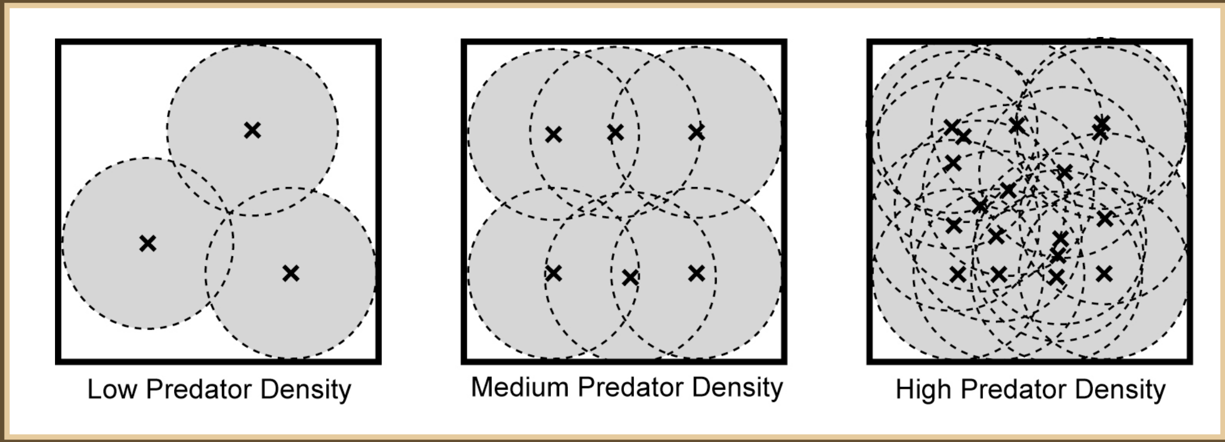
From Controversy to Consensus: The Indirect Interference Functional Response



Lev Ginzburg
Stony Brook University

Chris Jensen
Stony Brook University
Pratt Institute

Describing predator-prey systems:

$$\frac{dN}{dt} = \underbrace{\boxed{rN(1 - N/K)}}_{\text{Prey Growth}} - \underbrace{\boxed{f(\cdot)\,P}}_{\text{Consumption}}$$

$$\frac{dP}{dt} = \underbrace{\boxed{e\,f(\cdot)\,P}}_{\text{Predator Growth}} - \underbrace{\boxed{\mu\,P}}_{\text{Predator Death}}$$

Where N is prey density and P is predator density

Competing Functional Responses

$f\,(N)$

Holling Type II
"prey dependent"

$f\,(N, iP)$

Beddington-DeAngelis
"predator dependent"

$f\,(N/P^m)$

Hassell-Varley-Holling
"predator dependent"

$f\,(N/P)$

Arditi-Ginzburg
"ratio dependent"

Where N is prey density and P is predator density

Three Consequential Differences:

- Response of different trophic levels to system enrichment
- Length of trophic chains in relation to system enrichment
- Stability of trophic interaction

There has been much theoretical debate about which functional response should be used…

But what do experiments tell us?

