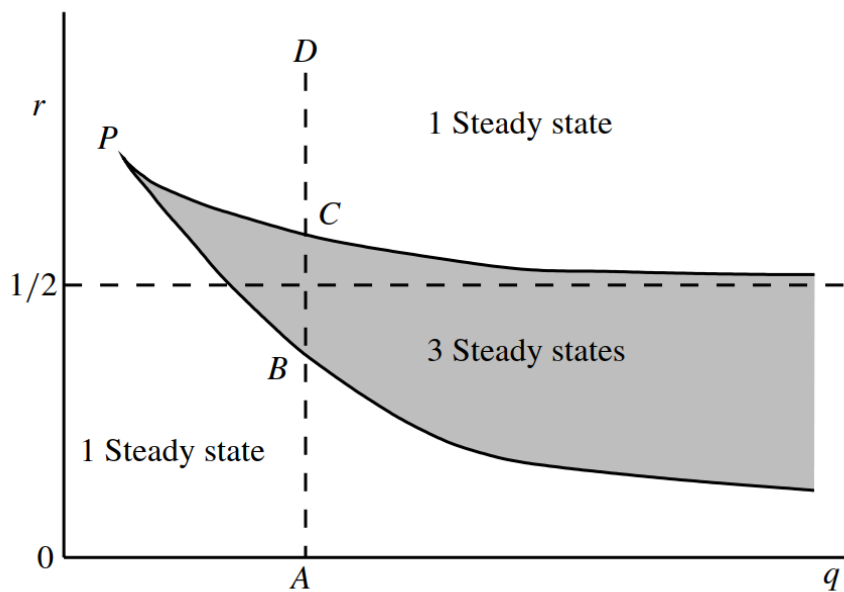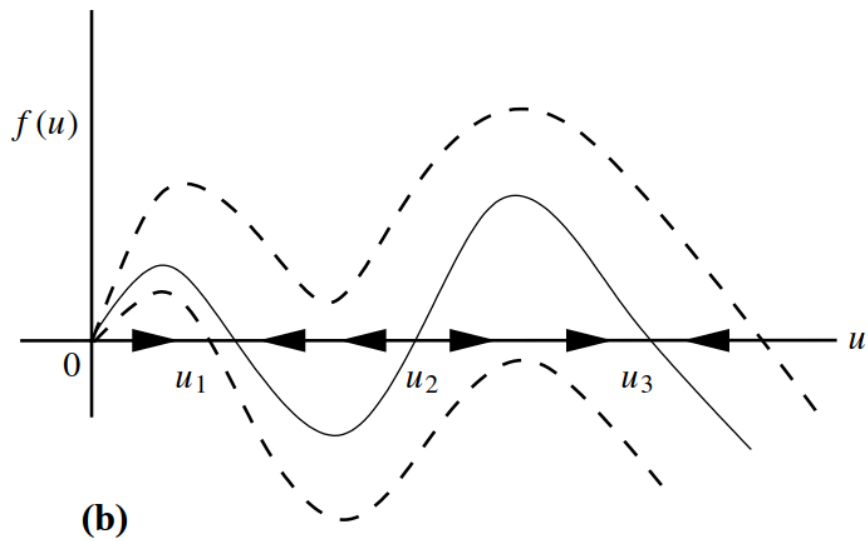
(b)

