Composing Models

1   Overview

This exercise asks you to struggle with something unfamiliar—representing ecological processes with mathematical models. This is truly hard work, but the rewards can be enormous if you master this skill. To get the most out of the problems below, you must work in your groups without consulting any external sources. You are a clever bunch and could easily look these things up, but that would defeat the point of this exercise. Be prepared to show me how your thinking evolved, what you tried, what worked and what didn't. The benefit of this work comes from practicing a process, not getting an answer "right". You also may need time alone in your room.

   The answers are shown in an answer sheet on the web page. This is because seeing the answer quickly after struggling with a problem is vital to learning. In your lab report, please describe your best result for each problem before you looked at the answers. Don't rush these–to get maximum benefit you really must force your thinking in new ways. This can be frustrating, but it will be rewarding if you stay with it.

2   Problems

2.1   Holling's disc equation

In preparation for this exercise, we derived a model of functional response for herbivores. Your task is to derive a model for predators. C. S. Holling (1959) composed the disc equation, a model of the type II functional response of predators to prey numbers:

$$\frac{dV}{dt}\frac{1}{P} = \frac{\alpha V}{1 + \alpha h V} \tag{1}$$

In a type II model, the per-capita rate of capture of prey by a predator increases asymptotically with increasing numbers of prey. I want you to derive the disc equation, the right hand side of equation 1. You should define relevant quantities symbolically and put them together in an equation that portrays how prey capture by predators responds to prey density. After a little algebra (remember algebra?) you should be able to obtain equation 1. The point of this exercise, of course, is the process you go through to derive the model. Check your units. If you want to use computer algebra systems like Maple or Matlab to hep your rusty algebra, that's fine.

Here is a small hint. It is important to your success in the next exercise that V is prey *number* and not prey *density*.[1] Think about defining α such that it has the total area occupied by the prey in its denominator, a trick known as variable rescaling. This allows the prey capture rate to be a function of prey density, while preserving V as a unitless quantity, number of prey as needed in the next problem.

Derivation of disc equation

A = total area of habitat containing predators and prey (area).

a = search rate (area/time)

γ = the probability than an encounter with prey results in a capture.

Let $\alpha = \gamma$ a/A, (1/time)

h = handling time (time), the time require to consume 1 prey.

V = number of prey in A

P = number of predators in A

We assume that handling precludes searching.

h = time required to consume one prey (time)

αV = prey capture rate, (1/time)

$\dfrac{1}{\alpha V}$ = time required to capture 1 prey (time)

Therefore, the prey capture rate per predator is

$$\frac{dV}{dt}\frac{1}{P} = \frac{1}{h + \dfrac{1}{\alpha V}} = \frac{\alpha V}{1 + \alpha V h}$$

Checking units:

$$\frac{dV}{dt}\frac{1}{P} = \frac{1/\text{time}}{1 + 1/\text{time} \cdot \text{time}} = \frac{1}{\text{time}}$$

2.2 Modifying the Lotka-Voltera predator-prey equations

The Lotka-Voltera equations are a true classic in community ecology and ecological modeling, widely used to portray the dynamics of predators and prey and as a starting point for modeling interactions in food webs. The model assumes that the growth rate of the prey population and the death rate of the predators are proportionate to population size. [2]As I showed you in class, the per capita rate of capture of prey by predators (P) is assumed to be a linear function of prey numbers, i.e.,

$$\frac{dV}{dt}\frac{1}{P} = \beta V \tag{2}$$

If we assume that the predator population grows at a per capita rate $= r$ (units $= 1/\text{time}$) in the absence of predators and that the predator population declines at per capita rate m (units $=$

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[1]Although it is often defined as prey density in derivations of the disc equation as I showed in lecture.
[2]Put in a more fancy way, they are first order processes.

1/time) in the absence of prey and that the predators are able to convert prey into new predators with efficiency ϵ (unitless), we can form balance equations for the numbers of predators and prey as

$$\frac{dV}{dt} = rV - \beta VP \tag{3}$$

$$\frac{dP}{dt} = \epsilon\beta VP - mP \tag{4}$$

The product βV is called the functional response because it gives the number of prey consumed per predator per unit time (i.e., $\frac{1}{P}\frac{dV}{dt} = \beta V$). Linear functional responses are called Type I, which is what we have here. A more realistic function response is saturating, where the per capita rate of capture reaches an asymptote as prey density increases.

Rewrite the differential equations for the Lotka-Voltera predator prey model using the following changes in assumptions. First, assume that the functional response is not Type I (linear) as in the example, but instead is Type II (asymptotic). Use the disc equation of Holling to represent the Type II response in the Lotka-Voltera model. Second, make the assumption that the per capita rate of growth of the prey population (in the absence of predation) declines linearly with prey numbers and that the growth rate is 0 when $V = K$.

Answer to Lotka-Voltera problem

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \frac{\alpha PV}{1 + \alpha hV} \tag{5}$$

$$\frac{dP}{dt} = \frac{\epsilon\alpha PV}{1 + \alpha hV} - mp \tag{6}$$

2.3   Modeling dispersal by plants

David Tilman and colleagues (1997) adapted Richard Levin's now famous metapopulation model (Levins, 1969) to represent dispersal by plants. The model is derived as follows.

