C. Exploitation (predation) (APE CH.6)

Definition:

\[
\frac{\partial \ln V}{\partial P} < 0
\]

\[
\frac{\partial \ln P}{\partial V} > 0
\]

where \( V \) is the population of victims & \( P \) is the population of predators

1. Primitive linear model by Lotka & Volterra:

\[
\frac{dV}{dt} = rV - kPV
\]

\[
\frac{dP}{dt} = \beta kPV - dP
\]

The zero-isoclines: \( P=r/k \) (a horizontal line)

& \( V=d/\beta k \) (a vertical line).

There must be an equilibrium. Trajectories will oscillate around it with \textit{Neutral} stability.
2- An additive model incorporating linear competition among the victims:

\[
\frac{dV}{dt} = rV\left(\frac{K-V}{K}\right) - kPV
\]

\[
\frac{dP}{dt} = \beta kPV - dP
\]

The zero-isoclines: \( P = \frac{r}{k}[1 - \frac{V}{K}] \) (a negatively sloped straight line with derivative: \(-\frac{r}{kK}\))

& \( V = \frac{d}{\beta k} \) (a vertical line).

There may be an equilibrium. Trajectories will oscillate around it, getting closer and closer with time.
We call that a **Stable focus**.
3- Functional responses of predators: How does the rate of exploitation vary as \( V \) grows?

Type I — Linear response. Example \( kV \).

Type II — Saturating response. Example \( k\left(\frac{V}{\chi + V}\right) \) — The Half-saturation Equation or Holling Disk Equation. (The variables of the Holling Disk Equation appear with different letters and in slightly different form but they are mathematically equivalent.) \( \chi \) is known as the Half-saturation constant because at \( V = \chi \), the rate of exploitation equals \( k/2 \). The rate asymptotes at \( k \) whereas \( \chi \) determines the curvature of the functional response.

Other types of functional responses exist, too.
4- Isoclines of a two-species predation system -- the simple, robust model without direct interaction amongst the predators or a refuge for their victims.
Technical mutualism among victims by sharing the burden of predation.

Another example: *Gerbillus allenbyi* collecting together in one hectare when threatened by owl overflights in both ha.
Stability properties of the equilibrium:

*When victims compete near the equilibrium, it is stable.*
*When victims are mutualistic near the equilibrium, it is unstable and the trajectory unwinds to a limit cycle.*
5- Stabilizing features of predation

Habitat complexity/predatory proficiency: Experiments of Gause (rarefaction) and of Huffaker.
Huffaker works with two mites (V= *Eotetranychus sexmaculatus*, a fruit eater & P= *Typhlodromus occidentalis*, a mite eater). He raises them in trays with oranges that are replenished regularly, but the P destroy the V and then become extinct themselves. He increases the complexity of the lab environment by adding more oranges, embedding them in a maze of Vaseline lines deposited on the tray surfaces, replacing some of the oranges with rubber balls and covering most of the orange surfaces to prevent their being used. Finally, with a 252-orange system and only 1/20\(^{th}\) of each orange exposed for feeding, he gets the system to cycle three times before \(V=0\)! Later an even more complex system lasts several years (until getting infected and being destroyed due to an outside organism).

So what is correct? Is heterogeneity stabilizing the predation or is predatory inefficiency the source of stability?

Leo Luckinbill settles the issue in 1973 (*Ecology* 54:1320-27 Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*). Gause had shown that these very two species do not last together in the lab unless one adds gravel to the bottom of the aquaria. But Luckinbill adds methyl cellulose instead. Water with MC is much more viscous than water alone. The viscosity slows down both species:

<table>
<thead>
<tr>
<th></th>
<th><em>Paramecium aurelia</em></th>
<th><em>Didinium nasutum</em></th>
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<tbody>
<tr>
<td></td>
<td>Plain medium</td>
<td>with methyl cellulose</td>
</tr>
<tr>
<td>Velocity ((\mu)sec)</td>
<td>1923</td>
<td>47</td>
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</tbody>
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And the methyl cellulose system is stable.
Refugia
Utida’s experiment with parasitoid wasps and bean weevils; a mysterious refuge produces a limit cycle.
6- Some applications

Biological control: Volterra's principle of biocides
Eutrophication: the paradox of enrichment