

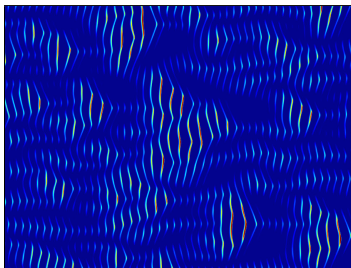
# Ecological Dynamics

## Predation (2 / 2)

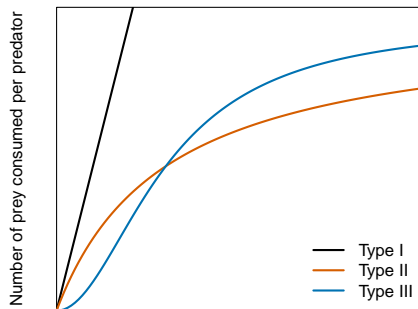
Dr. Tarik C. Gouhier  
<tarik.gouhier@gmail.com>

Northeastern University  
<http://blackboard.neu.edu>

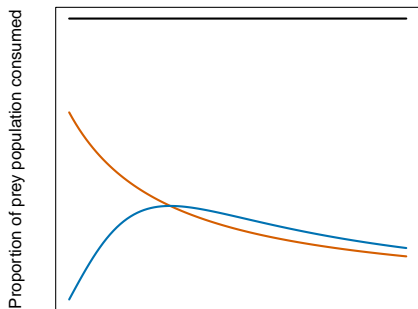
March 19, 2015



## Further refining the model: more realistic predation



Abundance of prey ( $N$ )



Abundance of prey ( $N$ )

There are three types of functional responses that describe how predators respond to increasing prey abundance (Holling, 1959a,b):

- **Type I:** linear relationship
- **Type II:** nonlinear saturating relationship
- **Type III:** nonlinear sigmoidal relationship

# Deriving the type II functional relationship

The type II functional response is by far the most widely used method for modeling predator satiation.

Its derivation is based on partitioning total time  $t$  spent feeding into the time the predator spends searching for prey  $t_s$  and the time spent handling prey once it is captured  $t_h$ :

$$t = t_s + t_h$$

Letting  $n$  be the number of prey captured in time  $t$  and  $h$  the handling time per prey, we can express the time handling prey as:

$$t_h = hn$$

## Deriving the type II functional relationship

Similarly, we can express the total time searching for prey  $t_s$  as a function of prey abundance  $N$ , prey captured  $n$  and attack rate  $a$ :

$$n = Nat_s$$

This can be rearranged to yield:

$$t_s = \frac{n}{aN}$$

We can now substitute these terms into the original equation to yield:

$$t = \frac{n}{aN} + hn$$

We now multiply the second term by  $\frac{aN}{aN} = 1$ :

$$t = \frac{n}{aN} + \frac{aNhn}{aN}$$

# Deriving the type II functional relationship

Factoring by  $n$  yields:

$$t = n \left( \frac{1 + aNh}{aN} \right)$$

We can now rearrange the equation to obtain the *per capita* consumption rate  $n/t$ :

$$\boxed{n/t = \frac{aN}{1 + aNh}}$$

When the handling time per prey  $h$  is low, the denominator is very small and the type II functional response becomes equivalent to the type I functional response.

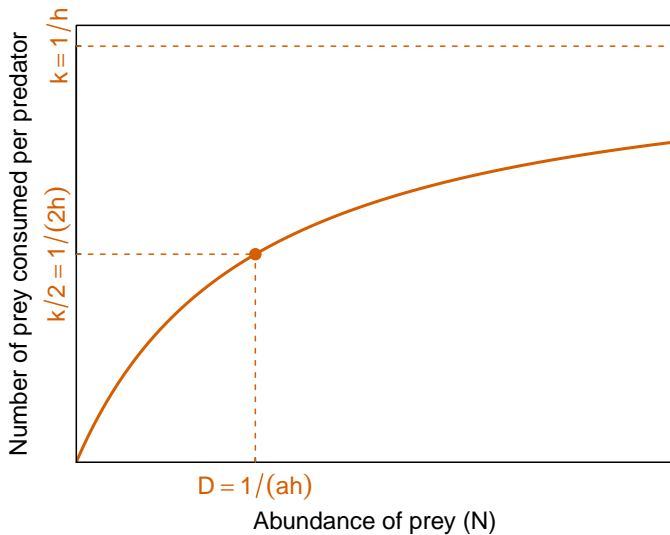
## Deriving the type II functional relationship