Experiments that consider response to enrichment

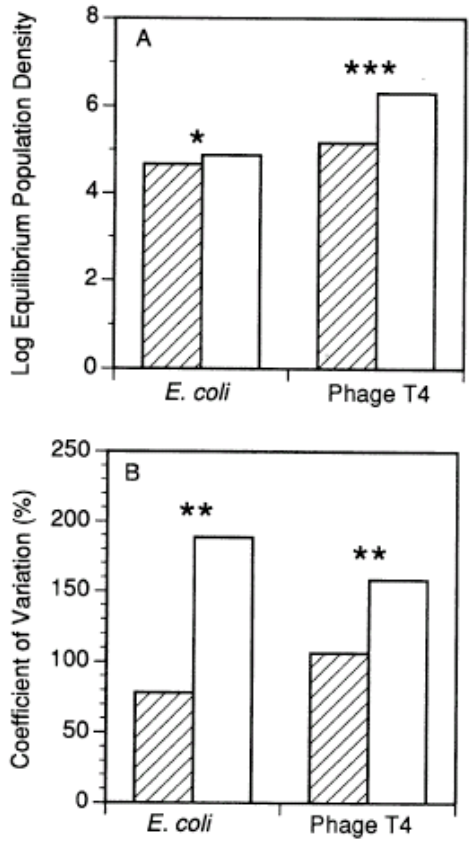
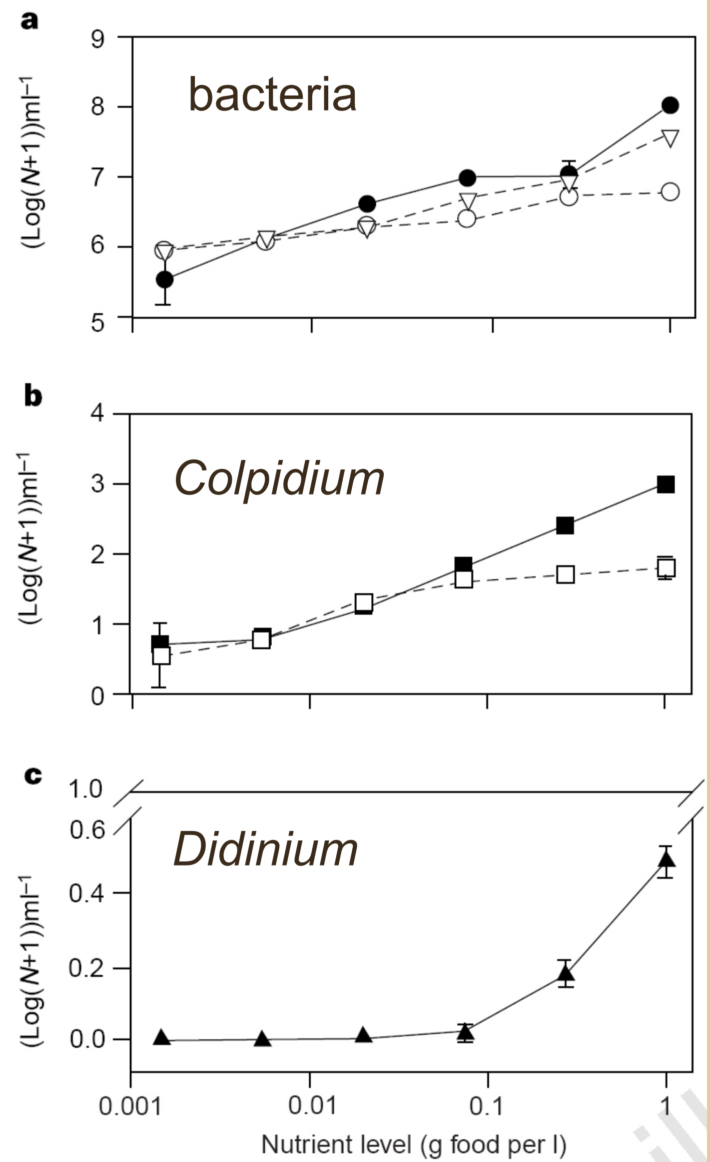


FIG. 4. Effect of glucose input concentration on equilibrium densities and population instability of *E. coli* and bacteriophage T4 populations interacting in a chemostat. Equilibrium population density is estimated as the grand mean of the mean population densities in three replicate chemostats. The equilibrium population densities (viruses/mL or bacteria/mL) have been log-transformed in this figure. Instability is estimated as the coefficient of variation of population densities averaged across three replicate chemostats. Stars indicate statistical significance: $*0.01 < P < 0.05$; $**0.001 < P < 0.01$; $***\ P < 0.001$. (A) equilibrium density, (B) instability. Key: striped bars = 0.1 mg/L glucose treatment; open bars = 0.5 mg/L glucose treatment.

Bohannan and Lenski 1997:

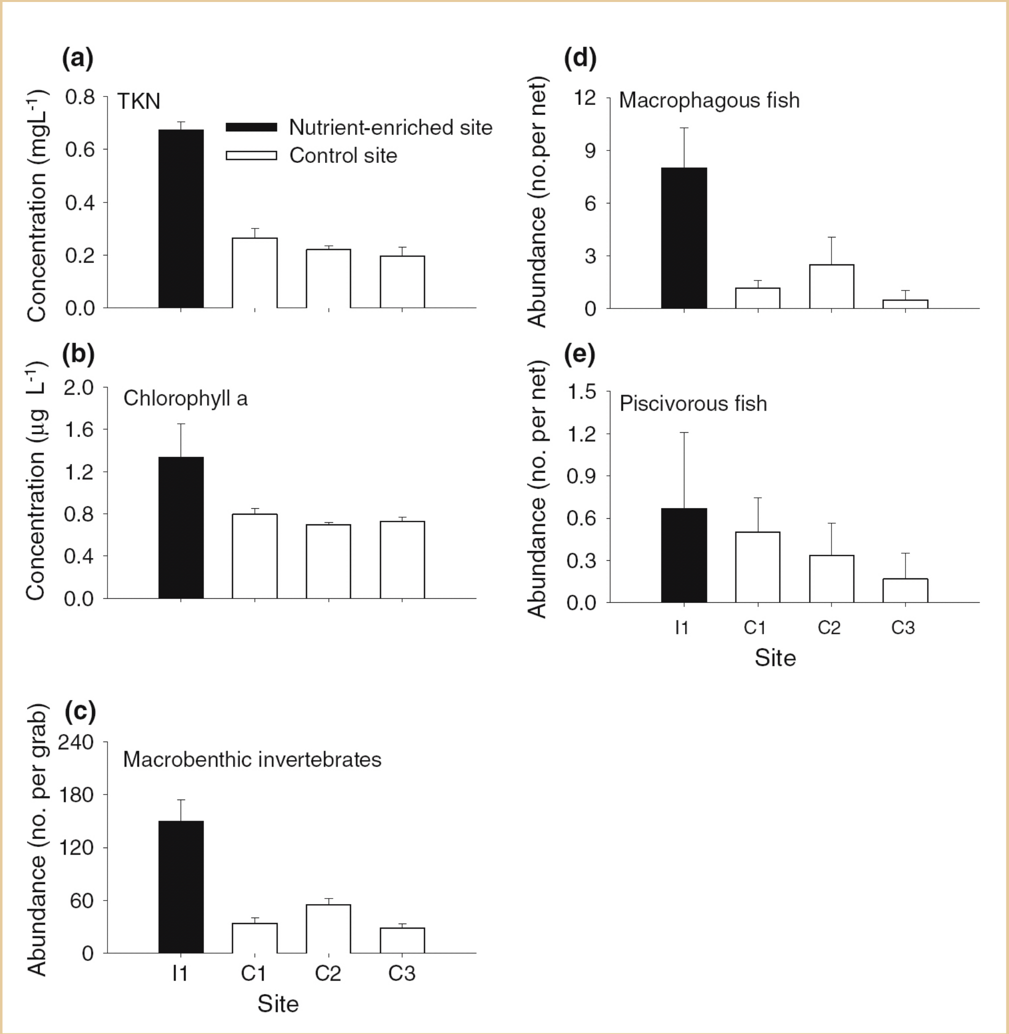
- Both levels respond positively to enrichment.



