# Summary of Primary Population Models

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## 1 Introduction

In class we have discussed several population models. These notes are meant to supplement and in some respects summarize our discussion of these models. I mean for them to work with other class notes and the text book – not replace them.

## 2 Exponential Growth Model

### 2.1 Equation

The exponential growth model is:

$$\frac{dN}{dt} = rN, \tag{1}$$

where $\frac{dN}{dt}$ is the population growth rate, $N$ is the population size or density, and in a *closed* population $r = b - d$ is the intrinsic growth rate when $b$ and $d$ are the population's instantaneous specific birth and death rates. In an *open* population we would add immigration and emigration processes to the consideration of the intrinsic growth rate by defining $r = b + i - d - e$, where $i$ and $e$ are the specific rates of immigration and emigration, respectively. What are the units of the variables and parameters?

Equation 1 is a continuous time differential equation. While it tells us the population growth rate, it does not tell us the population size. We can, however, integrate equation 1 and then use it to project or predict the population size. The integration result is:

$$N_t = N_0 e^{rt}, \tag{2}$$

where $N_t$ is the population size at time $t$, $N_0$ is the initial population size, and $r$ is the exponential growth rate[1].

### 2.2 Model Assumptions

- The population is closed. There is no immigration or emigration. This assumption can be relaxed as described above.

[1] In this equation, *e is the base of the natural logarithm and it is equivalent to 2.718*

- The birth and death rates ($b$ and $d$) are constant
- There is no genetic structure
- There is no age or size structure
- The population grows continuously with no time lags.

# 3 Logistic Growth: Intraspecific Competition

The logistic growth model is:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{3}$$

where $\frac{dN}{dt}$ is the population growth rate, $N$ is the population size or density, and $r = b - d$ is the intrinsic growth rate when $b$ and $d$ are the population's instantaneous specific birth and death rates, and $K$ is the environmental carrying capacity.

Like the exponential growth model, we must integrate equation 3 to determine the population size at a given time. This equation has an exact analytical solution, which is:

$$N_t = \frac{K}{1 + \left[(k - N_0)/N_o\right] e^{-rt}} \tag{4}$$

## 3.1 Model Assumptions

- carrying capacity is constant
- linear density dependence

## 3.2 Equilibrium Analysis

We can use the model to learn about characteristics of the modeled population. One useful technique is to find the equilibrium's of the population. That is, we will find where the population growth rate equals zero $\left(\frac{dN}{dt} = 0\right)$

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{5}$$

$$0 = rN\left(1 - \frac{N}{K}\right) \tag{6}$$

There are two ways 6 can be true. First, $rN = 0$ which can be true in the population size is zero. This is classified as an unstable equilibrium, because any increase in the population will cause the population to move away from this equilibrium. The second way that equation 6 can be true is if $\left(1 - \frac{N}{K}\right) = 0$. This occurs when $N = K$. This is a stable equilibrium because if the population size/density is above or below $K$, the population growth rate will change to drive the population towards $K$.

# 4 Lotka-Volterra Interspecific Competition

## 4.1 Equations

Recall that we modeled density-dependent *intraspecific* competition by adding the logistic function to the exponential growth model as follows:

$$\frac{dN_i}{dt} = r_i N_i \left( \frac{K_i - N_i}{K_i} \right), \tag{7}$$

Where $\frac{N_i}{dt}$ is the rate of population change in species $i$, $r_i = b_i - d_i$ is the intrinsic growth rate if species $i$, and $K_i$ is the carrying capacity for species $i$.

Here we are modifying the logistic equations as suggested by A.J. Lotka and V. Volterra to incorporate the effect of *interspecific* competition between two species (number 1 and 2). This modification is:

$$\frac{dN_1}{dt} = rN_1 \left( \frac{K_1 - N_1 - f(N_2)}{K_1} \right) \tag{8}$$

$$\frac{dN_2}{dt} = rN_2 \left( \frac{K_2 - N_2 - f(N_1)}{K_2} \right). \tag{9}$$

We are now working with a system of differential equations that shows how two species are interacting, and we are accounting for the behavior of both species. As formulated above, interspecific competition reduces the growth rate by some function $f$ of the second species.

As is often the case, the interspecific competition function in the equations above $f(N_i)$ can be replaced with many types of functions. However, the simplest and most commonly used function multiplies the competitor density by a constant number as follows:

$$\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \tag{10}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 - \beta N_1}{K_2} \right). \tag{11}$$

In equations (10 and 11), $\alpha$ and $\beta$ are the *competition coefficients*. As stated in Gotelli (2008) "we can define $\alpha$ as the per capita effects of species 2 on the population growth of species 1, *measured relative to the effects of species 1*" (p. 102).

## 4.2 Model Assumptions

As we have modified the logistic equations most of the assumptions of the logistic and exponential growth models are also made here. However, there are three additional assumptions we have made:

- Resources are in limited supply;
- Competition coefficients $\alpha$ and $\beta$ and the carrying capacities $K_1$ and $K_2$ are constants; and
- Density dependence is linear.

