Lotka-Volterra model

- Lotka-Volterra model can be used to model other kinds of interactions between species:

\[
\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 - \alpha_{21} N_2}{K_1}\right), \quad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 - \alpha_{12} N_1}{K_2}\right)
\]

<table>
<thead>
<tr>
<th>Interaction</th>
<th>(\alpha_{12})</th>
<th>(\alpha_{21})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competition</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Predator-prey</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Parasitism</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Commensalism</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Mutualism</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

- Strengths of interactions depend on magnitudes of \(a_{ij}\)’s.
Lotka-Volterra predator-prey model

• Ex., let:
  – $N_1$ be the population size of the predator ($P$).
  – $N_2$ be the population size of the prey ($V$ for victim).

\[ K_1 = 400, \ K_2 = 800 \]
\[ \alpha_{12} = -0.5, \ \alpha_{21} = 0.5 \]

Predator populations generally have smaller carrying capacities than prey populations.

$K_1=400, K_2=800, \alpha_{12}=-0.5, \alpha_{21}=0.50$
Lotka-Volterra predator-prey model

- If the prey are very abundant, then prey densities will exceed predator densities even with predation:

\[ K_1 = 400, K_2 = 2000 \]
\[ \alpha_{12} = -0.5, \alpha_{21} = 0.5 \]
Lotka-Volterra predator-prey model

- If the prey provide more value to the predator (more positive value of $\alpha_{21}$), the predators are enhanced and prey are more suppressed:

$$K_1 = 400, \quad K_2 = 800$$

$$\alpha_{12} = -0.5, \quad \alpha_{21} = 1$$

$K_1=400, K_2=800, \alpha_{12}=-0.50, \alpha_{21}=1.00$

$K_1=400, K_2=800, \alpha_{12}=-0.50, \alpha_{21}=1.00$
Lotka-Volterra predator-prey model

• If the predator is more efficient (more negative value of $\alpha_{12}$), the prey are more suppressed:

$$K_1 = 400, \ K_2 = 800$$

$$\alpha_{12} = -1.5, \ \alpha_{21} = 0.5$$

![Graph of Lotka-Volterra model with parameters $K_1=400$, $K_2=800$, $\alpha_{12}=-1.5$, $\alpha_{21}=0.5$. The graph shows the population sizes of predator and prey over time.](image)
Lotka-Volterra predator-prey model

- If the predator is even more efficient (even more negative value of $\alpha_{12}$), the prey are even more suppressed:

  \[ K_1 = 400, \quad K_2 = 800 \]
  \[ \alpha_{12} = -2, \quad \alpha_{21} = 0.5 \]
Lotka-Volterra predator-prey model

- If the predator is too efficient (even more negative value of $\alpha_{12}$), the prey can be driven to extinction:

$$K_1 = 400, \ K_2 = 800$$

$$\alpha_{12} = -2.5, \alpha_{21} = 0.5$$
Lotka-Volterra predator-prey model

- The L-V logistic-based (competition) model always proceeds to logistic-style equilibria.
  - Sigmoidal growth or decline to an equilibrium.
- However, **cyclical** predator-prey and parasite-host patterns are commonly observed in nature:
  - Especially when species interactions are tightly coupled.

![Graph showing population cycles of hare and lynx](image)

- Form of logistic-based model is incapable of mimicking such behavior.

![Graph showing changes in red grouse density](image)
Lotka-Volterra cyclical predator-prey model

• Lotka and Volterra proposed a non-logistic form of predator-prey model for one predator species and one prey species, tightly coupled.
  – Original motivation: to understand fluctuations in the catch of predaceous fish.

