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
α	maximum predator attack rate
μ	maximum predator death rate
e	predator conversion efficiency
h	handling time
K	carrying capacity of prey

General Predator-Prey Equations:

$$\frac{dN}{dt} = rN(1 - N/K) - \underline{f(\bullet)}\, P$$

$$\frac{dP}{dt} = e\,\underline{f(\bullet)}\, P - \mu P$$

Which functional response should be employed?

$$f(\cdot)?$$

$$f(\mathrm{N}) \longleftrightarrow f(\mathrm{N,P}) \longleftrightarrow f(\mathrm{N/P})$$

"Limit Myths"

Asymptotic Functional Responses:

$$f(N) = \frac{\alpha N}{1 + \alpha h N}$$

(Holling 1965)

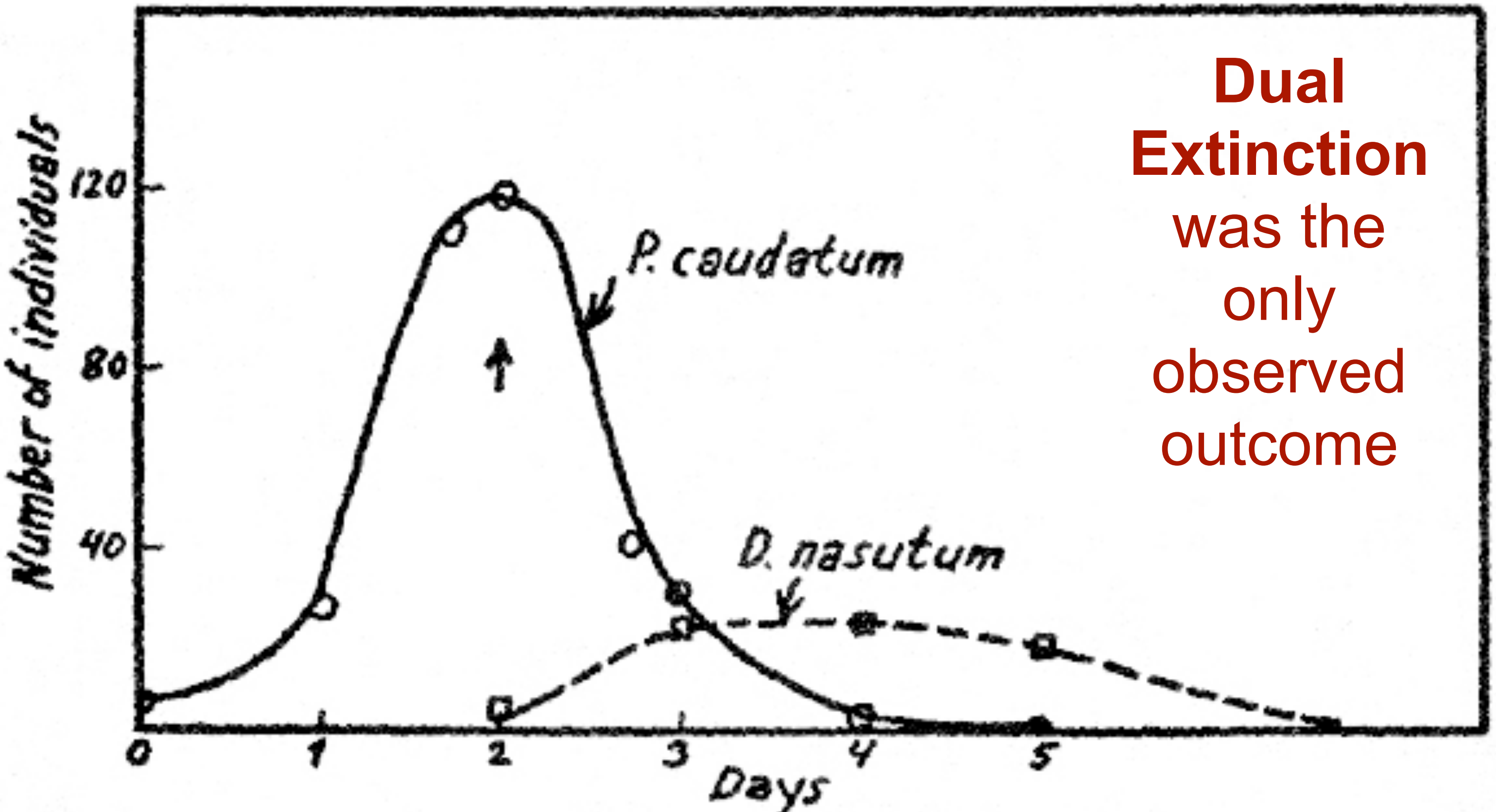
$$f(N/P) = \frac{\alpha N/P}{1 + \alpha h N/P}$$

(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”