The type II functional relationship can also be expressed in Monod or Michaelis-Menton form by defining the **maximum consumption rate**  $k = \frac{1}{h}$  and the **half-saturation constant**  $D = \frac{1}{ah}$ , and by multiplying the numerator and denominator by  $\frac{1}{ah}$ :

$$n/t = \frac{kN}{D + N}$$

These two formulations are equivalent and often used interchangeably in the literature.

# Visual depiction of type II functional relationship



# The type III functional relationship

- The type III functional response can also be used to model the *per capita* consumption rate of predators:  $n/t = \frac{kN^2}{D^2 + N^2}$
- This sigmoidal relationship can come about when predators switch to prey as they become more abundant or when foraging has both fixed and variable costs
- The type II and type III functional relationships behave similarly when prey abundance is high



# Estimating type II functional relationships from data

The parameters of the type II functional relationship can be estimated from data via regression.

To do so, regress the reciprocal of the type II against  $N' = \frac{1}{N}$  to obtain the attack rate  $a$  and the handling time per prey  $h$ :

$$\frac{1 + ahN}{aN} = \underbrace{\frac{1}{a}}_{\text{slope}} \cdot \frac{1}{N} + \underbrace{h}_{\text{intercept}} = \underbrace{\frac{1}{a}}_{\text{slope}} \cdot N' + \underbrace{h}_{\text{intercept}}$$

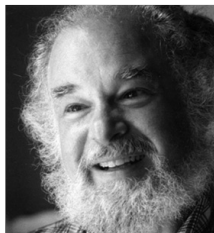
The parameters of the Monod version of the type II can also be estimated by regressing the reciprocal of the type II against  $N' = \frac{1}{N}$  to obtain the maximum consumption rate  $k$  and the half-saturation constant  $D$ :

$$\frac{D + N}{kN} = \underbrace{\frac{D}{k}}_{\text{slope}} \cdot \frac{1}{N} + \underbrace{\frac{1}{k}}_{\text{intercept}} = \underbrace{\frac{D}{k}}_{\text{slope}} \cdot N' + \underbrace{\frac{1}{k}}_{\text{intercept}}$$

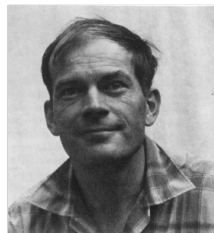
# The Rosenzweig-MacArthur predator-prey model

## The Rosenzweig-MacArthur predator-prey model

Rosenzweig and MacArthur (1963) integrated density-dependent growth of the prey and saturating consumption by the predator to create a more realistic depiction of predator-prey interactions.



**Michael Rosenzweig**



**Robert H. MacArthur**

# The Rosenzweig-MacArthur predator-prey model

$$\begin{aligned}\frac{dN}{dt} &= rN \left( 1 - \frac{N}{K} \right) - \frac{aNP}{1 + ahN} \\ \frac{dP}{dt} &= \frac{abNP}{1 + ahN} - mP\end{aligned}$$

Where  $r$  and  $K$  are the prey's growth rate and carrying capacity and  $a$ ,  $b$ ,  $h$  and  $m$  are the predator's attack rate, efficiency (number of predators produced per prey consumed), handling time and mortality.

The Rosenzweig-MacArthur model has two boundary equilibria and one interior equilibrium. We will now determine their stability.