Figure 1.6. Parameter domain for the number of positive steady states for the budworm model (1.8). The boundary curves are given parametrically (see Exercise 1) by $r(a) = 2a^3/(a^2 + 1)^2$, $q(a) = 2a^3/(a^2 - 1)$ for $a \geq \sqrt{3}$, the value giving the cusp point P.
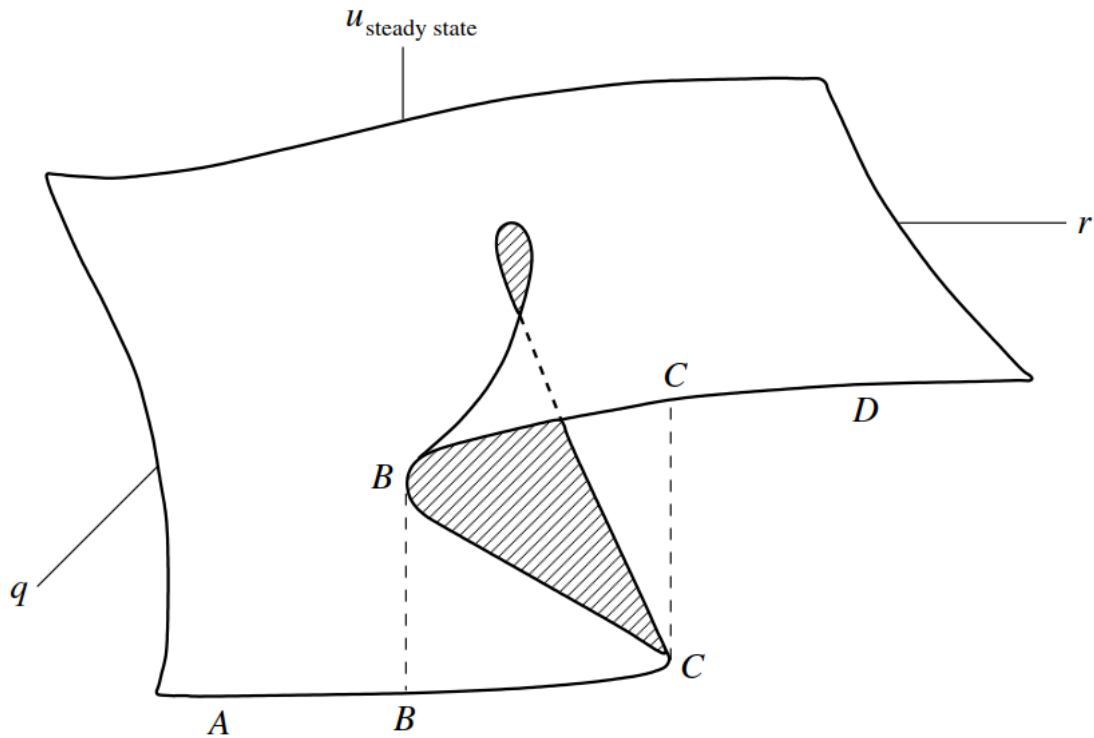
Cusp catastrophe:

Figure 1.7. Cusp catastrophe for the equilibrium states in the $(u_{\text{steadystate}}, r, q)$ parameter space. As r increases from A, the path is $ABCCD$ while as r decreases from D, the path is $DCBBA$. The projection of this surface onto the r, q plane is given in Figure 1.5. Three equilibria exist where the fold is.

As r increases along ABCD there is a discontinuous jump up at C while as r decreases from D to A there is a discontinuous jump down at B. (refer fig 1.6)

This is an example of a ***cusp catastrophe***, shown in Figure 1.7 where the letters A, B,C and D correspond to those in Figure 1.6. Note that Figure 1.6 is the projection of the surface onto the r,q plane with the shaded region corresponding to the fold.

(The smaller steady state u1 is the refuge equilibrium while u3 is the outbreak equilibrium)

Catastrophes in perception:

This section talks about sudden changes in visual perception.

Figure 1.8. Series of pictures exhibiting abrupt (catastrophic) visual change during the variation from a man's face to a sitting woman. (After Fisher 1967)

An experiment which demonstrates the sudden jump from seeing the face of a man to the picture of the woman was described by Zeeman (1982).

The experiment consisted of showing the series three times starting with the man's face, picture 1, going up to the woman, picture 8, then reversing the sequence down to 1 and again in ascending order. The students were told to write down the numbers where they noticed a major change in their perception.

The predictions were that during the first run through the series, that is, from 1 to 8, the perception of most of the audience would be locked into the figure of the face until it became obvious that the picture was in fact a woman at which stage there would be sudden jump in perception. As the pictures were shown in the reverse order the audience was now aware of the two possibilities and so could make a more balanced judgement as to what a specific picture represented. The perception change would therefore more likely occur nearer the middle, around 5 and 4. During the final run through the series the change would again occur near the middle. *This matched the results of the experiment.*

Comparing this with budworms' hysteresis, there is a fundamental difference. In the latter there is a definite and reproducible hysteresis while in the former this hysteresis effect occurs only once after which the dynamics is single valued for each stimulus.
(The hysteresis effect refers to a phenomenon where the response of the population to environmental conditions exhibits a delay or lag, often due to the interplay of multiple factors such as resource availability, predator-prey dynamics, and reproductive behavior.)

