

## Non-Linear Models

- Focus on more sophisticated interaction models between systems.
- These lead to *non-linear*, rather than linear, DEs; often not soluble exactly in analytical form so use *Phase-Plane Analysis*.
- This is a method where a system of DEs is reduced to a single DE, e.g.

$$\frac{dx}{dt} = f(x, y) \tag{5.13}$$

$$\frac{dy}{dt} = g(x, y)$$

for some non-linear functions  $f, g$ , is written in terms of  $x, y$  only.

- Resulting curves plotted in  $(x, y)$  plane are known as *phase-plane trajectories*.

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## Non-Linear Models Cont'd

- This section considers three types of interaction models:
  - 1 Mutually destructive interaction,
  - 2 Interaction beneficial to one or the other species,
  - 3 Mutually beneficial interaction (symbiosis)
- Then we proceed to the modelling of infectious diseases.

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## Non-Linear Models Cont'd: Guerrilla Combat

### The Guerrilla Combat Model

- Can model Combat btw occupying & guerrilla force (with some assumptions) as 2 coupled DEs.
- Combat models used to understand what factors affect battle outcomes e.g. how many occupying needed for victory.
- Let number of 'friendly' soldiers be  $x$  & 'enemy' (i.e. guerrilla forces) be  $y$  at time  $t$ .
- Assume
  - Large numbers permit use of continuous variables.
  - Major attrition factor is number of soldiers killed by opponents.
  - No prisoners taken & both use only gunfire (reasonable in guerrilla combat).

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## Non-Linear Models Cont'd: Guerrilla Combat

- If  $\delta x$  &  $\delta y$  are changes in armies by opponents' gunfire then

$$\delta x = -R_y P_y y \delta t \text{ and } \delta y = -R_x P_x x \delta t \quad (5.14)$$

This says that number of soldiers hit in a small time  $\delta t$  is equal to product of

- 1 firing rate of each soldier (const.  $R_x, R_y$  for each army),
  - 2 probability single shots hit targets ( $P_x, P_y$  for each army, subscript is side firing),
  - 3 the number of soldiers firing.
- Firing rates  $R_x, R_y$  are assumed constant,

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## Non-Linear Models Cont'd: Guerrilla Combat

- $P_x, P_y$  depend on whether target is exposed/ hidden.
- For 'friendly' troops, make  $P_y$  constant as each single shot has same hit probability.
- For hidden targets,  $P_x$  is ratio of area  $\alpha$  exposed, to total area occupied by enemy soldiers, so  $P_x = \alpha y/A$ .
- Put into Eqn.(5.14) & letting  $\delta x, \delta y, \delta t \rightarrow 0$ :

$$\begin{aligned} \frac{dx}{dt} &= -ay \\ \frac{dy}{dt} &= -bxy \end{aligned} \quad (5.15)$$

where  $a = R_y P_y$  and  $b = R_x \alpha/A$  are positive constants.

- Eqn(5.15) are *Lanchester's Linear Law* for undirected fire.

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## Non-Linear Models Cont'd: Guerrilla Combat

- Eqns.(5.15) have equilibrium point  $(X, Y)$

$$0 = -aY \text{ and } 0 = -bXY \quad (5.16)$$

i.e. Guerrilla army defeated with  $X$  unspecified.

- But phase-plane analysis shows some initial conditions give opposite outcomes.
- Taking Eqn.s(5.15) & dividing one by other get:

$$\frac{dy}{dx} = \frac{b}{a}x \quad (5.17)$$

This is first-order separable & may be integrated:

$$y = \frac{b}{2a}x^2 + K \quad (5.18)$$

where  $K = y_0 - \frac{b}{2a}(x_0)^2$  is a constant.

