Gause, Luckinbill, Veilleux and What to Do: Distinguishing between the Prey-Dependent and Ratio-Dependent Limit Myths

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Parameters:

- $r$: maximum prey growth rate
- $\alpha$: maximum predator attack rate
- $\mu$: maximum predator death rate
- $e$: predator conversion efficiency
- $h$: handling time
- $K$: carrying capacity of prey
General Predator-Prey Equations:

\[
\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - f(\bullet)P
\]

\[
\frac{dP}{dt} = ef(\bullet)P - \mu P
\]
Which functional response should be employed?

\[ f(\cdot)? \]

\[ f(N) \leftrightarrow f(N, P) \leftrightarrow f(N/P) \]

“Limit Myths”
Asymptotic Functional Responses:

\[ f(N) = \frac{\alpha N}{1 + \alpha hN} \]  

(Holling 1965)

\[ f(N/P) = \frac{\alpha N/P}{1 + \alpha hN/P} \]  

(Arditi and Ginzburg 1989)
Possible Outcomes of a Predator-Prey System:

1) Complete consumption of prey followed by starvation of the predator ("Dual Extinction").
2) Oscillatory or non-oscillatory coexistence of predator and prey ("Coexistence")
3) Starvation of the predator followed by ‘escape’ of the prey ("Predator Extinction").
“Gause Loops”

Dual Extinction was the only observed outcome

(Gause 1934)
Reducing the frequency of contact between prey and predators, along with food limitation of prey, allows for Coexistence.
Veilleux 1979:

The attack rate of predators is a function of the nutritional status of the prey.

(Veilleux 1979)
The efficiency of predators is a function of the nutritional status of the prey.
Shifts in parameter space produce changes in qualitative outcomes:

<table>
<thead>
<tr>
<th>Food Concentration:</th>
<th>Outcome:</th>
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<tbody>
<tr>
<td>1.35 – 1.80</td>
<td>52% Dual Extinction, 48% Predator Extinction</td>
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<tr>
<td>0.59 – 1.13</td>
<td>Coexistence</td>
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<td>0.18 – 0.45</td>
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(Veilleux 1979)
Is *dual extinction* the result of stochastic or deterministic processes?
Prey-Dependent Predator Extinction:
Prey-Dependent Coexistence:

![Graph showing predator and prey population sizes](image)
Prey-Dependent Dual Extinction:

Diagram showing the relationship between predator and prey population sizes.
Rich Dynamics of Ratio-Dependence:

(Berezovskaya et al. 2001)
Veilleux Experiment in Berezovskaya Space:

(Berezovskaya et al. 2001)
Dual Extinction or Coexistence (depends on initial abundances)

\[ \nu = \frac{\alpha}{r} \]

\[ \mu = \frac{e}{(rh)} \]
# Comparison of Predicted Outcomes:

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$K$ is not independent of $r$:

(Veilleux 1979)
The Paradox of Enrichment:

decreasing $r$
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Searching for the better “Limit Myth” using the *Didinium-Paramecium* system:

1) Confirm $r$-dependence of $K$ in *Paramecium-Didinium* system.

2) Revisit the experiments of Gause, Luckinbill, and Veilleux to explore the changes in qualitative outcomes generated by manipulations of $r$. 
Confirming the $r$-dependence of $K$:

1) The growth rate ($r$) of the prey in isolation can be reduced by imposing proportional mortality at frequent, regular intervals.

2) Decrease $r$ and observe the average equilibrium abundance ($K$):
   - $H_0 = \text{decreasing } r \text{ should have no effect on the average equilibrium abundance } (K)$.
   - $H_a = \text{decreasing } r \text{ should reduce the average equilibrium abundance } (K)$. 
Gause, Luckinbill, and Veilleux redirected:

1) Using the methods of Luckinbill and Veilleux, produce **coexistence** in the *Paramecium-Didinium* system.

2) Decrease $r$ via experimental manipulation:
   - $H_0 =$ decreasing $r$ in stable system should **maintain stability** (Prey-dependent prediction).
   - $H_a =$ decreasing $r$ in stable system should **destabilize the system** (Ratio-dependent prediction).
Acknowledgements:

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Rich Dynamics of Ratio-Dependence:

Outcome can depend on parameter values and/or initial values ($N$ & $P$):

1) Dual Extinction for any initial values
2) Coexistence for any initial values
3) Predator Extinction for any initial values
4) Both Dual Extinction and Coexistence are possible, outcome depends on initial values
5) Both Predator Extinction and Dual Extinction are possible, outcome depends on initial values

(Berezovskaya et al. 2001)
Coexistence and Dual Extinction under Ratio-Dependence*:

\[ \alpha > r + \mu \quad \rightarrow \quad \text{dual extinction} \]

\[ \alpha < r + \mu \quad \rightarrow \quad \text{coexistence} \]

(Ginzburg et al. 1974)

* Works for certain area of initial abundances, with adequate predator growing ability.
Notation Confusion:

Prey growth function:

\[ rN(1 - N/K) = rN - \gamma N^2 \]

\[ \gamma = \frac{r}{K} \quad \text{and} \quad K = \frac{r}{\gamma} \]