# Analyzing the Rosenzweig-MacArthur model

To assess the stability of the equilibria, we must first write the Jacobian matrix  $\mathbf{J}$  by taking the partial derivatives of each population growth rate  $\dot{N}$  and  $\dot{P}$  with respect to each variable  $N$  and  $P$ :

$$\mathbf{J} = \begin{bmatrix} r - \frac{2rN}{K} - \frac{aP}{(a+ahN)^2} & -\frac{aN}{1+ahN} \\ \frac{abP}{(1+ahN)^2} & \frac{abN}{1+ahN} - m \end{bmatrix}$$

We now assess the stability of the extinction equilibrium  $\{\hat{N} = 0, \hat{P} = 0\}$ :

$$\mathbf{J}(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}$$

## Analyzing the Rosenzweig-MacArthur model

To determine the eigenvalues, we subtract  $\lambda \mathbf{I}$  from  $\mathbf{J}(0, 0)$  and find the characteristic polynomial by computing the determinant:

$$0 = (r - \lambda_1)(-\gamma - \lambda_2)$$

There are two solutions to this equation:  $\lambda_1 = r$  and  $\lambda_2 = -m$ . This means that the extinction equilibrium is a saddle point because it will be stable for  $P$  as long as  $m > 0$  but unstable for  $N$  as long as  $r > 0$ .

We now determine the stability of the  $N$  equilibrium  $\{\hat{N} = K, \hat{P} = 0\}$ :

$$\mathbf{J}(K, 0) = \begin{bmatrix} -r & -\frac{aK}{1+ahK} \\ 0 & \frac{abK}{1+ahK} - m \end{bmatrix}$$

## Analyzing the Rosenzweig-MacArthur model

The determinant of the jacobian yields the following characteristic polynomial:

$$0 = (-r - \lambda_1) \left( \frac{abK}{1 + ahK} - m - \lambda_2 \right)$$

There are two solutions to this equation:  $\lambda_1 = -r$  and  $\lambda_2 = \frac{abK}{1+ahK} - m$ .

This means that the  $N$  equilibrium will be stable as long as  $m > \frac{abK}{1+ahK}$  (i.e., predator mortality greater than maximum predator growth due to prey consumption).

We are now ready to analyze the interior equilibrium:

$$\hat{N} = \frac{m}{a(b - hm)}$$
$$\hat{P} = \frac{r}{aK} \left[ K + N(ahK - 1) - ahN^2 \right]$$

# Analyzing the Rosenzweig-MacArthur model

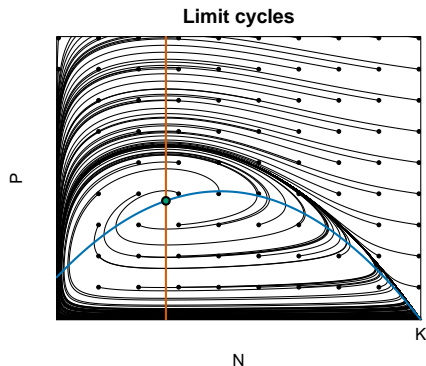
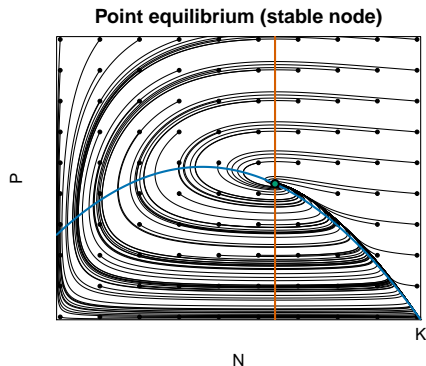
The stability of this equilibrium is going to be fairly painful to analyze using the traditional eigenvalue approach.

Thankfully, May (1973) developed a semi-graphical approach for determining the stability of the interior equilibrium in this model.