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## Non-Linear Models Cont'd: Guerrilla Combat

- Fig 5.3 shows different parabolic solutions for different  $K$ .
- As  $x, y > 0$  (+ive numbers),  $\dot{x}, \dot{y} < 0$  so curves go to  $(0, 0)$ .
  - 'Friendly' wins when  $x > 0$  &  $y = 0$ , i.e.  $K < 0$  & thus  $y_0 < \frac{b}{2a}(x_0)^2$  at  $t = 0$ .
  - 'Away' wins when  $x = 0$  &  $y > 0$ , so  $K > 0$  & so  $y_0 > \frac{b}{2a}(x_0)^2$ .
  - All dead when

$$K = 0 \text{ \& so } \frac{y_0}{(x_0)^2} = \frac{b}{2a}.$$

- Guerrillas have advantage as  $b \ll a$  cos ratio of areas  $\alpha/A \ll 1$ ,
- So two armies are evenly matched if  $x_0$  is large and  $y_0$  is relatively small.

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## Non-Linear Models Cont'd: Guerrilla Combat

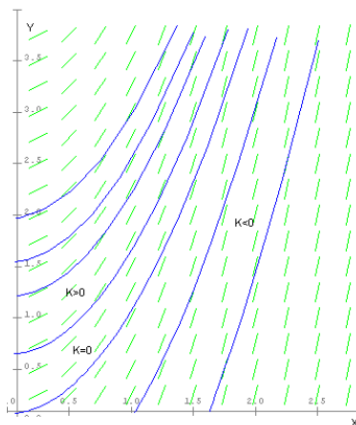


FIGURE 5.3 : Guerrilla Combat Phase-Plane Plot

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## Non-Linear Models Cont'd: Predator-Prey

### The Predator-Prey Model

- Guerrilla Combat is mutually destructive (i.e. any interaction results in pop'n decrease).
- More usual for pop'n increase of one species ↓ & other ↑, - *predator-prey*.
- First models by Lotka (1925) & Volterra (1926) for fish in Mediterranean.
- Lotka-Volterra model is based on a number of assumptions:
  - 1 Prey grow in an unlimited way when no predation.
  - 2 Predators depend on prey to thrive/ survive.
  - 3 Predation rate depends on likelihood that a predator encounters a victim.
  - 4 Predator pop'n growth rate  $\propto$  rate of predation.

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## Non-Linear Models Cont'd: Predator-Prey

- These can be expressed mathematically as:

$$\begin{aligned}\frac{dx}{dt} &= ax - bxy \\ \frac{dy}{dt} &= -cy + dxy\end{aligned}\tag{5.19}$$

where  $x, y$  are prey & predator numbers &  $a, b, c, d$  are positive constants.

- in Eqn.(5.19a), item 1 is the  $ax$  term & item 2 the  $-bxy$  term.
- in Eqn.(5.19b),  $dxy$  term corresponds to item 3 &  $-cy$  term corresponds to item 4.

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## Non-Linear Models Cont'd: Predator-Prey

- Note: Eqn.s(5.19) depend on 4 parameters  $a, b, c, d$
- Removing dimensions by putting  $x = \frac{c}{d}u, y = \frac{a}{b}v, \& t = \frac{1}{a}\tau$ , Eqn.s(5.19) become:

$$\begin{aligned} \frac{du}{d\tau} &= u(1-v) \\ \frac{dv}{d\tau} &= \gamma v(u-1) \end{aligned} \quad (5.20)$$

where  $\gamma = \frac{c}{a}$ .

- In the  $u, v$  phase plane, these give:

$$\frac{dv}{du} = \gamma \frac{v(u-1)}{u(1-v)} \quad (5.21)$$

with equilibrium points at  $(\bar{u}, \bar{v}) = (0, 0)$  &  $(\bar{u}, \bar{v}) = (1, 1)$ .

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## Non-Linear Models Cont'd: Predator-Prey

- Integrate this directly to give solution for the trajectories:

$$\gamma u + v - \ln u^\gamma v = H \quad (5.22)$$

for some  $H > H_{min} = 1 + \gamma$ .

- $H_{min}$  is minimum of  $H$  over all  $(u, v)$  & it occurs at  $u = v = 1$ .
- For a given  $H > H_{min}$ , trajectories given by Eqn.(5.22) are closed & given in Fig. 5.4(a).