Models for interacting populations

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.

E.g. - lions hunting deers

(ii) If the growth rate of each population is decreased then it is competition.

E.g. - competition between lions and tigers for food

(iii) If each population's growth rate is enhanced then it is called mutualism or symbiosis.

E.g. - flowering plants and pollinators

Predator-prey models: Lotka-Volterra systems

If N(t) is the prey population and P(t) that of the predator at time t then Volterra's model is,

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

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

a,b,c,d are positive constants.

There are several assumptions in this model, such as -

(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.

To analyze the model, we again apply nondimensionalization the system by writing

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

and it becomes

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

Solving these equations analytically leads us to

$$\alpha u + v - \ln u^{\alpha} v = H, \qquad\qquad (3.6)$$

where H > Hmin is a constant: Hmin = 1 + α is the minimum of H over all (u,v) and it occurs at u = v = 1. For a given H > 1 + α, the trajectories (3.6) in the u-v plane are closed.
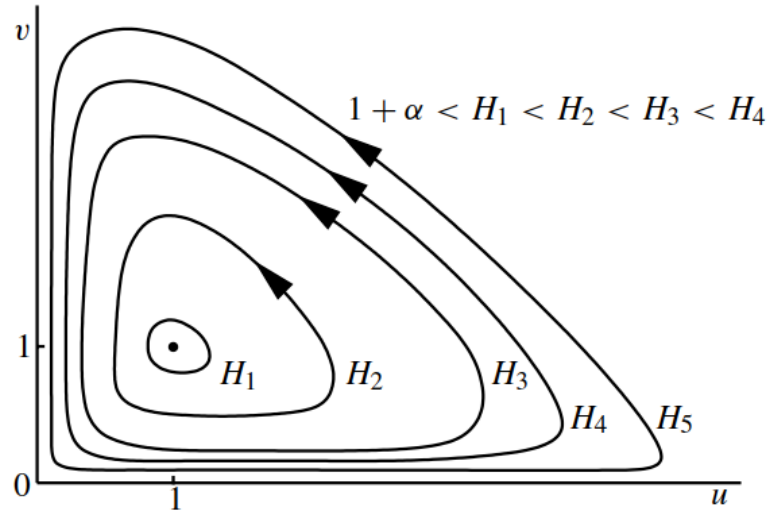

Figure 3.1. Closed (u, v) phase plane trajectories, from (3.6) with various H, for the Lotka–Volterra system (3.4): $H_1 = 2.1$, $H_2 = 2.4$, $H_3 = 3.0$, $H_4 = 4$. The arrows denote the direction of change with increasing time τ.

The initial conditions, u(0) and v(0), determine the constant H in (3.6) and hence the phase trajectory in Figure 3.1.

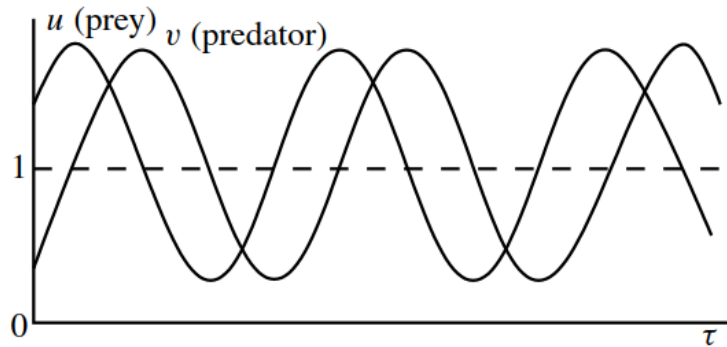Closed trajectories in u-v plane implies periodic solutions in τ for u and v.

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 $u(0) = 1.25$, $v(0) = 0.66$.

Limitation of Lotka-Volterra model:

From Figure 3.1, we can see that 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 H4 which passes close to the u and v axes. Then any small perturbation will move the solution onto another trajectory which is not close to the original H4 everywhere. Thus a small perturbation can have a very marked effect, at the very least on the amplitude of the oscillation.

Steady state analysis:

In 3.4, we can see that the common solutions are (0,0) and (1,1). These are called singular points. Linearisation about the singular points determines the type of singularity and the stability of the steady states.