• Modeling growth of the prey population:
  – Growth of prey population is some function of the numbers of both prey and predators:
    \[ \frac{dV}{dt} = f_V (V, P) \]
  – Assume that the predators are the only force limiting growth of the prey population.
  – In the absence of the predator, the prey population increases exponentially:
    \[ \frac{dV}{dt} = rV \]
Lotka-Volterra cyclical predator-prey model

• Potential for increase of the prey population is offset by losses that occur when predators are present:
  – Rate of change of prey density  $V = (\text{intrinsic growth rate of prey}) \times (\text{prey density})$ – loss of prey due to predation:
    \[
    \frac{dV}{dt} = rV - \alpha VP
    \]
  – Assumes that losses to predation are proportional to the product of predator and prey numbers.
  • Mass-action assumption, analogous to a chemical reaction:
    – Predators and prey encounter each other randomly.
    – Homogeneous in space and time.
Lotka-Volterra cyclical predator-prey model

- The proportionality constant $\alpha$ measures capture efficiency:

$$\frac{dV}{dt} = rV - \alpha VP$$

- This is *not* the competition coefficient of the logistic-based model, but is analogous.
- Measures the effect of a predator on the specific (per capita) growth rate of the prey: $\frac{1}{V} \frac{dV}{dt}$
- The larger $\alpha$ is, the more the specific growth rate of the prey population is depressed by the addition of a single predator.
  - Filter-feeding whale: large $\alpha$.
  - Predaceous spider: small $\alpha$. 
Lotka-Volterra cyclical predator-prey model

• **Modeling growth of the predator population:**
  – Analogous equation: growth of predator population is a different function of the numbers of predators and prey:
    \[ \frac{dP}{dt} = f_P(P,V) \]
  – Assume that predator is an extreme **specialist**:
    • Feeds only on prey population with no alternate source of prey.
    • (Assumption can later be relaxed.)
  – If prey population is absent, the predator population **declines** exponentially:
    • \( q \) is the **specific mortality (death) rate**: \[ \frac{dP}{dt} = -qP \]
Lotka-Volterra cyclical predator-prey model

• Positive growth of predator population occurs only when prey population is present:
  • Rate of change of predator density \( P \) = growth of predator population due to predation – (specific death rate of predator) * (predator density).
    \[
    \frac{dP}{dt} = \beta VP - qP
    \]

• Term \( \beta VP \) assumes mass-action, random encounters of predators and prey.

• Proportionality constant \( \beta \) is a measure of conversion efficiency: ability of predators to convert each new victim into additional specific growth rate for the predator population: \( \frac{1}{P} \frac{dP}{dt} \)
  – Moose captured by wolves: large \( \beta \)
  – Single seed consumed by granivorous bird: small \( \beta \).
Lotka-Volterra cyclical predator-prey model

• So: the new L-V predator-prey model comprises the coupled differential equations for prey and predator populations:

\[
\frac{dV}{dt} = rV - \alpha VP \\
\frac{dP}{dt} = \beta VP - qP
\]

Solved using numerical integration

• Mass-action assumption important.
  – Reasonable for moderate predator and prey densities.
  – Low prey densities: predators may search more thoroughly, actively seeking prey.
  – High prey densities: predators reduce search effort due to satiation.
Lotka-Volterra cyclical predator-prey model

- Model displays periodic solutions (limit cycles):

  ![Graph showing predator-prey population dynamics](image)

  **Time trajectories**
  **Phase plot for different initial conditions**
Lotka-Volterra cyclical predator-prey model

- **Cyclical behavior** not explicitly built into model.
- Lagging cyclical behavior is an **emergent property**.

\[
\begin{align*}
V_0 &= 600, \quad P_0 = 200 \\
r &= 0.01, \quad q = 0.05 \\
\alpha &= 0.0001, \quad \beta = 0.0001
\end{align*}
\]

- Time trajectories
- Phase plot (State space)
Lotka-Volterra cyclical predator-prey model

• Equilibrium solutions:
  – Equilibrium is a point at which population size ($V$ or $P$) does not change.
  – Set each equation to zero and solve for population size.
    
    \[
    \frac{dV}{dt} = rV - \alpha VP \\
    rV = \alpha VP \\
    r = \alpha P \\
    \hat{P} = \frac{r}{\alpha}
    \]
  – Predicts the specific number of predators that maintains the prey population at zero growth.
  – Determined by ratio of growth rate of prey ($r$) to the capture rate of the predators ($\alpha$).
    • Faster the prey growth rate, the more predators are needed.
    • Higher the capture efficiency, the fewer predators are needed.
Lotka-Volterra cyclical predator-prey model

- As with the L-V competition model, can plot isoclines in the phase space to evaluate the joint equilibrium.
  - Prey equilibrium yields a horizontal prey isocline.