The key insight is that the predator's ZNGI ( $\hat{N}$ ) is a vertical line but the prey's ZNGI is an inverted parabola.

The stability of the interior equilibrium will depend on whether the ZNGI intersect in the ascending or descending part of the prey's ZNGI (May, 1973).

# Stability of interior equilibrium



The interior equilibrium will be a **stable node** if the ZNGI of the **predator** and the **prey** intersect in the descending part of the **prey's ZNGI**.

The model will exhibit **limit cycles** if the ZNGI of the **predator** and the **prey** intersect in the ascending part of the **prey's ZNGI** (May, 1973).



# Stability of interior equilibrium

To assess the stability of the interior equilibrium, we need to compute the partial derivative  $\frac{\partial \hat{P}}{\partial \hat{N}}$  to determine when prey's ZNGI reaches its maximum value:

$$\frac{\partial \hat{P}}{\partial \hat{N}} = \frac{r}{aK} \left[ ahK - 1 - \frac{2hm}{b - hm} \right] = 0$$

This is only possible if the term in the brackets is equal to zero:

$$0 = ahK - 1 - \frac{2hm}{b - hm}$$

## Stability of interior equilibrium

We can solve this equation with respect to any of these parameters, but for historical reasons, we will solve for  $K$ :

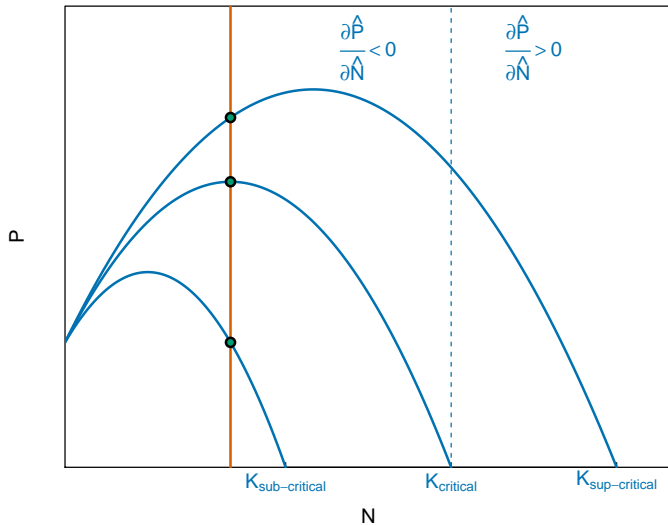
$$K_{\text{critical}} = \left(1 + \frac{2hm}{b - hm}\right) \cdot \frac{1}{ah}$$

This means that when  $K > K_{\text{critical}}$ ,  $\frac{\partial \hat{P}}{\partial \hat{N}} > 0$  so the ZNGI will intersect in the ascending part and the equilibrium will be a **limit cycle**.

Conversely, when  $K < K_{\text{critical}}$ ,  $\frac{\partial \hat{P}}{\partial \hat{N}} < 0$  so the ZNGI will intersect in the descending part and the equilibrium will be a **stable node**.

The transition from a stable node to a limit cycle is called a **Hopf bifurcation**.

# Stability of interior equilibrium



# The paradox of enrichment

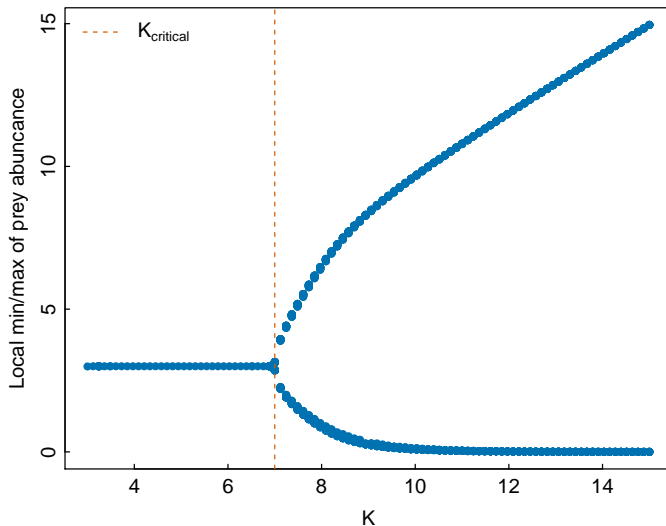
Rosenzweig (1971) coined the term **paradox of enrichment** based on this analysis.