- We assume that the environment consists of a large number (N) of discrete sites such that each site can be occupied by a single plant. The number of sites that are occupied, and hence the number of live plants, is given by N_o, $N_o \leq N$.

- We assume that the propagules that land on an empty site become established and that dispersal of propagules is random over all sites. All propagules can reach all sites.

- The rate of production of propagules per individual plant (i.e., per occupied site) is c (units = time-1) .

- The per capita death rate is m (units = time-1).

Compose a model that predicts the rate of change in the number of occupied sites $\left(\frac{dN_0}{dt}\right)$. To attack the problem, think of the overall rate of change as the difference between the colonization rate and the vacancy rate, i.e. rate of change in number of occupied sites = $\frac{dN_o}{dt}$ = colonization rate - vacancy rate. Concentrate on each term on the right hand side, then put them together. As a hint, the site colonization rate depends on the number of plants (occupied sites), the per capita rate of propagule production, and the proportion of sites that are not occupied. The vacancy rate depends on the number of occupied sites and the per capita death rate.

After your quick success with this problem[3], please compose a model of the rate of change in the *proportion* of sites that are occupied, that is, $\frac{dP}{dt}$=? As a hint, create a new variable, $p = \frac{N_o}{N}$, and do a little algebra. Use you model to solve for the proportion of sites that are occupied at equilibrium, that is when $\frac{dp}{dt} = 0$. What does this tell us about the proportion of sites that are unoccupied at steady state?

Answer to Tilman-Levins problem

The rate of change in occupied sites is:

$$\frac{dN_o}{dt} = cN_o\left(1 - \frac{N_o}{N}\right) - mN_o.$$

However, if we are interested in the proportion of sites that are occupied rather than the number of sites, we divide both sides by N and substitute , $p = \frac{N_o}{N}$:

$$\frac{dN_o}{dt}\frac{1}{N} = c\frac{N_o}{N}\left(1 - \frac{N_o}{N}\right) - m\frac{N_o}{N},$$

which, of course, is the Levins metapopulation model,

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[3]Of course, you recognize the form of this equation, reinforcing the truth that ecological modelers tend to use the same bag of tricks.

$$\frac{dp}{dt} = cp(1 - p) - mp.$$

At equilibrium,

$$p^* = 1 - \frac{m}{c},$$

leading to the somewhat surprising conclusion that a proportion of sites will always be unoccupied.

2.4 Toxins in a lake (50 points extra credit).

One of the reasons to use math to develop models of processes is that you can gain insight that you would never obtain without the rigor that math imposes on your thinking. The following problem is taken from Gurney and Nisbet (1998). We are interested in formulating a model of changes in the concentration of a toxic substance in a lake of with volume V (m^3) and a total mass of toxicant, Q (kg). The lake is fed by one river and drained by a second one. The inflowing river supplies water containing the toxin at concentration q_{in} (kg/m^3) at a rate of R_{in} (m^3/day). The river flowing out removes water (and the dissolved toxin at concentration q_{out}) at a rate R_{out}.

Develop rate equations for :

1. The volume of fluid in the lake (i.e. $\frac{dV}{dt}$) ,

2. The mass of toxin in the lake (i.e., $\frac{dQ}{dt}$),

3. The concentration of toxin in the lake (i.e., $\frac{dq}{dt}$).

Number 3. is surprisingly challenging. As a hint, you will need to use $Q = qV$ and exploit the product rule for differentiation. Of course, your remember the product rule? If not, here is a bit more of a hint, but please look up the product rule to understand this.

$$\frac{dQ}{dt} = \frac{d\,(q \cdot V)}{dt} = \frac{dq}{dt}V + \frac{dV}{dt}q$$

After you derive a general expression for $\frac{dq}{dt}$, simplify it under the assumption that the volume of the lake is constant (i.e. $\frac{dV}{dt} = 0$ and $R_{in} = R_{out} = R$).

Answer to lake problem

$$\frac{dV}{dt} = R_{in} - R_{out}$$

$$\frac{dQ}{dt} = R_{in}q_{in} - R_{out}q_{out}$$

To derive $\frac{dq}{dt}$:

1) $Q = qV$

2) $\frac{dQ}{dt} = \frac{dq}{dt}V + \frac{dV}{dt}q$

3) $\frac{dq}{dt}V = \frac{dQ}{dt} - \frac{dV}{dt}q$

Substitute $R_{in}q_{in} - R_{out}q_{out}$ for $\frac{dQ}{dt}$ in 3 and simplify

$$\frac{dq}{dt} = \frac{1}{V}\left(R_{in}q_{in} - R_{out}q_{out} - \frac{dV}{dt}q \right)$$

If the volume is constant, then

$$\frac{dq}{dt} = \frac{R}{V}(q_{in} - q_{out})$$

References

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Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.

Tilman, D. T., C. Lehman, and P. Kareiva, 1997. Population dynamics in spatial habitats. In D. Tilman and P. Kareiva, editors, *Spatial Ecology: The Role of Space in Populations Dynamics and Interspecific Interactions.*, pages 3–20. Princeton University Press, Princeton, New Jersey.