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## Non-Linear Models Cont'd: Predator-Prey

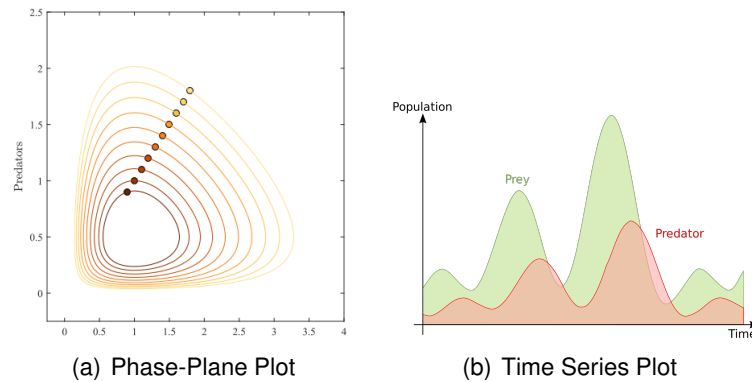


FIGURE 5.4 : Predator Prey Plots for  $\gamma = 2$

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## Non-Linear Models Cont'd: Predator-Prey

- As noted above, system's equilibrium points are  $(\bar{u}, \bar{v}) = (0, 0)$  &  $(\bar{u}, \bar{v}) = (1, 1)$ .
- As in the chemostat, write Jacobian  $\mathbf{A}(u, v)$  of Eqn.s(5.20) as:

$$\mathbf{A}(u, v) = \begin{pmatrix} 1 - v & -u \\ \gamma v & \gamma(u - 1) \end{pmatrix} \quad (5.23)$$

- At  $(\bar{u}, \bar{v}) = (0, 0)$  this reduces to diagonal matrix with eigenvalues  $\lambda_1 = 1$  &  $\lambda_2 = -\gamma$ .
- Hence, solutions *near*  $(0, 0)$  are

$$\mathbf{u}(t) = \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = c_1 \mathbf{x}_1 e^{\lambda_1 t} + c_2 \mathbf{x}_2 e^{\lambda_2 t}.$$

where  $\mathbf{x}_1, \mathbf{x}_2$  are e-vectors of  $\mathbf{A}$  at  $(0, 0)$ , as per Eqn.3.20

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## Non-Linear Models Cont'd: Predator-Prey

- Since  $-\gamma < 0 < 1$ , say that  $(0, 0)$  is a *saddle point* as solution

$$\mathbf{u}(t) = \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = c_1 \mathbf{x}_1 e^t + c_2 \mathbf{x}_2 e^{-\gamma t}. \quad (5.24)$$

has eigenvalues of different signs & so is like a saddle.

- Shows exp'l growth & decay of prey & predator respectively on the  $u, v$  axes referred to in items 1 & 2 above.
- As one  $\lambda_i > 0$  always, rhs of Eqn.5.24 increases exp'ly with  $t$  so  $(0, 0)$  is unstable equilibrium point.

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## Non-Linear Models Cont'd: Predator-Prey

- At the equilibrium  $(\bar{u}, \bar{v}) = (1, 1)$ , the Jacobian is:

$$\mathbf{A}(1,1) = \begin{pmatrix} 0 & -1 \\ \gamma & 0 \end{pmatrix} \quad (5.25)$$

e-values of which are imaginary  $\pm i\sqrt{\gamma}$ , so point is a *centre*.

- Mathematically complex eigenvalues are only stable if in left half of Argand Diagram.
- Since these lie *on* the axis, model is *unstable* mathematically.
- The reason for this can be seen qualitatively from Fig 5.4(a).
- Solutions are periodic, oscillating around a fixed point in the phase-plane of  $(u, v)$ , Fig 5.4(b)).