Specifically, he noted that enriching a system (increasing its carrying capacity  $K$ ) would destabilize it by inducing a shift from a stable node (point equilibrium) to a limit cycle.

Furthermore, enrichment beyond  $K_{\text{critical}}$  generates limit cycles of greater amplitude and, eventually, extinction of both the prey and the predator.

Rosenzweig (1971) hypothesized that the paradox of enrichment could explain the boom-and-bust dynamics sometimes observed when pests invade agricultural systems.

# The paradox of enrichment



# Full circle on predation

We have gone full circle when it comes to determining the dynamics of predator-prey systems:

- The Lotka-Volterra model indicated that oscillations were the only possible outcome
- Adding density-dependence for the prey yields an interior equilibrium that is always stable
- Finally, adding a type II functional response for the predator yields an intermediate scenario whereby the system can either experience a stable interior equilibrium or limit cycles
- Overall, this shows the importance of ensuring that the mathematical assumptions are relevant to the natural system being modeled

# Apparent competition

## Apparent competition

Holt (1977), Holt (1984) and Holt et al. (1994) showed that apparent competition, a process by which species are coupled via a common predator, could lead to exclusion even if the species were not competing for a common resource.

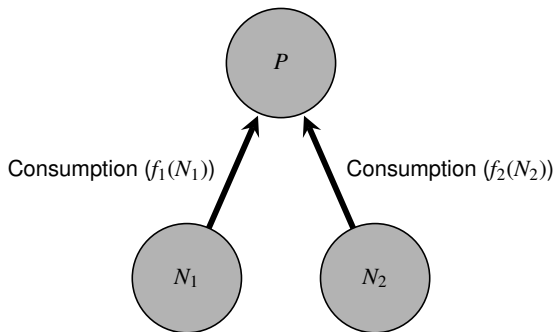


**David Tilman**



**Robert D. Holt**

# A diagram of apparent competition



Note that prey  $N_1$  and  $N_2$  are not necessarily competing for the same resources.



# Modeling apparent competition

Holt (1977) used mechanistic resource competition as a starting point to develop the following model demonstrating apparent competition:

$$\begin{aligned}\frac{dP}{dt} &= P \left( \sum_{i=1}^N a_i b_i N_i - m \right) + I - eP \\ \frac{dN_i}{dt} &= N_i (r_i - a_i P)\end{aligned}$$

Where  $a_i$ ,  $b_i$  are the predator attack rates and efficiencies for prey  $i$ ,  $m$  is predator mortality,  $I$  and  $e$  are predator immigration and emigration rates, and  $r_i$  is the growth rate of prey  $i$ .

Here, we will use the invasion criterion to determine when a second prey  $N_2$  can invade a system consisting of a single prey  $N_1$  and a generalist predator  $P$ .

# Modeling apparent competition

To do so, we solve the model at equilibrium:

$$P_1^* = \frac{r_1}{a_1}$$
$$N_1^* = \frac{m + e - \frac{I}{r_1/a_1}}{a_1 b_1}$$

For  $N_2$  to invade,  $\dot{N}_2 > 0$ :

$$\dot{N}_2 = N_2 (r_2 - a_2 P_1^*)$$

Hence,  $N_2$  can invade if  $\frac{r_2}{a_2} > P_1^*$ . Since  $P_2^* = \frac{r_2}{a_2}$ , the following must hold:

$$\boxed{P_2^* > P_1^*}$$

**This is known as the  $P^*$  rule: the prey with the highest  $P^*$  value will exclude all others.**

# Predation, competition and coexistence

## Keystone predation

Paine (1966, 1969) showed that the seastar *Pisaster ochraceus* played a critical role in promoting species diversity by preferentially consuming competitively dominant mussels in intertidal ecosystems on Tatoosh Island (Pacific Northwest). Holt et al. (1994) explored how predation could promote coexistence.