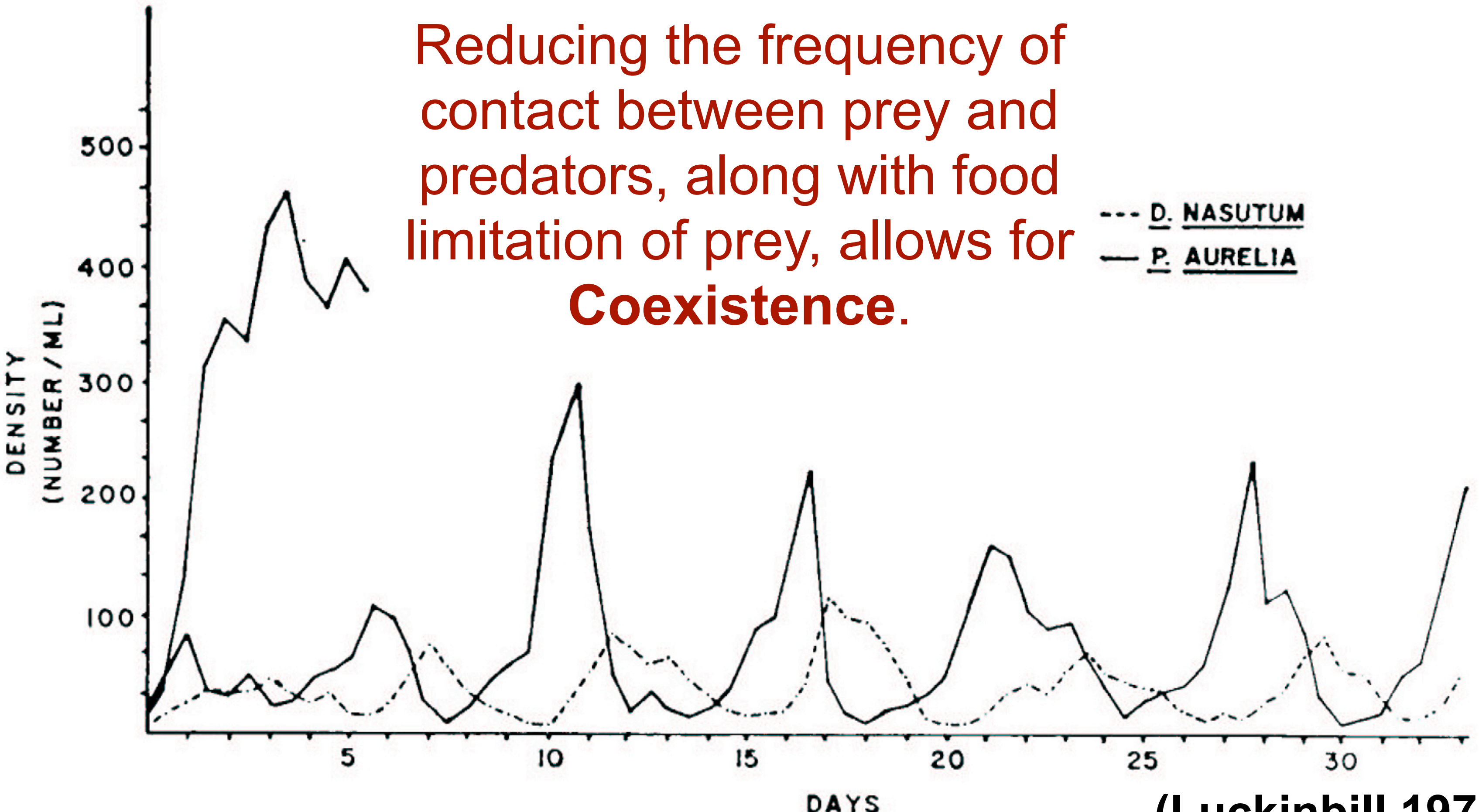


Dual Extinction was the only observed outcome

(Gause 1934)

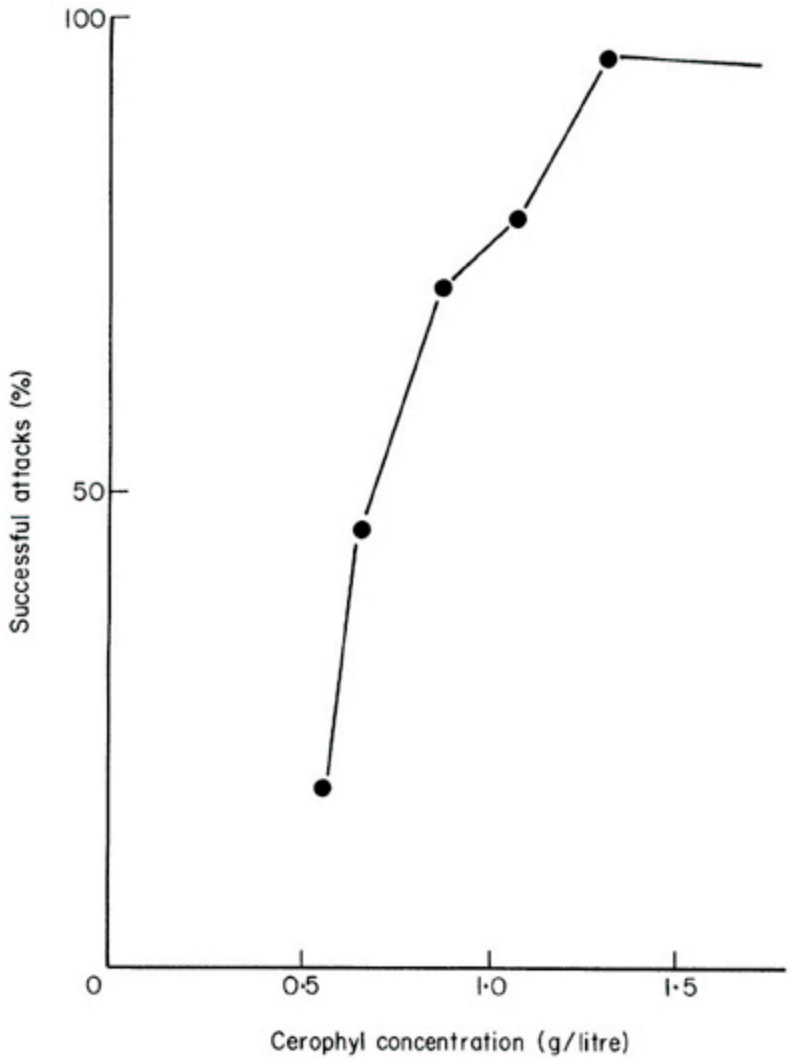
Luckinbill 1973:

Reducing the frequency of contact between prey and predators, along with food limitation of prey, allows for **Coexistence**.



