Two Interacting Populations: Predation

Bio 534, Fall 2011

1 Introduction

1.1 Objectives

- Consider primary types of interactions between two species
- Discuss consumer–resource interactions in general
- Investigate alternative ways of modeling predator–prey dynamics in detail
- Identify three general types of functional responses and contemplate when they might be ecologically relevant

2 Consumer–Resource Interactions

In this course we will focus our attention on Consumer–Resource interactions $(-, 0)$ in general, but spend most of our time discussing the more specific topic of Predator–Prey interactions. However, the modeling principles we learn can be applied broadly to the other interaction types.

3 Predation

3.1 Lotka–Volterra Formulation

A.J. Lotka and V. Volterra first formulated this simple strategic model independently in the 1920's.

Diagrams Consider both a Forrester type diagram for this system and a process tree representation.

This will be drawn on the board.

Equations Consider a closed prey population N_1 in a defined area A that has a constant "natural" per-capita mortality rate m_1 and birth rate b so that its *net growth rate* in the absence of predation is $r = b - m_1$. We then need to consider the additional per-capita prey mortality generated by a predator population N_2.

Assume that the prey are randomly distributed in A, that each predator can search an area A_s per time unit, and that a fraction σ of each predator–prey encounter results in a prey death. We can then define an *attack rate*, $\alpha = \sigma(A_s/A)$. Thus, each predator consumes an average of αN_1 prey. This is the predation *functional response*.

The predator population grows as new predators are created from the prey consumed. Let ϵ be the unitless efficiency of the predators ability to convert prey into predator individuals.

Therefore, our system of predator–prey equations are

$$\frac{dN_1}{dt} = \dot{N}_1 = \underbrace{rN_1}_{\text{growth}} - \underbrace{\alpha N_1 N_2}_{\text{predation}} \tag{1}$$

$$\frac{dN_2}{dt} = \dot{N}_2 = \underbrace{\epsilon\alpha N_1 N_2}_{\text{predation}} - \underbrace{m_2 N_2}_{\text{mortality}} \tag{2}$$

The model symbols are defined as follows:

Table 1: Definition of model variables and parameters

Symbol	Definition
State Variables	
N_1	Prey population density
N_2	Predator population density
Parameters	
r_1	intrinsic growth rate of prey
α	attack rate; per capita rate at which predators consume prey
$\alpha = \sigma(A_s/A)$	
A	area in which prey are randomly located
A_s	area searched per time
σ	prey encounter rate
ϵ	efficiency with which a predator converts captured prey into new predators
m_2	per capita death rate of predators

3.2 Equilibrium Analysis & Graphical Solutions

Like with the previous models we have studied, we can use the equilibrium values of the model to analyze the possible behavior of the model. Recall that the equilibrium of a model is where the rate of change is zero (i.e., the population is not changing). Thus, we identify the equilibriums by setting the differential equations equal to zero and then solving for the population density at those points.

For the Lotka–Volterra equations there are two types of equilibriums. The first is where $N_1 = N_2 = 0$. These are unstable and largely trivial equilibriums. The second set of equilibriums occur where the per-capita population change is zero. We can find this by setting $\dot{N}_1/N_1$ and $\dot{N}_2/N_2$ equal to zero as follows.

N_1 Equilibrium Population Density

$$\begin{aligned} \frac{\dot{N}_2}{N_2} &= \epsilon\alpha N_1 - m_2 \\ 0 &= \epsilon\alpha N_1 - m_2 \\ m_2 &= \epsilon\alpha N_1 \\ N_1^* &= \frac{m_2}{\epsilon\alpha} \end{aligned} \tag{3}$$

N_2 Equilibrium Population Density

$$
\begin{aligned}
\frac{\dot{N}_1}{N_1} &= r - \alpha N_2 \\
0 &= r - \alpha N_2 \\
\alpha N_2 &= r \\
N_2^* &= \frac{r}{\alpha}
\end{aligned}
\tag{4}
$$

State Space Graphs with Equilibrium Isoclines

Draw graphs on board

Example Numerical Realizations Figure 1 shows the dynamics of the basic Lotka–Volterra equations with $r = \alpha = 1$, $\epsilon = m_1 = 0.1$. Figure 1 (top) had initial population densities of $N_1 = 2$ and $N_2 = 1$, while the bottom panel had initial densities of 1 and 4.9, respectively. These are numerical approximations generated using the *lsoda* algorithm in R .