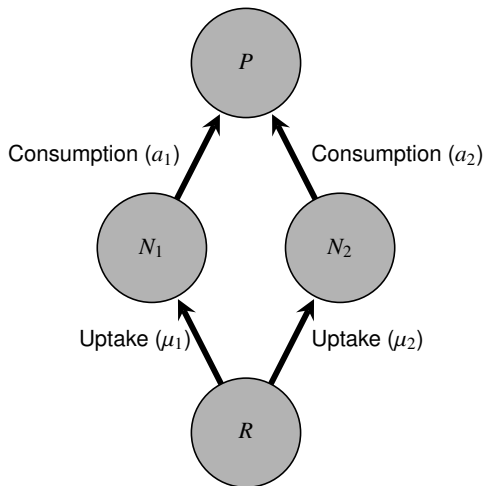


**Robert T. Paine**



**Robert D. Holt**

# A diagram of keystone predation



Note that prey  $N_1$  and  $N_2$  are now competing for a common resource.

# Modeling keystone predation

We can model keystone predation by extending the apparent competition model to include resource competition:

$$\begin{aligned}\frac{dP}{dt} &= P (a_1 b_1 N_1 + a_2 b_2 N_2 - m) \\ \frac{dN_1}{dt} &= N_1 (\mu_1 R - m_1 - a_1 P) \\ \frac{dN_2}{dt} &= N_2 (\mu_2 R - m_2 - a_2 P) \\ \frac{dR}{dt} &= S - \delta R - N_1 \mu_1 \frac{R}{Y_1} - N_2 \mu_2 \frac{R}{Y_2}\end{aligned}$$

# Modeling keystone predation

Here, it is sufficient to solve the  $\dot{N}_i = 0$  to understand the effect of keystone predation on coexistence:

$$R_1^* = \frac{m_1 + a_1 P_1^*}{\mu_1}$$
$$R_2^* = \frac{m_2 + a_2 P_2^*}{\mu_2}$$

Since  $R_1^* = R_2^*$  is necessary for the prey species to coexist, we have:

$$\frac{m_1 + a_1 P_1^*}{\mu_1} = \frac{m_2 + a_2 P_2^*}{\mu_2}$$

After some algebra, this yields:

$$P_1^* a_1 \mu_2 + \mu_2 m_1 = P_2^* a_2 \mu_1 + \mu_1 m_2$$

# Modeling keystone predation

Since  $P_1^* = P_2^*$  is necessary for the prey species to coexist, we have:

$$\frac{P_1^*}{P_2^*} = 1 = \frac{a_2\mu_1 + \mu_1m_2}{a_1\mu_2 + \mu_2m_1}$$

This can be rewritten as:

$$\mu_1 (a_2 + m_2) = \mu_2 (a_1 + m_1)$$

This last expression shows that prey species can coexist as long as the predator's preference offsets competitive differences (i.e., the predator preferentially consumes competitively dominant species).

# References

- Holling, C. 1959a. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist*, **91**:293–320.
- Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**:385–398.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**:197–229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist*, **124**:377–406.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, **144**:741–771.
- May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.



# References

- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist*, **100**:65–75.
- Paine, R. T. 1969. *Pisaster*-*tegula* interaction - prey patches, predator food preference, and intertidal community structure. *Ecology*, **50**:950–961.
- Rosenzweig, M. L. 1971. Paradox of enrichment - destabilization of exploitation ecosystems in ecological time. *Science*, **171**:385–387.
- Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist*, **97**:209–223.