(Luckinbill 1973)

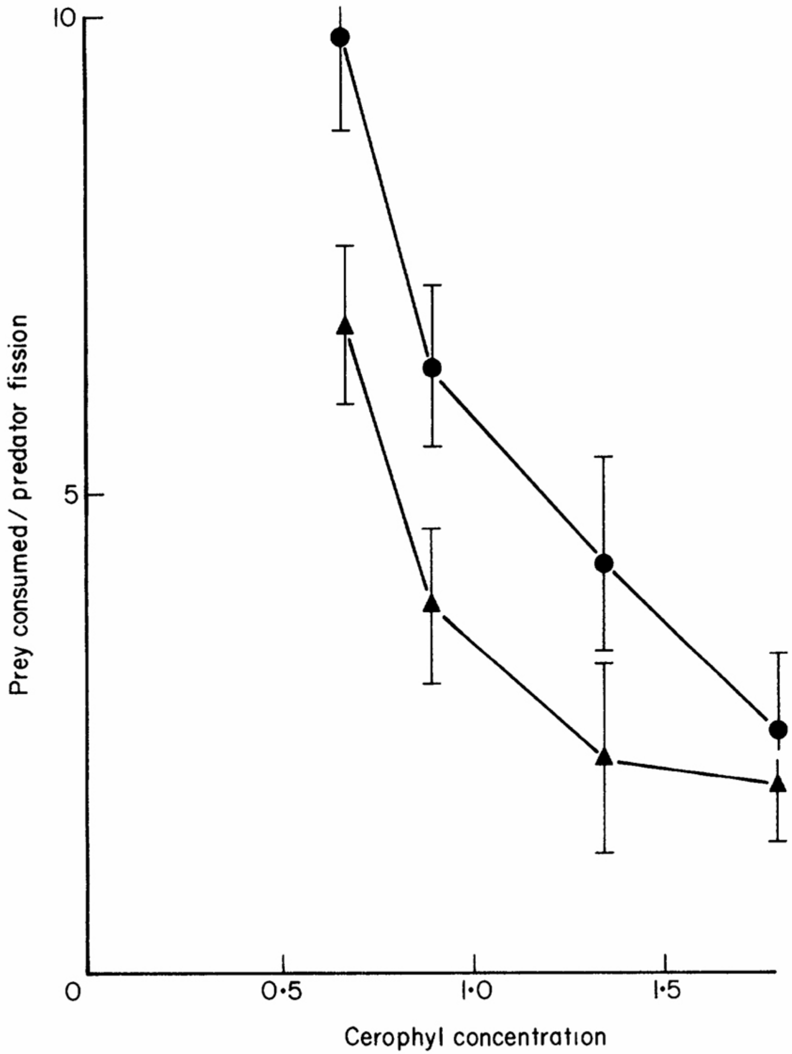
Veilleux 1979:



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

(Veilleux 1979)

Veilleux 1979:



The **efficiency** of predators is a function of the nutritional status of the prey.

(Veilleux 1979)

Shifts in parameter space produce changes in qualitative outcomes:

decreasing α

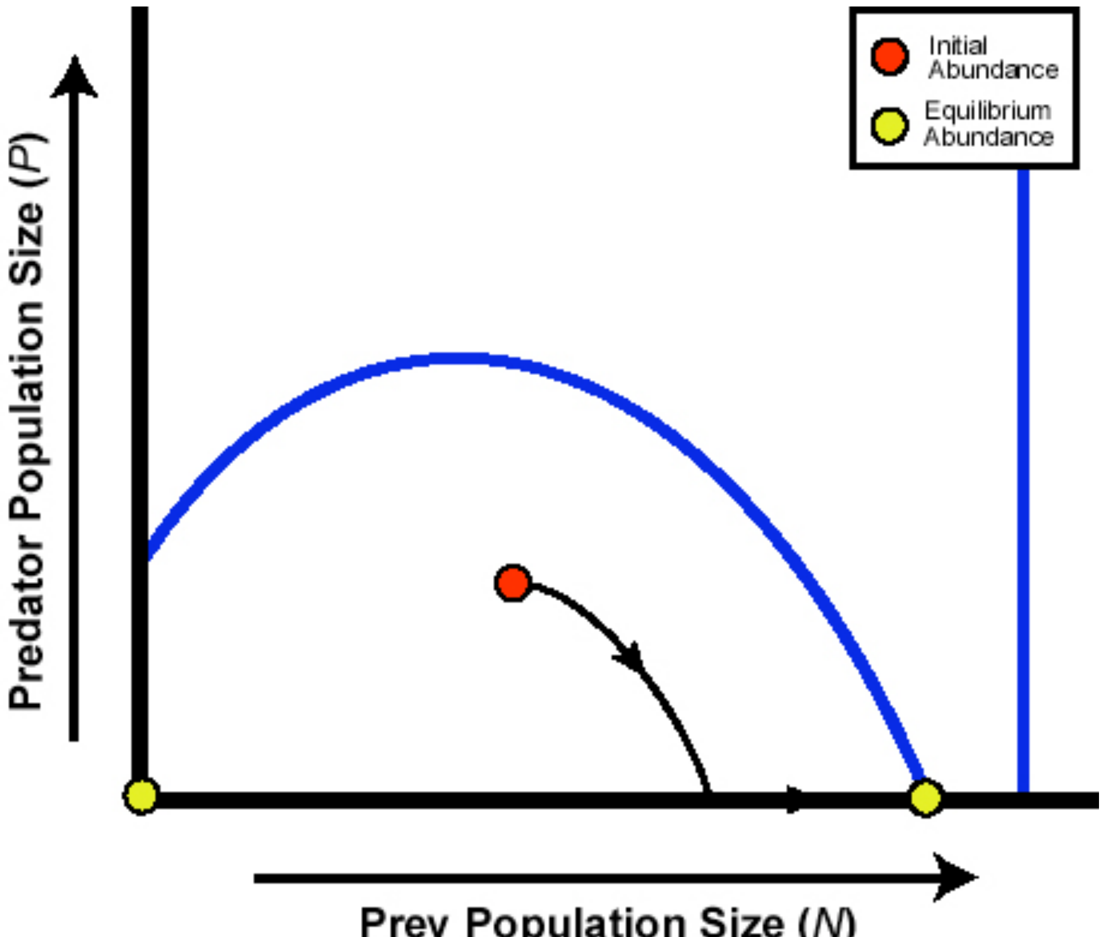
decreasing e

Food Concentration:	Outcome:
1.35 – 1.80	52% **Dual Extinction,** 48% **Predator Extinction**
0.59 – 1.13	**Coexistence**
0.18 – 0.45	**Predator Extinction**