3.3 Assumptions

Gotelli (2008) identifies four key assumptions of the Lotka–Volterra predation model. They are:

- Growth of the victim (prey) population is limited only by predation.
- The predator is a specialist that can persist only if the victim population is present. $N_1 = 0 \implies N_2 \to 0$
- Individual predators can consume an infinite number of victims. – predators are never satiated and experience no interference competition.
- Predator and victim encounter one another randomly in a homogeneous environment. – no spatial/temporal refuges

3.4 Adding Density Dependence

Diagram This will be drawn on the white board.

Equations

$$
\dot{N}_1 = \underbrace{rN_1\left(1 - \frac{N_1}{K_1}\right)}_{\text{growth}} - \underbrace{\alpha N_1 N_2}_{\text{predation}} \tag{5}
$$

$$
\dot{N}_2 = \underbrace{\epsilon \alpha N_1 N_2}_{\text{predation}} - \underbrace{m_2 N_2}_{\text{mortality}} \tag{6}
$$

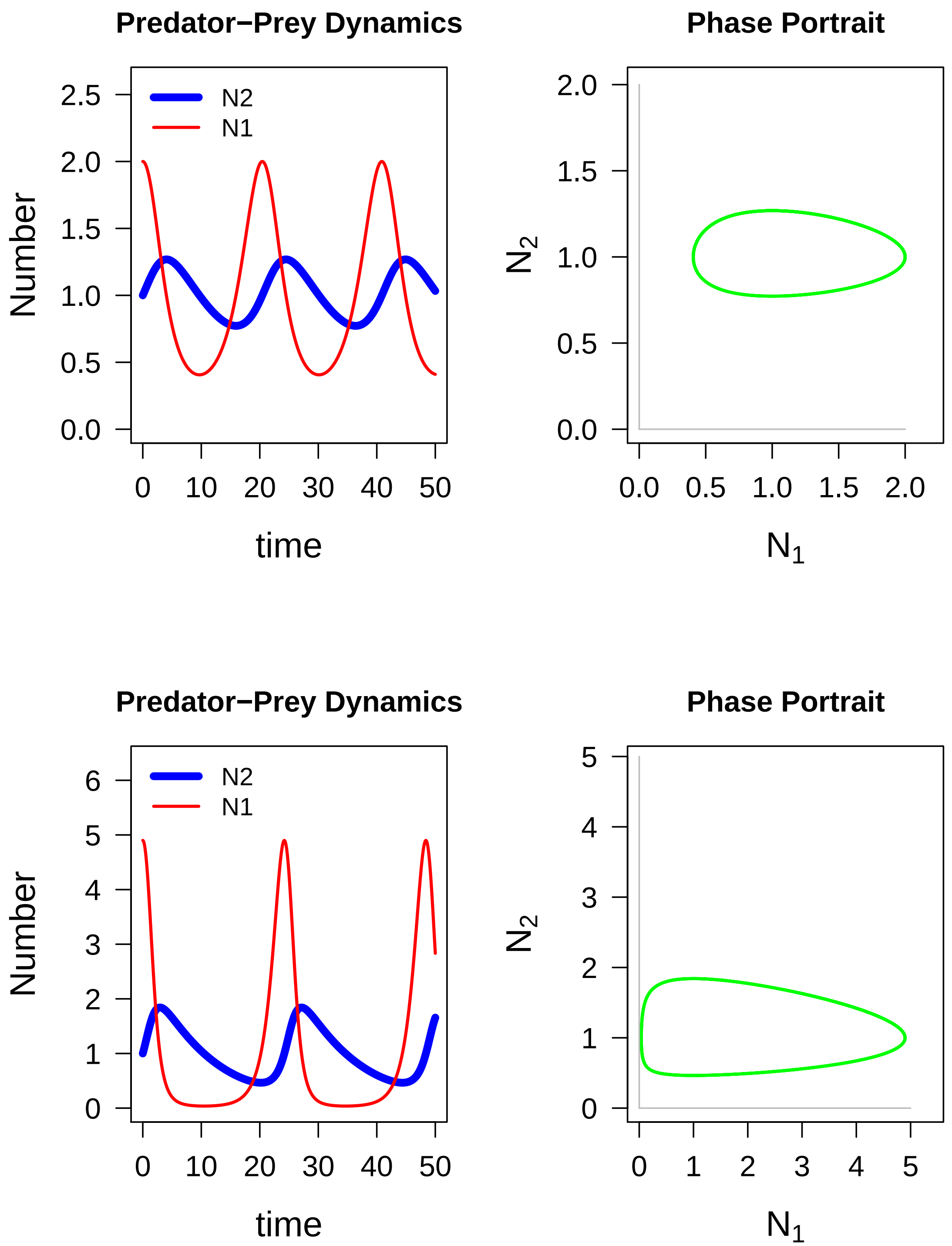

Figure 1: Dynamics of the classic Lotka-Volterra predation equations. The left panel shows the temporal dynamics of the two species and the right panel shows the phase portrait, or the state–space plot of the solution. Top panels are simulated with initial population densities of $N_1 = 2$ and $N_2 = 1$ while the bottom panels started at $N_1 = 1$ and $N_2 = 4.9$

Equilibrium Values In this case there are three sets of equilibriums: (1) $N_1 = N_2 = 0$, (2) $N_1 = K_1$ and $N_2 = 0$, and (3) where both species coexist $N_1 = N_1^*$ and $N_2 = N_2^*$. N_1^* and N_2^* can again be found by setting equations 5 and 6 equal to zero and solving for the respective population density, which generates