Kaunzinger and Morin 1998:

- All levels respond positively to enrichment.
- Top predator (*Didinium*) excluded at lower enrichment levels.

Bishop et al. 2006:



- Enriched site shows increased equilibrial densities at all trophic levels.

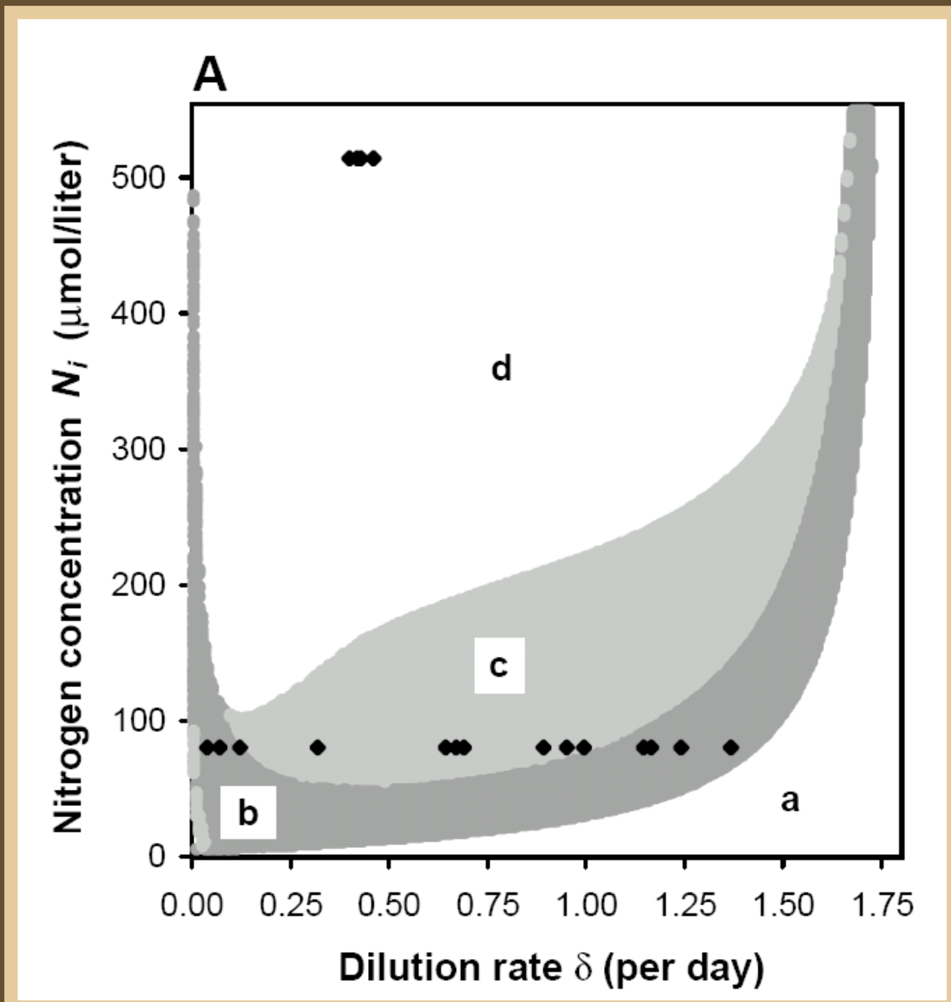
Veilleux 1979:

Table 1. Dynamic behaviour of Methyl Cellulose cultures

Cerophyl concentration (g per litre)	Number of runs	Time per cycle (h)	Response
1·80	17	96	Undamped oscillations, prey destroyed in all cases
1·58	9	117	Undamped oscillations, prey destroyed in six runs, predators die off first in three runs
1·35	18	134	Undamped oscillations, predators die off first
1·13	2	140	Large amplitude stable oscillations
1·01	4	158	Stable oscillations
0·90	20	162	Stable oscillations
0·77	6	145	Stable oscillations
0·68	18	156	Stable oscillations
0·59	2	—	Statistically random fluctuations—quasiequilibrium
0·45	10	—	Predator dies off
0·18	10	—	Predator dies off

- Pattern of stability in response to enrichment looks like Holling II [***f (N)***] or Beddington-DeAngelis [***f (N,iP)***] predator dependence
- But, changing nutrient levels shown to affect other parameters.