- Around (0,0) -
  If x and y are small perturbations around (0,0), then 3.4 becomes

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

  The solution of which is of the form

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

  where B is an arbitrary constant column vector. The eigenvalues of the matrix A, λ, are 1 and $-\alpha$.
  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.

- Around (1,1) -
  x and y are small perturbations around (1,1), i.e., u = 1+x, v = 1+y. (3.4) becomes

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

with eigenvalues λ given by

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

The solution 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 l and m are eigenvectors.
Since Re(λ) = 0 the steady state is neutrally stable.
Since the eigenvalues are purely imaginary, (1,1) is a centre singularity.

The solutions in the neighbourhood of the singular u = v = 1 are periodic in τ with period $2\pi/\sqrt{\alpha}$. In dimensional terms from (3.3), this period is T = $2\pi\sqrt{(a/d)}$, i.e., 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.

In 3.7, 3.8, A is called the community matrix. The stability depends on its eigenvalues. If Re λ > 0 then the steady state is unstable while if both Re λ < 0 it is stable. The critical case Re λ = 0 is termed neutral stability.

Lotka-Volterra model, when applied to Canadian lynx–snowshoe hare interaction, did not give intuitive results, rather suggested that hares were eating the lynx. Gilpin (1973) gave a possibly correct explanation, that when hare population was more, the fur trappers may have hunted lynx (more profitable than hare), and would have found other jobs when hare population was low.

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.

Generalizing to multiple prey and predator species:

consider the generalized Lotka–Volterra predator–prey system with k prey species and k predators, which prey on all the prey species but with different severity.
Then our model looks like

$$\frac{dN_i}{dt} = N_i \left[a_i - \sum_{j=1}^{k} b_{ij} P_j \right]$$

$$i = 1, \ldots, k \qquad\qquad (3.10)$$

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

Stability analysis:

- This system has a trivial steady state with $N_i = P_i = 0$ for all i.

   The community matrix in this case will be a diagonal matrix, and hence, the 2k eigenvalues are

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

Since some eigenvalues are positive, the steady state is unstable.

- Another steady state is the column vector solution N*, P*, given by

$$\mathbf{BP^* = a, \ CN^* = d}$$

   a, d are column vectors, B, C are k*k matrices.

   Linearizing about the steady state, and finding the eigenvalues of the community matrix A, we get that *sum of them = 0.*

   Since the elements of A are real, the eigenvalues, if complex, occur as complex conjugates. Thus there are two cases: all the eigenvalues are purely imaginary or they are not.
   - If all Re λi = 0 then the steady state (N*,P*) is neutrally stable as in the 2-species case.
   - If there are λi such that Re λi ≠ 0 then, since they occur as complex conjugates, at least one exists with Re λ > 0 and hence (N*,P*) is unstable.

Comparing this with the 2-species case, we see that in the non-trivial steady state, a possibility of instability has come up. We conclude a fairly general and important result that **'complexity usually results in instability rather than stability.'**

Limit cycle -

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.

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 will not be discussed.
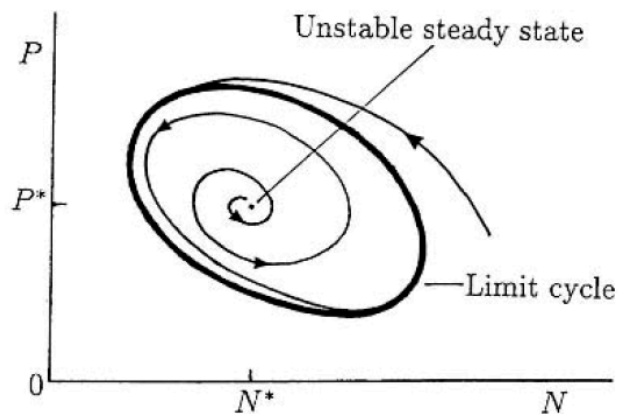

Figure 3.4. Typical closed predator–prey trajectory which implies a limit cycle periodic oscillation. Any perturbation from the limit cycle tends to zero asymptotically with time.

Realistic Predator-Prey models:

Some of the changes to lotka-volterra model can be-
1) Prey would have a logistic growth and not the unbounded Malthusian in absence of predators.
2) The predation term, which is the response of the predator to some change in the prey density, should show saturation, as a reflection of the limited predator capability.
    Can be achieved by using PNR(N), where NR(N) saturates for N large, instead of bNP, as in the Lotka–Volterra model.