$$N_1^* = \frac{m_2}{\epsilon\alpha} \qquad \text{and} \qquad N_2^* = \frac{r}{\alpha}\left(1 - \frac{m_2}{\epsilon\alpha K_1}\right). \tag{7}$$

Thus, coexistence is possible if the predator has some excess production when the prey is at its carrying capacity, $K_1 \geq \frac{m_2}{\epsilon\alpha}$.

Numerical Realizations Figure 2 shows the dynamics of the Lotka–Volterra equations with prey intraspecific competition, where the parameters are defined as above and $K_1 = 10$. These simulations were begun at initial population densities of $N_1 = 3$ and $N_2 = 0.1$ in Figure 2 (top), while they were 3 and 1.5, respectively, in Figure 2 (bottom).

Additional Thoughts Gurney and Nisbet (1998) note that the amplitude of the predator–prey cycles generated by this system of equations is unrealistically dependent upon the initial population equations.

4 Alternative Functional Responses for Predation

Holling identified three possible types of functional responses which are shown in Figure 3. Recall that a **functional response** is a description of how the number of prey eaten per predator changes with prey density. The classic Lotka-Volterra formulation of predation uses a linear or **Type I** functional response, $f_p(N_1) = \alpha N_1$. In most cases, however, it would be better to use a **Type II** functional response because most real consumers will reach a satiation level at which their consumption rate slows or stops. A **Type III** functional response might be appropriate if the encounter rate or attack rate increases as a function of prey density $\alpha = f(N_1)$. Case (2001) suggests that this might occur if as a predator gains experience with a prey it develops a *search image* that improves its ability to locate the prey.