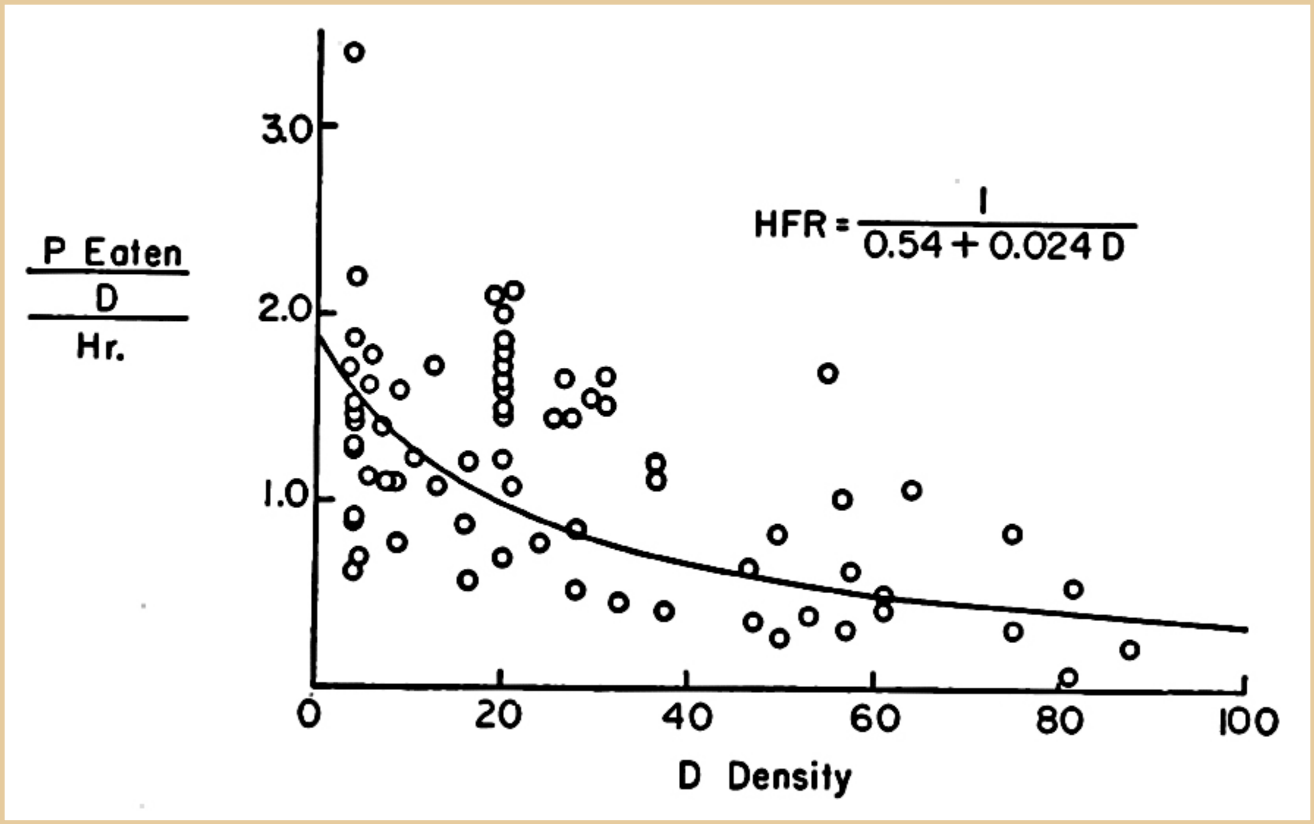
Fussmann et al. 2000:



- Pattern of stability in response to enrichment looks like Holling II [***f (N)***] or Beddington-DeAngelis [***f (N,iP)***] predator dependence
- But, prey extinction not shown (present at higher nitrogen concentrations?)