### 4.3 Equilibriums and Isoclines for Lotka-Volterra Competition

We can use state space graphs, equilibriums, and isocline analysis to anticipate the range of possible behaviors in our system of equations without having to solve them for specific solutions. These are powerful techniques for analyzing the general possible behavior of a model.

As we have done previously, we can find the equilibrium population densities ($\hat{N}$) for each of the Lotka–Volterra competition equations. Again, we do this by setting both equations (10 and 11) equal to zero and solving for the equilibrium densities as follows.

$$\frac{dN_1}{dt} = 0 = r_1 N_1 \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \tag{12}$$

$$\frac{dN_2}{dt} = 0 = r_2 N_2 \left( \frac{K_2 - N_2 - \beta N_1}{K_2} \right). \tag{13}$$

Now lets solve them for equilibrium densities in tern. Notice that an unstable equilibrium occurs when $r_1 N_1$ or $r_2 N_2$ equal zero. Other equilibriums will take the form of a line, and we can find them as:

$$0 = \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right) \tag{14}$$

$$0 = 1 - \left( \frac{N_1 + \alpha N_2}{K_1} \right) \tag{15}$$

$$1 = \left( \frac{N_1 + \alpha N_2}{K_1} \right) \tag{16}$$

$$K_1 = (N_1 + \alpha N_2) \tag{17}$$

$$\hat{N}_1 = K_1 - \alpha N_2 \tag{18}$$

I will live it to you to do the algebra to find the equilibrium value $\hat{N}_2$. However, we can summarize the equilibrium values as:

$$\hat{N}_1 = K_1 - \alpha N_2 \tag{19}$$

$$\hat{N}_2 = K_2 - \beta N_1 \tag{20}$$

Notice that the equilibriums are no longer points—they are straight lines in two dimensional space. These are the zero growth isoclines that we plotted in *state-space* and used to determine the possible dynamics of the model given particular population information. To plot the lines on the graph, you can find their intercepts by sequentially replacing $N_1$ or $N_2$ with zero.

# 5 Lotka-Volterra Predation Equations

In Chapter 14, we use two new Lotka-Volterra equations to explore predation. Notice their similarity to the equations we have used previously.

### 5.1 equations

$$\frac{dN_1}{dt} = \underbrace{r_1 N_1}_{\text{Growth}} - \underbrace{cN_1N_2}_{\text{Predation}} \quad (21)$$

$$\frac{dN_2}{dt} = \underbrace{b\,\underbrace{cN_1N_2}_{\text{Predation}}}_{\text{Births}} - \underbrace{dN_2}_{\text{Mortality}} \quad (22)$$

In these equations $N_1$ is the population density of the victim (prey) and $N_2$ is the population density of the predator, $r_1$ is the intrinsic growth rate of species 1, $c$ is the per capita rate at which predators consume their prey, $b$ is the efficiency with which food is converted into predator individuals (aka the birth rate), and $d$ is a specific mortality or death rate for species 2.

### 5.2 Equilibriums and Isoclines

Again we can use the isoclines of the equations to anticipate the dynamics of the coupled populations. Your text book shows this nicely, but here I will summarize it for you. Again, the technique is to set the equations equal to zero and solve for the equilibrium population density.

**Victim Population**

$$0 = rN_1 - cN_1N_2 \quad (23)$$
$$rN_1 = cN_1N_2 \quad (24)$$
$$cN_2 = r \quad (25)$$
$$\hat{N}_2 = r/c \quad (26)$$

**Predator Population**

$$0 = b(cN_1N_2) - dN_2 \quad (27)$$
$$b(cN_1N_2) = dN_2 \quad (28)$$
$$bcN_1 = d \quad (29)$$
$$\hat{N}_1 = d/bc \quad (30)$$
$$(31)$$

See the figures in the book (Smith and Smith, Fig. 14.2) for graphing and using these isoclines.

# 6 Modeling Mutualisms

We can modify the outcome of a pair of interacting mutualists by slightly modifying the Lotka-Volterra interspecific competition models shown in equations (10 and 11). Instead of subtracting a term for the effect of the second species, we will add a function to model the benefit. One example parallel to the interspecific equations is:

$$\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 - N_1 + \alpha N_2}{K_1} \right) \tag{32}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 + \beta N_1}{K_2} \right). \tag{33}$$

Instead of subtracting $\alpha N_2$ we are now adding it. Thus, $\alpha$ now represents the positive effect of $N_2$ on species 1. See the "Quantifying Ecology 15.1" section in your text on p. 326 for more information about this.

# References

Gotelli, N.J. 2008. A Primer of Ecology (fourth edition). Sinauer Associates, Inc., Sunderland, MA.

Kot, M. 2001. Elements of Mathematical Ecology. Cambridge University Press, Cambridge UK.