- If predator population is less than equilibrium, prey population will increase.
- If predator population is greater than equilibrium, prey population will decrease.
Lotka-Volterra cyclical predator-prey model

- Equilibrium solution for predators:

\[
\frac{dP}{dt} = \beta VP - qP \\
0 = \beta VP - qP \\
\beta VP = qP \\
\beta V = q \\
\hat{V} = \frac{q}{\beta}
\]

- Predator is controlled by a fixed number of prey.
  - Greater the death rate of the predators \( (q) \), the more prey are needed to keep the predator population from declining.
  - Greater the conversion efficiency of the predators \( (\beta) \), the fewer prey are needed to maintain the predators at equilibrium.
Lotka-Volterra cyclical predator-prey model

- **Predator isocline** is a **vertical line** representing the critical size of the prey population.

- To the left, there are not enough prey to support the predator population, so it declines.
- To the right, there is an excess of prey, so the predator population increases.
Lotka-Volterra cyclical predator-prey model

- Simultaneous isoclines:
  - For competition model, there were 4 ways that the pair of isoclines could be placed in phase space.
  - For predation model, only one possible pattern:
    - Isoclines cross at 90°.
    - But dynamics are more complex.
    - Intersection of isoclines is an unstable equilibrium.
    - Otherwise trajectories move in approximate ellipse.
Lotka-Volterra cyclical predator-prey model

- Approximate ellipse in phase space translates into cyclical trajectories over time.
  - Populations cycle smoothly from minimum to maximum.
  - Might hit axis: extinction.
  - Peak of predator population occurs when prey population is at midpoint, and vice versa.
  - Peaks displaced by quarter cycle.
  - Period of cycle (C) is approximately: \( C = \frac{2\pi}{\sqrt{rq}} \)
Lotka-Volterra cyclical predator-prey model

Phase plot (State space)

Time trajectories

Number of predators or prey

One prey cycle

Prey

Predators

Time
Lotka-Volterra cyclical predator-prey model

- Example:

\[
V_0 = 600, \ P_0 = 200
\]
\[
r = 0.01, \ q = 0.05
\]
\[
\alpha = 0.0001, \ \beta = 0.0001
\]
Lotka-Volterra cyclical predator-prey model

- **Assumptions** of cyclical L-V model:
  - Closed populations, no time lags.
  - Parameters constant.
  - Predator and prey populations tightly coupled:
    - Growth of prey population limited only by predation.
    - Predator is a specialist that can persist only with the prey population.
  - Predators and prey encounter one another randomly in a homogeneous environment (mass-action).
    - No prey refuges or cooperation among prey.
  - Individual predators can consume an infinite number of prey.
    - No satiation.
    - No interference or cooperation among predators.
- Many **modifications of model** to relax assumptions.
Lotka-Volterra cyclical predator-prey model

- Incorporating a carrying capacity for the prey species:
  - Expect that prey population will be limited by other resources.
  - Can modify prey portion of model to incorporate carrying capacity:
    \[
    \frac{dV}{dt} = rV - \alpha VP \quad \text{(Original model)}
    \]
    \[
    \frac{dV}{dt} = rV - \alpha VP - cVV \quad \text{(With carrying-capacity term)}
    \]
    \[
    = rV - \alpha VP - cV^2
    \]
  - Prey population decrease by the presence of predators \((\alpha VP)\) and by its own abundance \((cV^2)\).
Lotka-Volterra cyclical predator-prey model

• Graph of modified prey isocline in phase space:
  – Straight line with negative slope.
  – Crosses prey axis at $V = r/c$.
    = Max possible population size in absence of predators.
    • Equivalent to logistic growth model with $K = r/c$.
  – Trajectories spiral inward to stable equilibrium point.
    • Equilibrium size for prey population decreases when predators present.
    • Presence of other limiting factors dampens cycling.