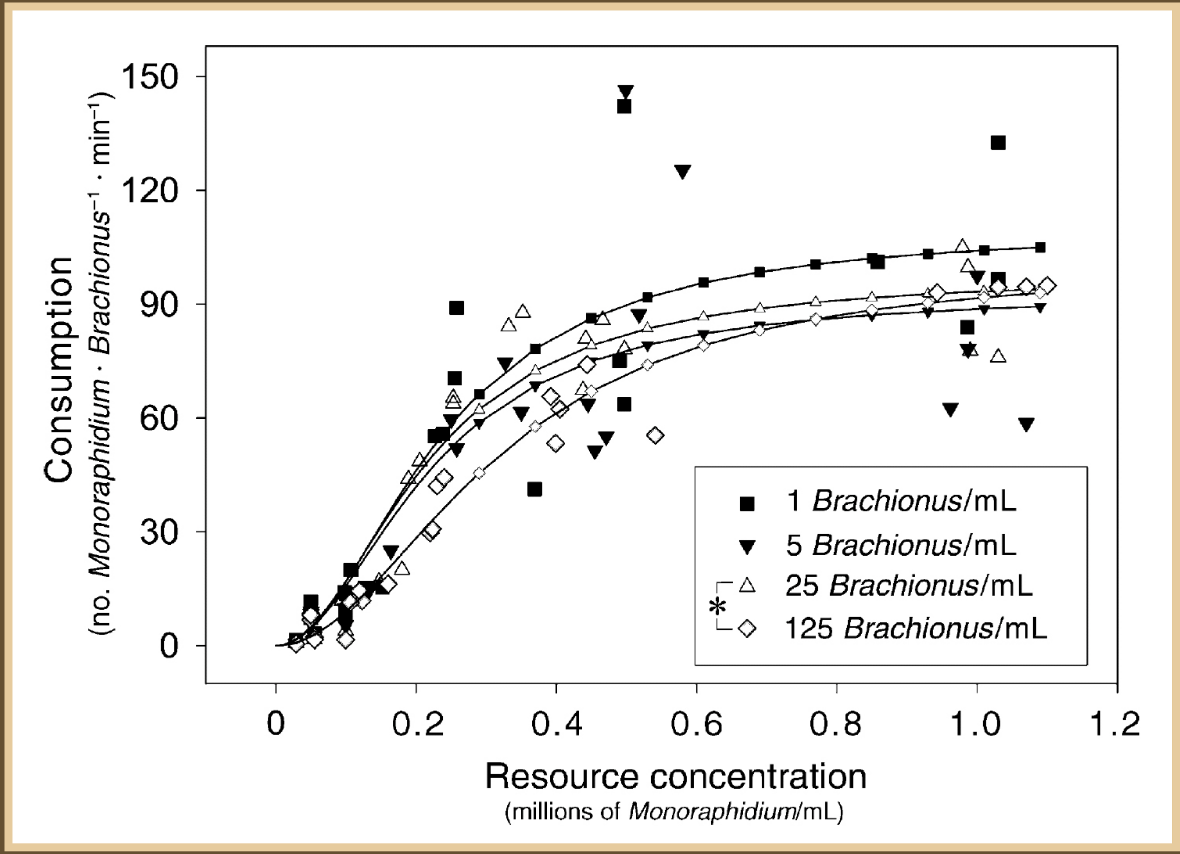
Experiments that directly measure functional response

Salt 1974:



Strong predator dependence is detected when consumption is measured over a discrete interval.

Fussmann et al. 2005:



When consumption is measured on a near instantaneous time scale, there is no detectable predator dependence.

Direct vs. Indirect Interference:

Direct Interference:

$$f\,(N, iP) = \frac{aN}{1 + ahN + iP}$$

Beddington-DeAngelis

Indirect Interference:

$$f\,(N, P) = ??????????$$

???????????

The fallacy of instantism:

- Many theorists take the *dt* in differential equations to be literally “an instant”.
- Under a less strict interpretation, we can think of *dt* being a discrete, biologically-relevant interval.
- Determining the correct *dt* to consider relies on a strong understanding of the biological details of a predator-prey system.

What consumption interval?

$dt \approx$ generation time

$dt \approx$ time of behavior

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

Prey Growth

Consumption

$dt \approx$ generation time

$dt \approx$?

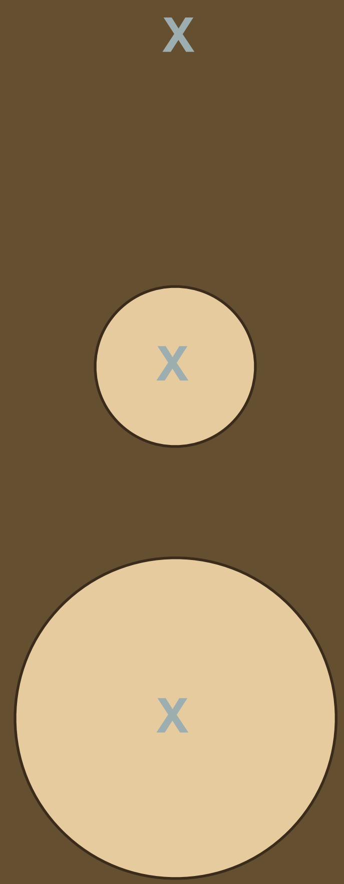
$$\frac{dP}{dt} = \boxed{e\,f(\bullet)\,P} - \boxed{\mu\,P}$$