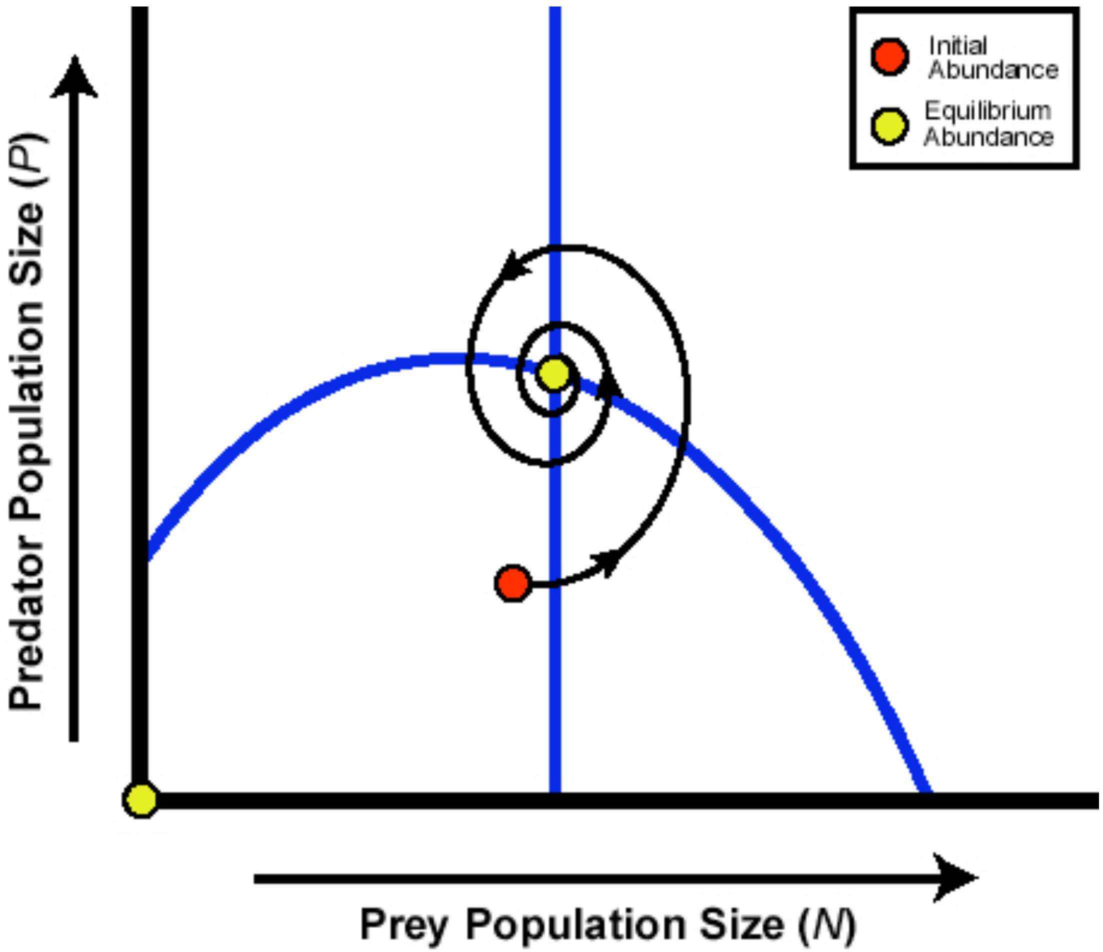
(Veilleux 1979)

Is *dual extinction* the result of stochastic or deterministic processes?

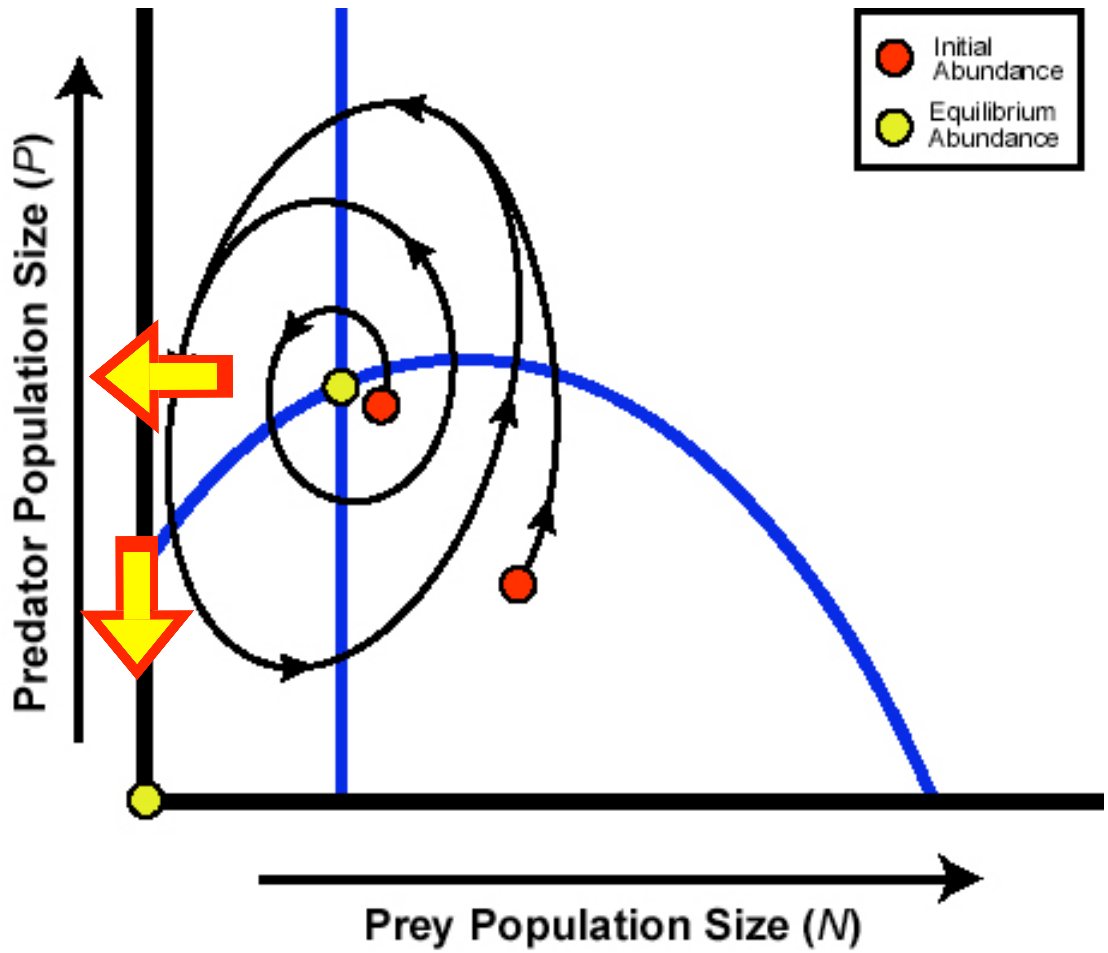
Prey-Dependent
Predator Extinction:



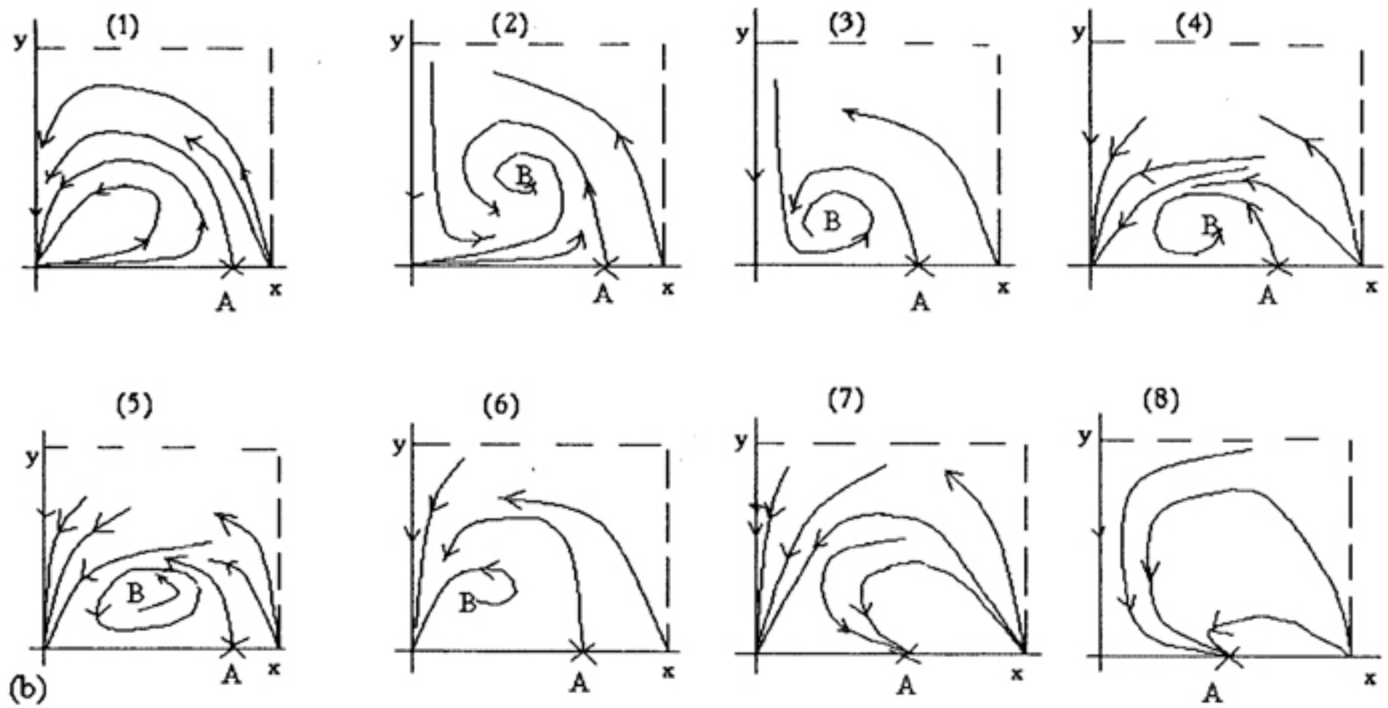
Prey-Dependent Coexistence:



Prey-Dependent
Dual Extinction:

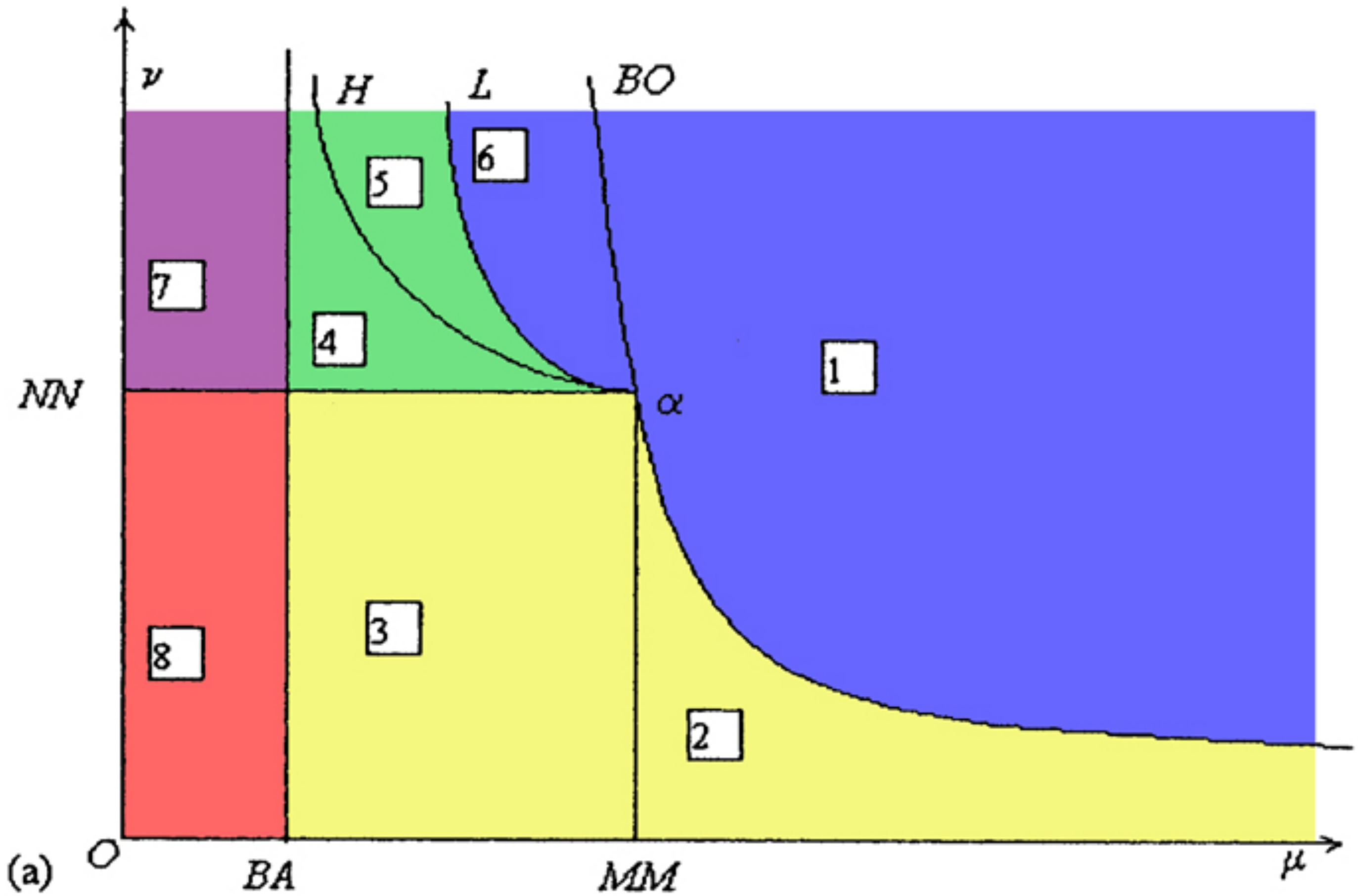


Rich Dynamics of Ratio-Dependence:

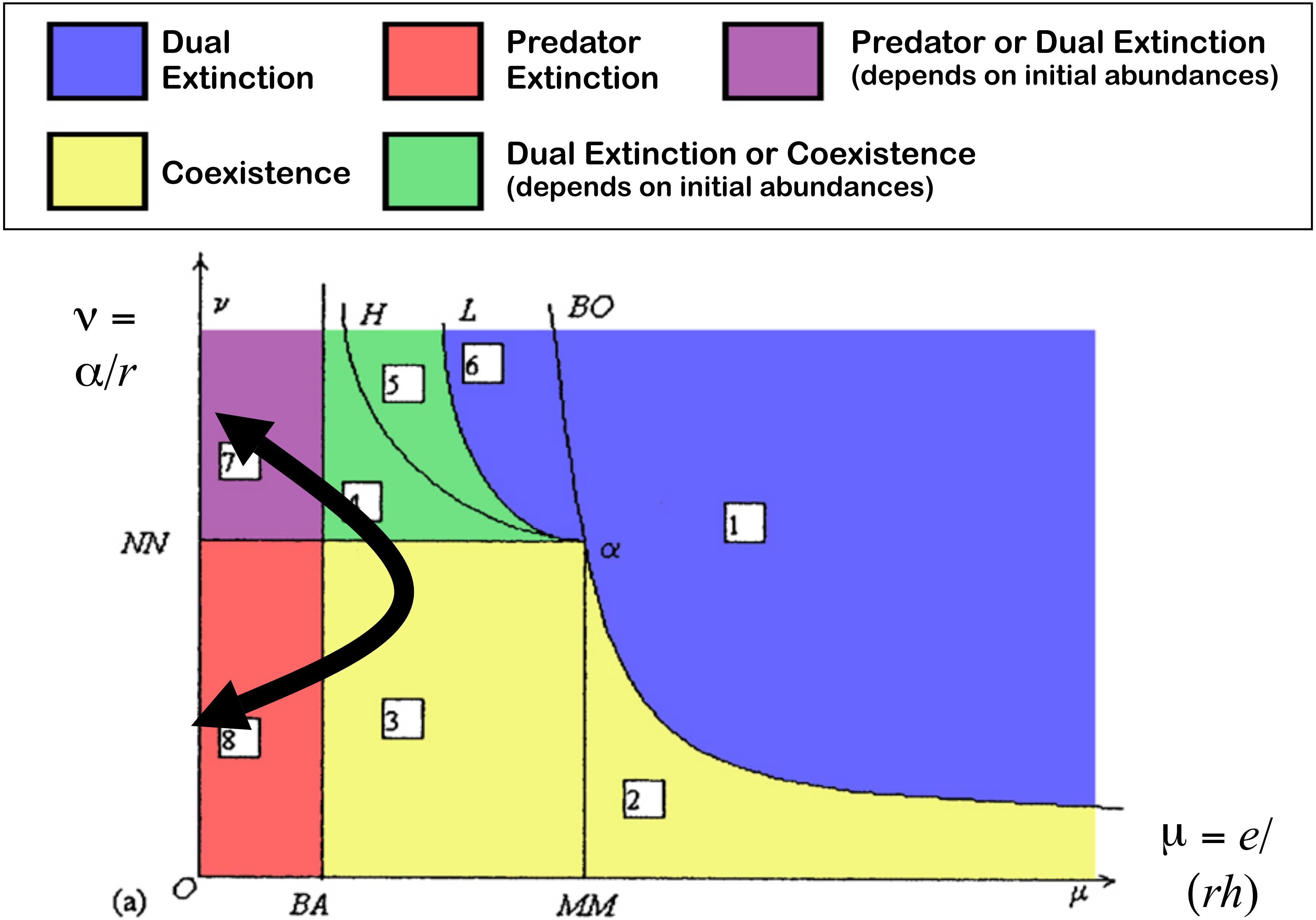


(Berezovskaya *et al.* 2001)