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## Non-Linear Models Cont'd: Predator-Prey

- Different trajectories correspond to different initial conditions in Fig 5.4(a)
- These are closed curves for different values of  $H$  in Eqn.(5.22).
- Viewing areas round the centre  $(1, 1)$  as quadrants, look at slopes given by Eqn.s(5.20) & hence trajectories' directions.
  - If 1st quadrant is closest to the origin, Eqn.s(5.20) shows  $\dot{u} > 0, \dot{v} < 0$
  - Shows that prey increase & predators decrease.
  - So phase-plane trajectories move in a counter-clockwise direction.

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## Non-Linear Models Cont'd: Predator-Prey

- Although attempts have been made using LV model in real-world oscillatory phenomena, instability issue remains.
- However model allows conclusions to be drawn on qualitative behaviour of such a system
- Using purely mathematical methods and very simple assumptions about the system.
- Most important is that systems like Eqn.s(5.19) give rise to the existence of periodic solutions.

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## Non-Linear Models Cont'd: Symbiosis

### Symbiosis

- 3rd interaction model is *symbiosis* where interaction benefits all species.
- Model has form:

$$\begin{aligned}\frac{dx}{dt} &= \mu_1 x \left( 1 - \frac{x}{K_1} + c_{12} \frac{y}{K_1} \right) \\ \frac{dy}{dt} &= \mu_2 y \left( 1 - \frac{y}{K_2} + c_{21} \frac{x}{K_2} \right)\end{aligned}\quad (5.26)$$

- $x, y$  grow logistically in absence each other with different carrying capacities  $K_1, K_2$  respectively.
- Positive parameters  $c_{12}, c_{21}$  show positive effect that each species has on the other.

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## Non-Linear Models Cont'd: Symbiosis

- Setting  $u_1 = \frac{x}{K_1}, u_2 = \frac{y}{K_2}$ , &  $\tau = \mu_1 t$ , Eqn.(5.26) goes to:

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1 (1 - u_1 + \alpha_{12} u_2) \\ \frac{du_2}{d\tau} &= \xi u_2 (1 - u_2 + \alpha_{21} u_1)\end{aligned}\quad (5.27)$$

where (non-dim'l) parameters given by  $\xi = \mu_2/\mu_1$ ,  
 $\alpha_{12} = c_{12}K_2/K_1$  &  $\alpha_{21} = c_{21}K_1/K_2$ .

- The steady-states of Eqn.(5.27) are given by:  
 $(\dot{u}_1, \dot{u}_2) = (0, 0) \equiv (u, v) = (0, 0)$  or  $(1 + \alpha_{12}u_2, 1 + \alpha_{21}u_1)$
- Leads to 4 cases:

$$(0, 0) \text{ or } (0, 1) \text{ or } (1, 0) \text{ or } \left( \frac{1 + \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}, \frac{1 + \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right)$$

where final case is only relevant if  $\alpha_{12}\alpha_{21} < 1$ .

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## Non-Linear Models Cont'd: Symbiosis

- Next, can find Jacobian matrix, at a steady-state  $(\bar{u}_1, \bar{u}_2)$ :

$$\mathbf{A}(\bar{u}_1, \bar{u}_2) = \begin{pmatrix} 1 - 2\bar{u}_1 + \alpha_{12}\bar{u}_2 & \alpha_{12}\bar{u}_1 \\ \xi\alpha_{21}\bar{u}_2 & \xi(1 - 2\bar{u}_2 + \alpha_{21}\bar{u}_1) \end{pmatrix} \quad (5.28)$$

- So at the equilibrium points, get

$$\text{for } (0, 0) \quad \mathbf{A} = \begin{pmatrix} 1 & 0 \\ 0 & \xi \end{pmatrix}$$

$$\text{for } (1, 0) \quad \mathbf{A} = \begin{pmatrix} -1 & \alpha_{12} \\ 0 & \xi(1 + \alpha_{21}) \end{pmatrix}$$

$$\text{for } (0, 1) \quad \mathbf{A} = \begin{pmatrix} 1 + \alpha_{12} & 0 \\ \xi\alpha_{21} & -\xi \end{pmatrix}$$