Predator Growth

Predator Death

Consumption should be measured over the same interval as other processes

Prey depletion and home range:



Zero home range = instantaneous time scale

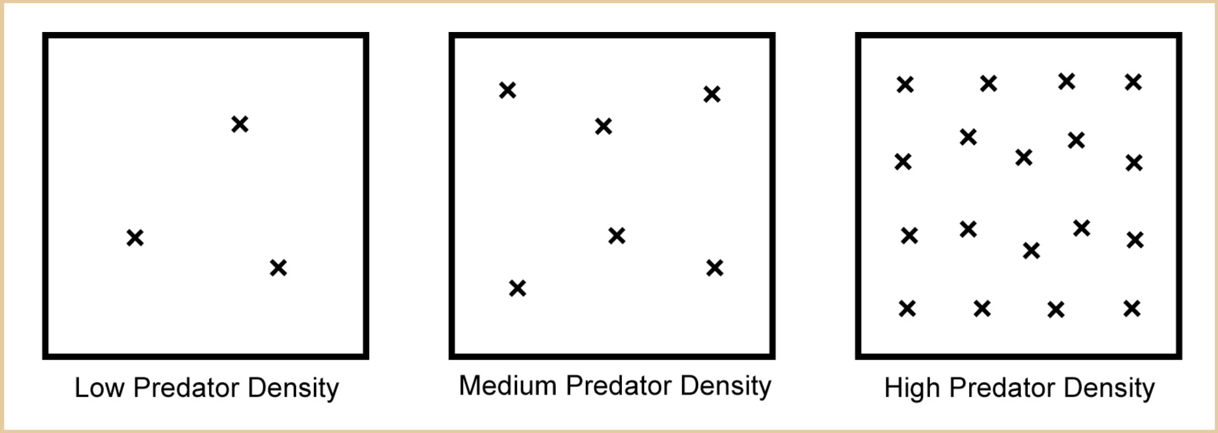
Small home range = relatively small *dt*

Large home range = relatively large *dt*

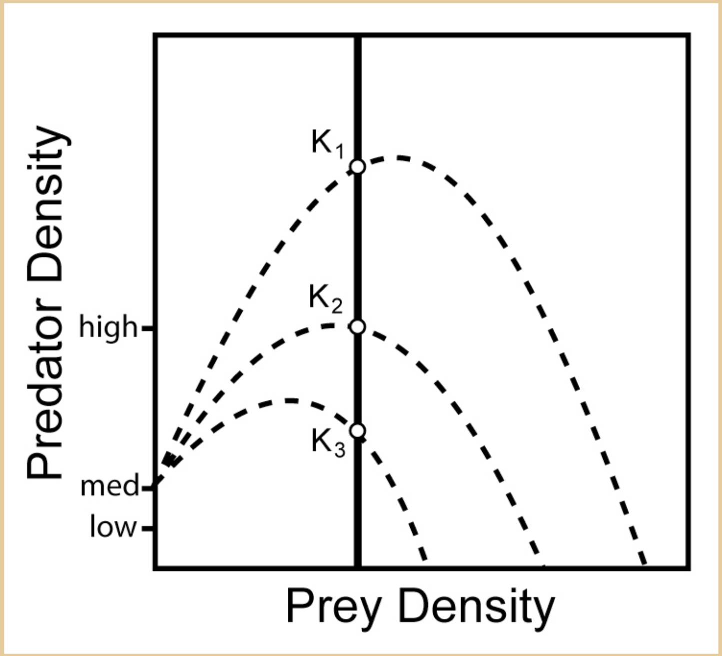
Our model:

- We consider home range as a proxy for the appropriate consumption interval.
- We assume that prey are uniformly distributed over a two-dimensional space.
- We assume that predators behaviorally minimize overlap of home range with other predators.

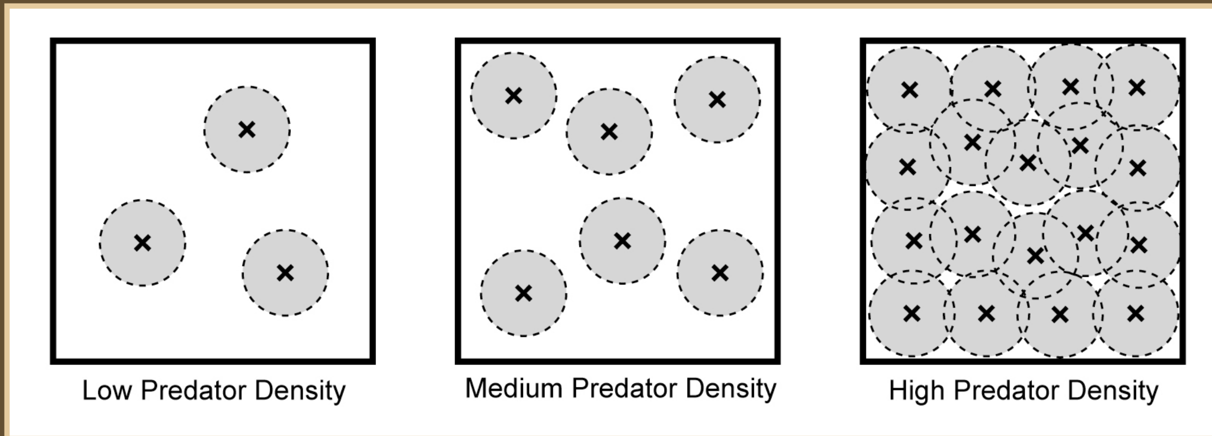
Zero Home Range:



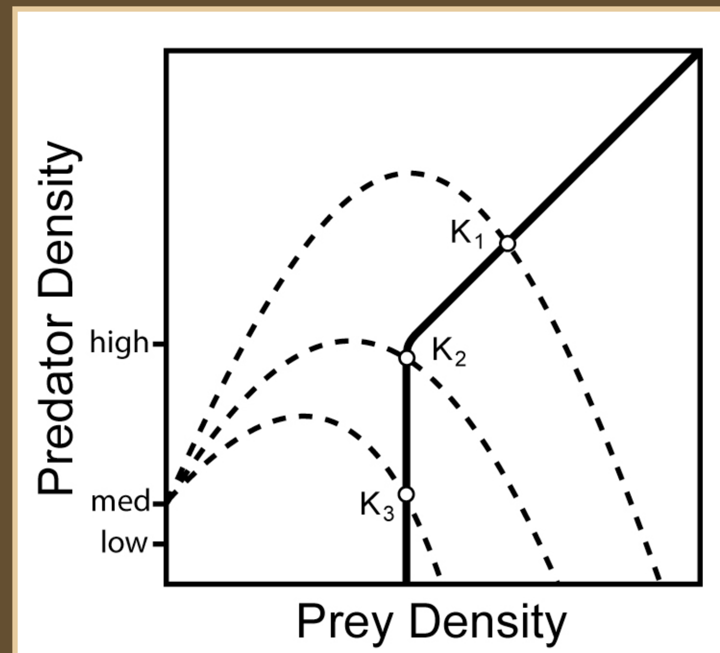
- Even at very high densities, predators cannot share prey.
- At all natural predator densities, predator isocline is vertical.
- System enrichment leads to increases in equilibrial predator density, but equilibrial prey density remains constant.
- Paradox of enrichment possible.



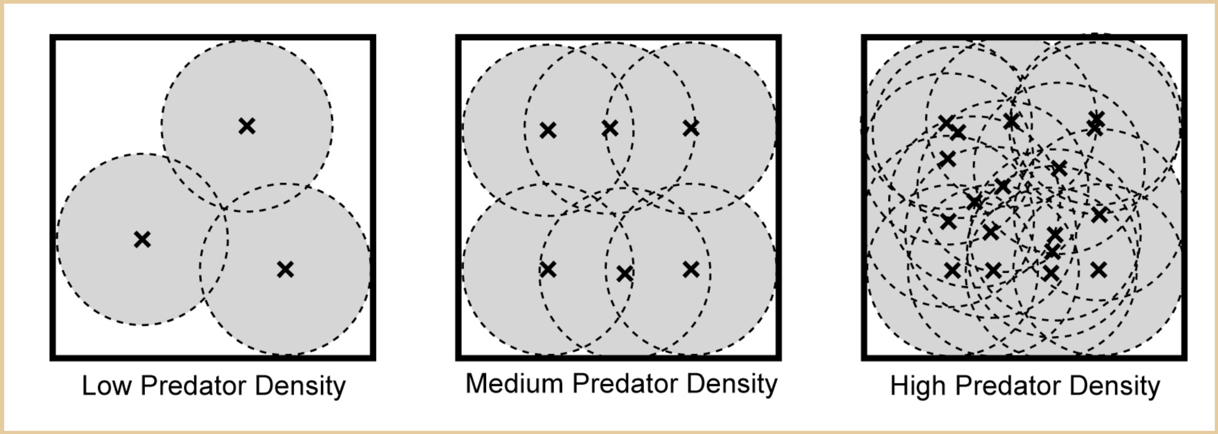
Small Home Range:



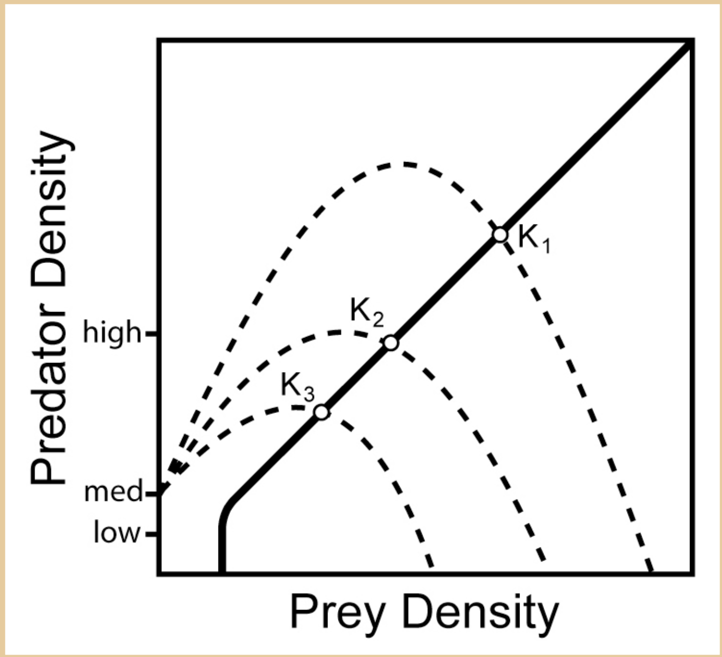
- At high densities, predators begin to share prey.
- The predator isocline slants at the density where sharing begins.
- At low levels of enrichment there is no increase in prey density; higher levels enrichment cause increases in both predator and prey.
- Paradox of enrichment absent.



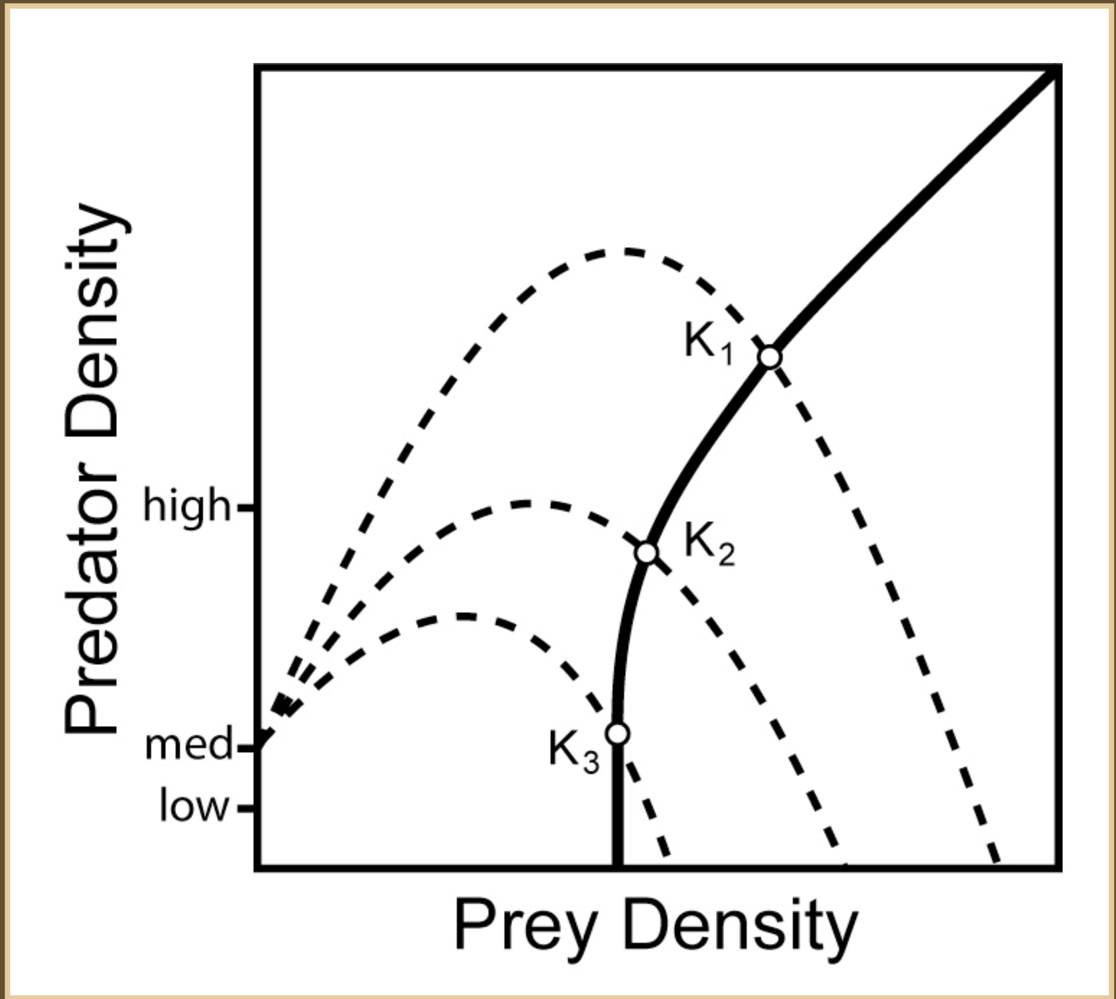
Large Home Range:



- Predators share prey at all but the lowest densities.
- For most natural predator densities, predator isocline is slanted.
- All but the lowest levels of enrichment lead to proportional increases in predator and prey densities.
- Paradox of enrichment absent.



What if the assumption of a territorial predator is relaxed?



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