Veilleux Experiment in Berezovskaya Space:



(Berezovskaya *et al.* 2001)



Dual Extinction
Predator Extinction
Predator or Dual Extinction
(depends on initial abundances)
Coexistence
Dual Extinction or Coexistence
(depends on initial abundances)
ν = α/r
ν
H
L
BO
5
6
7
4
1
NN
α
3
8
2
μ = e/(rh)
(a)
O
BA
MM
μ

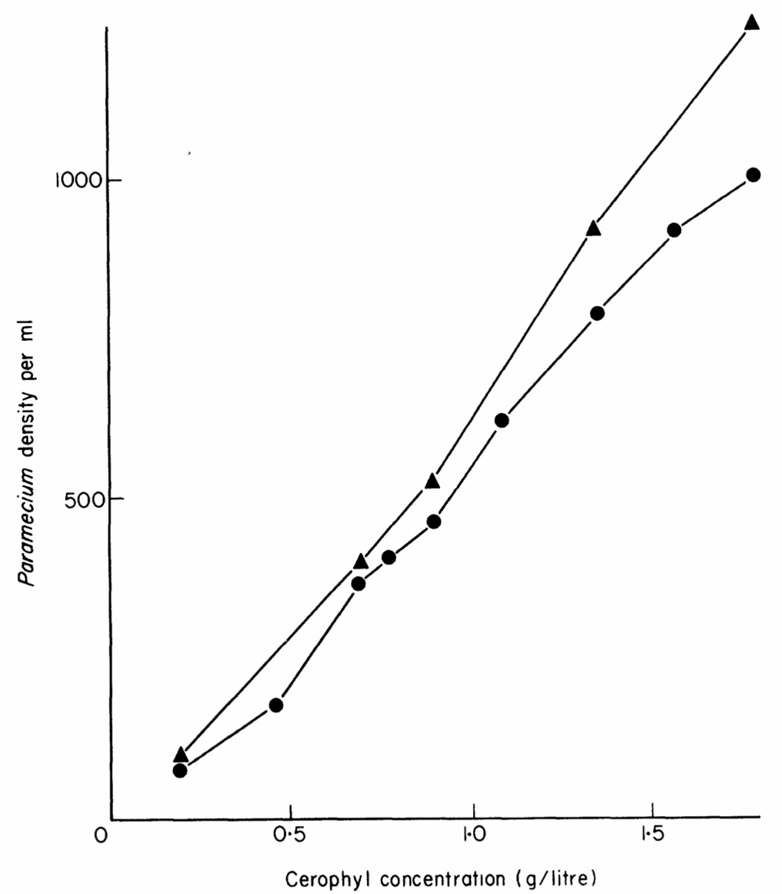
Comparison of Predicted Outcomes:

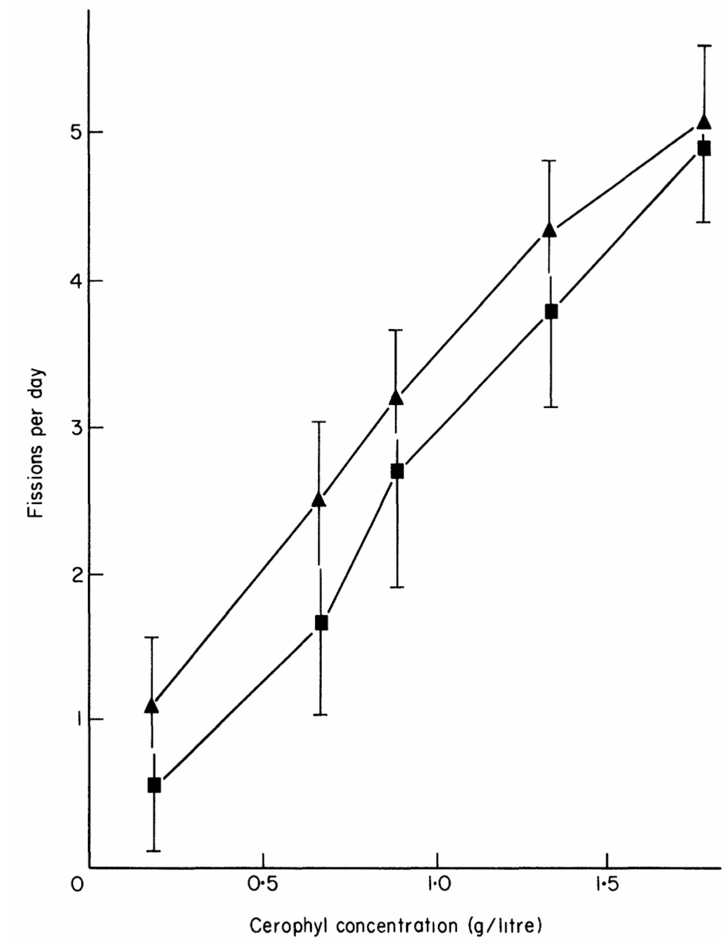
Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$\alpha \downarrow$	**DE → CoEx**	**DE → CoEx**
$r \downarrow$	***no change***	**CoEx → DE**
$\mu \downarrow$	**CoEx → DE**	**CoEx → DE**
$e \downarrow$	**DE → CoEx**	**DE → CoEx**
$h \downarrow$	**CoEx → DE**	**CoEx → DE**