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## Non-Linear Models Cont'd: Symbiosis

$$\text{for } \left( \frac{1 + \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}, \frac{1 + \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} \right),$$

$$\mathbf{A} = \frac{1}{1 - \alpha_{12}\alpha_{21}} \begin{pmatrix} -(1 + \alpha_{12}) & \alpha_{12}(1 + \alpha_{12}) \\ \xi\alpha_{21}(1 + \alpha_{21}) & -\xi(1 + \alpha_{21}) \end{pmatrix}$$

- $\alpha$ 's +ive,  $\Rightarrow$  (0, 0) is unstable node, (1, 0) & (0, 1) saddles.
- 4th steady-state has e-values given by zeros of characteristic polynomial of Jacobian, hence

$$\lambda^2 - \text{trace}(\mathbf{A})\lambda + \det(\mathbf{A}) = 0 \quad (5.29)$$

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## Non-Linear Models Cont'd: Symbiosis

- Stability requires  $\Re(\lambda_1, \lambda_2)$  being -ive, only true if coeffs of eqn(5.29) +ive
- Thus need  $\text{trace}(\mathbf{A}) < 0$  - always true for  $\alpha_{12}\alpha_{21} < 1$  and

$$\det(\mathbf{A}) > 0 \equiv \frac{\xi(1 + \alpha_{12})(1 + \alpha_{21}) [1 + \alpha_{12}\alpha_{21}]}{1 - \alpha_{12}\alpha_{21}} > 0$$

which is again satisfied with  $\alpha_{12}\alpha_{21} < 1$ .

- See this on phase-plane plots in Fig 5.5 (a),(b).
- Here  $\alpha_{12} = 0.5$ ,  $\alpha_{21} = 0.25$  &  $\xi = 2$  in Fig 5.5(a) (i.e.  $\alpha_{12}\alpha_{21} < 1$ )
- Gives a stable equilibrium (i.e. stable node) for the fourth case at  $(\frac{12}{7}, \frac{10}{7})$ .
- Fig 5.5(b) shows a similar plot with  $\alpha_{12} = 1.5$ ,  $\alpha_{21} = 1.25$  &  $\xi = 2$  (i.e.  $\alpha_{12}\alpha_{21} > 1$ ) giving instabilities everywhere.

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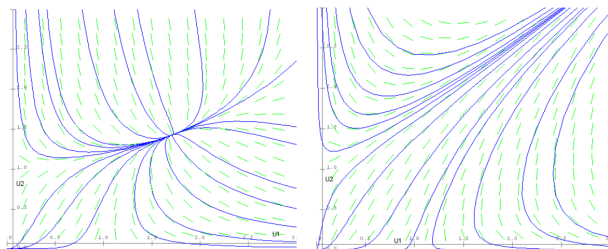
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## Non-Linear Models Cont'd: Symbiosis



(a)  $(u_1, u_2)$  for  $\alpha_{12}\alpha_{21} < 1$  (b)  $(u_1, u_2)$  for  $\alpha_{12}\alpha_{21} > 1$

FIGURE 5.5 : Symbiosis Phase-Plane Plots

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# Non-Linear Models Cont'd: The Chemostat Revisited

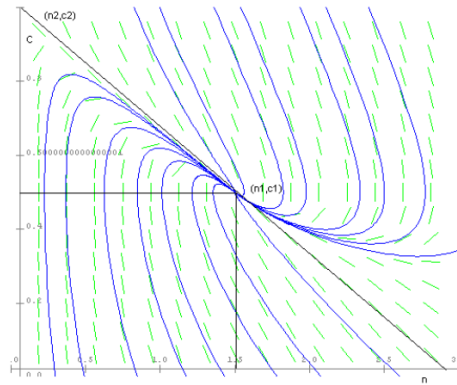


FIGURE 5.11 : Chemostat Phase-Plane Plot,  $\alpha_1 = 3, \alpha_2 = 1$

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