Discrete-Time Models in Biology

This entire section of the course focuses on how we can use mathematics to mimic biological situations in which it is reasonable to view the underlying biological variables as changing at discrete time intervals. We have already seen several examples of this. When we discussed matrix models for populations structured by age, using the Leslie model, we projected the age structure forward one time period by multiplying the vector of the population's age structure by the transition matrix to get the population structure one time unit later. Another example arose when we analyzed simple population genetics models in which we determined the gene frequency in the population at the next generation from the gene frequencies in the previous generation.

The types of models we will discuss now are designed for populations with discrete generations (e.g. many insects and plants), in which we can think of the next generation as being produced dependent upon the size of the current generation. Thus the state variable that describes the population will typically be x_n or the population size (or density) at generation n. These models are in some sense easier than the matrix models such as the Leslie model since at each time period we are only following a single state variable (the total population size) rather than a vector of state variables (the age structure). Even though they are simpler, these models still serve as the basis for many very practical applications, including many models in fisheries and insect pest management.

The key assumption in discrete-time models is that there is a fixed time period, the time step (often a year, or a generation time), which is appropriately chosen so that the population size at the next time step is a simple function of the population size at a previous (sometimes several previous) time steps. There are many situations in which this is clearly an approximation, for example human populations breed and reproduce continuously, not at fixed time steps. The next term in this course sequence will show how to produce models for continuously breeding populations (this is part of calculus), but in some cases discrete-time models are an adequate representation of even continuously breeding populations to be useful. Thus much of human demography (the study of the structure of human populations) utilizes discrete-time matrix models (typically using 5 years as the time step, so a human population is broken into age classes 0-4 years old, 5-9 years old, etc.), even though humans breed continuously.

We will start with the simplest possible population model in discrete time, in which we view each individual in the population as replacing themselves with b individuals in the next generation. What do we expect to happen in this case as time passes? Obviously if b > 1 we expect that the population will increase and if b < 1 the population will decrease since each individual is not completely replacing themselves. Here you may wonder what it means if we let b = 1.5 since it is not clear that .5 individuals makes sense (what does half an individual mean – the right half of a baby if Solomon really did let it be cut in two?). At least two interpretations make sense here. One is that the state variable for the model is density (individuals per m^2 is one potential measurement of density) so that b = 1.5 means that for each unit of density currently present, the population has 1.5 units of

density at the next time step. Another interpretation is that $b = 1.5$ represents the average number of new individuals produced per individual present the previous generation, where this average is taken over the entire population. Thus, $b = 1.5$ would arise if half the individuals produce one offspring and die, and the other half produce two offspring and then die. The average reproduction rate is thus 1.5 individuals per time step.

This simple model is described by letting x_n be the population size at generation n so that $x_{n+1} = b\ x_n$ and clearly then $x_n = x_0 b^n$ where x_0 is the initial population size. What happens here as we look at the population after many generations? If $b > 1$, then x_n gets larger and larger, while if $b < 1$ then x_n gets as close as you might want to zero by choosing n large enough. This model is called Geometric Growth or Malthusian Growth (after Thomas Malthus, who first described the implications of geometric growth on human populations as eventually outstripping the potential for agricultural production of food). You have already seen geometric growth since when you plot x_n versus n on semi-log paper, you get a straight line. Geometric growth is the same as exponential growth, except in discrete time.

If we write down the list $x_0, x_1, x_2, x_3, \dots$ then we get the list of population sizes indexed by the generation. Mathematically, this list is called a sequence - it is determined by a rule (a function) that assigns some number (here it is population size) to each non-negative integer (the generation). As we argued above, if the sequence is geometric (formed from the geometric growth model above), then the sequence gets closer and closer to zero (but never quite reaching it) as n gets larger, if $b < 1$. We say then that the sequence has a limit, which is zero. If $b > 1$, then x_n continues growing as n increases, never approaching anything, so no limit exists.

The idea of a "limit" therefore means that a sequence of numbers x_n approaches a particular value as n gets larger and larger. If the sequence represents population size, then the population size approaches some "limiting value", an equilibrium value, as time goes on. We have seen an example of this in the Leslie model, in which the population structure approached the structure of the eigenvector of the dominant eigenvalue. Just think of the limit as the long term population size, if it exists. Clearly, in the real world there are numerous factors which cause populations to vary in time, so an equilibrium size is just an approximation.