Comparison of Predicted Outcomes:

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$\alpha \downarrow$	DE $\rightarrow$ CoEx	DE $\rightarrow$ CoEx
$r \downarrow$	***no change***	CoEx $\rightarrow$ DE
$\mu \downarrow$	CoEx $\rightarrow$ DE	CoEx $\rightarrow$ DE
$e \downarrow$	DE $\rightarrow$ CoEx	DE $\rightarrow$ CoEx
$h \downarrow$	CoEx $\rightarrow$ DE	CoEx $\rightarrow$ DE

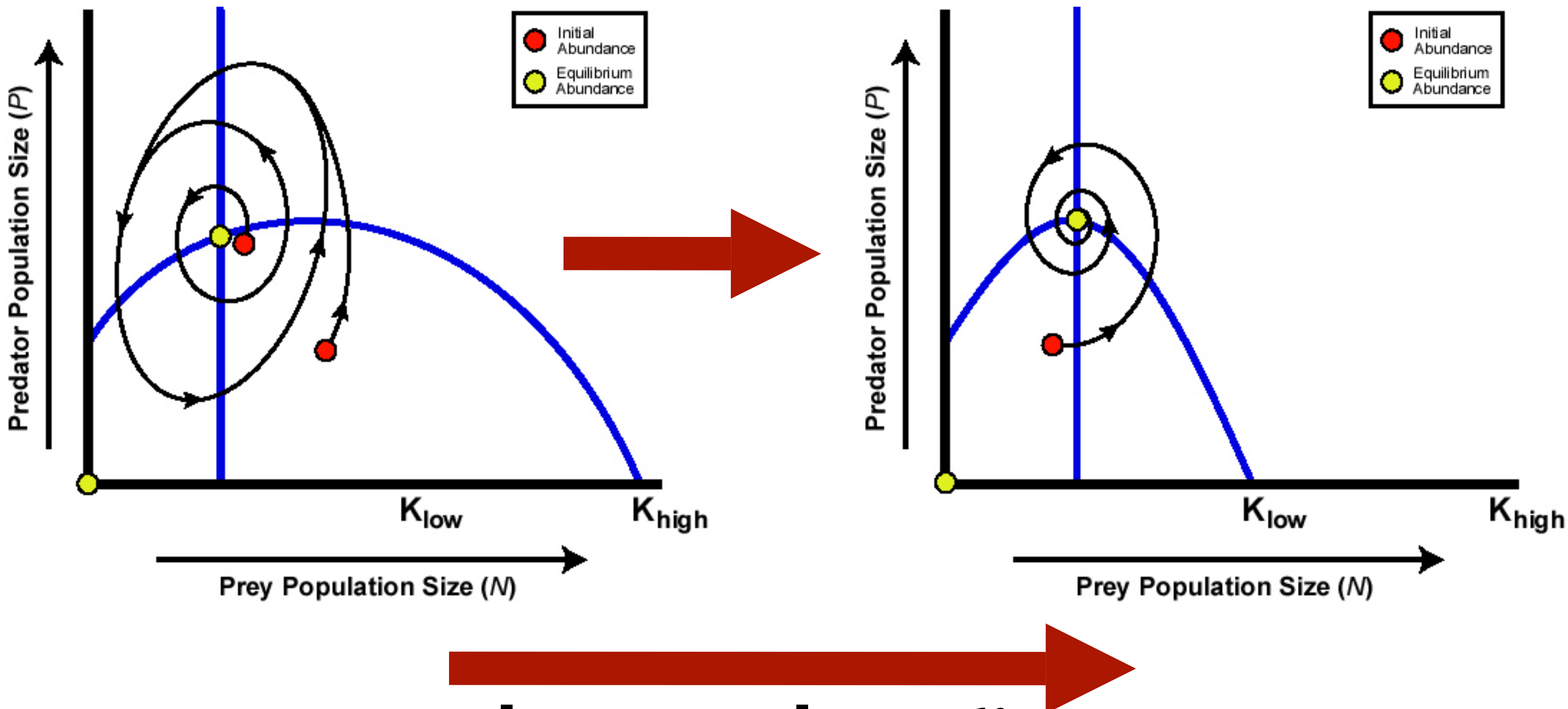
K is not independent of *r* :





(Veilleux 1979)

The Paradox of Enrichment:



decreasing r

Comparison of Predicted Outcomes:

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$\alpha \downarrow$	DE → CoEx	DE → CoEx
$r \downarrow$	DE → CoEx	CoEx → DE
$\mu \downarrow$	CoEx → DE	CoEx → DE
$e \downarrow$	DE → CoEx	DE → CoEx
$h \downarrow$	CoEx → DE	CoEx → DE

Comparison of Predicted Outcomes:

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$\alpha \downarrow$	DE $\rightarrow$ CoEx	DE $\rightarrow$ CoEx
$r \downarrow$	DE $\rightarrow$ CoEx	CoEx $\rightarrow$ DE
$\mu \downarrow$	CoEx $\rightarrow$ DE	CoEx $\rightarrow$ DE
$e \downarrow$	DE $\rightarrow$ CoEx	DE $\rightarrow$ CoEx
$h \downarrow$	CoEx $\rightarrow$ DE	CoEx $\rightarrow$ DE

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 = decreasing *r* should have **no effect** on the average equilibrium abundance (*K*).
   - H_a = decreasing *r* 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).

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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*:

$$\alpha > r + \mu \longrightarrow \text{dual extinction}$$

$$\alpha < r + \mu \longrightarrow \text{coexistence}$$

(Ginzburg *et al.* 1974)

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

Notation Confusion:

Prey growth function:

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

$$\gamma = \frac{r}{K} \qquad K = \frac{r}{\gamma}$$