First, lets rewrite our equations with our new functional notation.

$$\dot{N}_1 = \underbrace{rN_1\left(1 - \frac{N_1}{K_1}\right)}_{\text{growth}} - \underbrace{f_p(N_1)N_2}_{\text{predation}} \tag{8}$$

$$\dot{N}_2 = \underbrace{\epsilon f_p(N_1)N_2}_{\text{predation}} - \underbrace{m_2 N_2}_{\text{mortality}} \tag{9}$$

Now we can consider alternative ways of modeling the predation functional response $f_p(N_1)$.

Type II

Monod

$$f_p(N_1) = a_{max}\frac{N_1}{N_1 + k_1} \tag{10}$$

a_{max} is the maximum per-capita uptake rate or capture rate, and k_1 is the 1/2 saturation point.

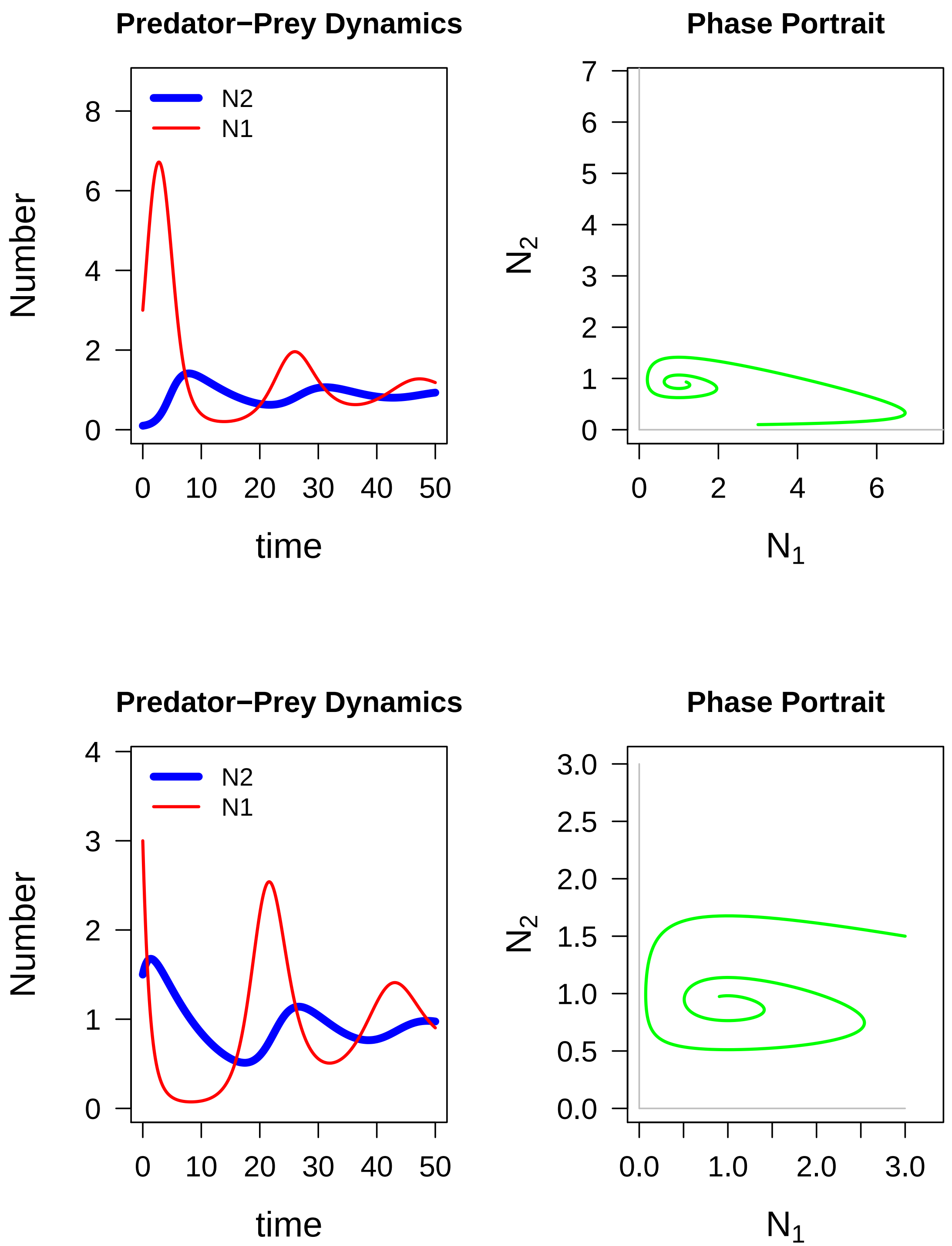

Figure 2: Dynamics of the Lotka-Volterra predation with density dependent growth of the prey population. The top graphs show the outcomes when initial densities were $N_1 = 3$ and $N_2 = 0.1$, while the bottom panels show the results when initial densities were $N_1 = 3$ and $N_2 = 1.5$.

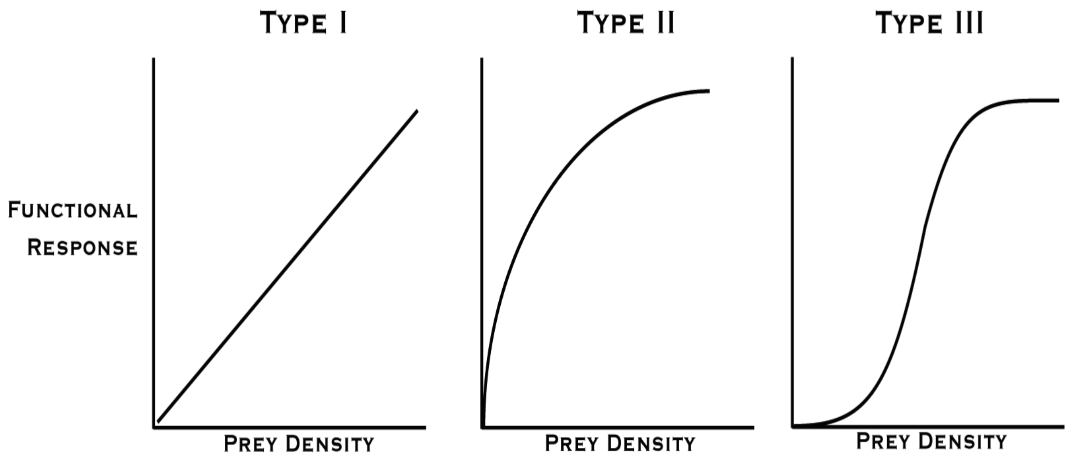

Figure 3: Three types of functional response identified by C.S. Holling

Holling's Disk Equation

$$f_p(N_1) = \frac{aT_sN_1}{1 + aT_hN_1} \tag{11}$$

Where a is the prey encounter rate, T_s is the time spent searching for prey, and T_h is the prey handling time.

Type III

Generalized Monod

$$f_p(N_1) = a_{max}\frac{N_1^b}{N_1^b + k_1^b} \tag{12}$$

In this equation a_{max} and k_1 are the same as in the previous Monod equation, and $b > 1$ causes the function to adopt a sigmoid shape. An increase in b might represents a stronger increase in the foraging effort as food abundance increases.

5 Summary

In today's lecture we have explored two species dynamics through the lens of population ecology and continuous time models of predator–prey dynamics. Along with discussing specific details of a number of ways to model predation, we have established a general way of describing the predation functional response. In the literature, there are numerous alternative formulations of predation that make different assumptions about the way the process operates. Haefner (2006) and Jost and Ellner (2000) describe a number alternatives in more detail.

References

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Gurney, W. S. C., and R. M. Nisbet. 1998. Ecological dynamics. Oxford University Press, New York.

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Jost, C., and Ellner, S. 2000. Testing for predator dependence in predator–prey dynamics: A non-parametric approach. Proc. R. Soc. Lond. 267: 1611–1620.