Math 345 Intro to Math Biology
Lecture 3: Biological Models using Difference Equations

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A crash course of linear algebra

Let A be an $n \times n$ matrix with real-valued entries.
The numbers λ satisfying $Ax = \lambda x$ are called eigenvalues.
The corresponding $x(\neq 0) \in \mathbf{R}^n$ is called eigenvector associated with the eigenvalue.
An $n \times n$ matrix has exactly n eigenvalues (they could be same, but with different eigenvectors)
If v is an eigenvector, so is cv (c is a constant)

Eigenvalue and eigenvector of 2×2 matrix
$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \lambda \begin{pmatrix} x \\ y \end{pmatrix}, \begin{pmatrix} a-\lambda & b \\ c & d-\lambda \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$
solve $(a-\lambda)(d-\lambda) - bc = 0$ (characteristic equation) for eigenvalues λ_1, λ_2

Eigenvalues, eigenvectors for higher dimensional matrices: use Matlab to solve

Solution of matrix equation

Suppose that $x_n \in \mathbf{R}^k$ is the n-th generation population distribution.

Solution of $x_{n+1} = Ax_n$ (A is a $k \times k$ matrix):

$$x_n = c_1\lambda_1^n v_1 + c_2\lambda_2^n v_2 + \cdots + c_k\lambda_k^n v_k = \sum_{i=1}^{k} c_i\lambda_i^n v_i$$

where λ_i are eigenvalues, v_i are eigenvectors, and c_i are constants.

The eigenvalues can be ordered so that $|\lambda_1| \geq |\lambda_2| \geq \cdots \geq |\lambda_k|$, and λ_1 is called the dominant eigenvalue.

$x(n) \approx c_1\lambda_1^n v_1$ for large n

If $|\lambda_1| < 1$, then $x(n) \to 0$ as $n \to \infty$ (extinction)
If $|\lambda_1| > 1$, then $x(n) \to \infty$ as $n \to \infty$ and $x(n) \approx c_1\lambda_1^n v_1$
$\frac{1}{\lambda_1^n} x(n) \approx c_1 v_1$
Let $w_1 = \frac{v_1}{sum(v_1)}$, then w_1 is the stable state distribution of the model

Perron-Frobenius Theorem: If A has non-negative entries and is power positive (there is a natural number n such that A^n has only positive entries), then the dominant eigenvalue of A is positive, and the associated eigenvector is also positive.

Structured population models

Physiologically structured: age, sex
Spatially structured: location
Methods of modeling:
1. introduce new continuous variables like age (s), location (x) in additional to time (t) (partial differential equation about functions $P(s,t)$ or $P(x,t)$ depending on more than one variables)
2. the structure has a finite number of state (a number of spatial patches, a number of age groups, two sexes), and use matrix model (difference or differential equations)

Leslie matrix model

Consider only the number of female in the population
Define $z(n) = (z_1(n), z_2(n), \cdots, z_k(n))^T$ be the population vector with $z_i(n)$ being the population of the i-th age group at time n. $z_1(n)$ is the population of the youngest group, and $z_k(n)$ is that of the oldest group.
For example, assume the $z_i(n)$ is the population of people age i in year n. We can assume $1 \le i \le 150$.
Let s_i be the survival rate from age $i-1$ to i, let m_i be the average reproduction rate per capita for age i. Then we can use a matrix model $z(n+1) = Lz(n)$ to describe the population growth, and L is a $k \times k$ matrix:

$$L = \begin{pmatrix} s_1 m_1 & s_1 m_2 & \cdots & s_1 m_{k-1} & s_1 m_k \\ s_2 & 0 & \cdots & 0 & 0 \\ 0 & s_3 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_k & 0 \end{pmatrix}$$

$0 < s_i < 1$ for $1 \le i \le k$, $m_i > 0$ only for $\alpha \le i \le \beta$ (fertile period)

<u>Solution</u>: $z(n) = c_1 \lambda_1^n v_1 + c_2 \lambda_2^n v_2 + \cdots + c_k \lambda_k^n v_k = \sum_{i=1}^{k} c_i \lambda_i^n v_i$

where λ_i: eigenvalues, v_i: eigenvectors, and c_i: constants.
$x(n) \approx c_1 \lambda_1^n v_1$ for large n when $\lambda_1 > 0$ is the dominant eigenvalue according to Perron-Frobenius Theorem since Leslie matrix is non-negative and power positive, ($\lambda_1 > 1$ growth, $\lambda_1 < 1$ extinction), and v_1 is the stable age distribution.

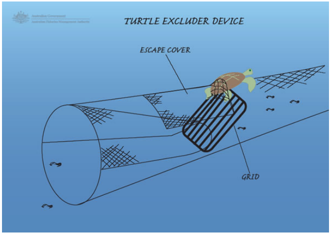
Saving the loggerhead turtles

In the 1980s, six of the seven species of sea turtles were on the endangered species list. These six endangered species includes all five species of sea turtles that live in the United States. The declines in these endangered populations were quite dramatic. For example, Kemp's Ridley turtles at Rancho Nuevo declined from approximately 40,000 individuals in 1947 to 500 individuals in 1987. Several factors potentially play an important role in these declines. Sea turtles lay their eggs on beaches and after hatching the turtles head back to the sea. The eggs and juvenile turtles are exposed to a variety of life threatening dangers: predation from seagulls and racoons, getting stuck in ruts dug into the sand by dune buggies, urban lighting misdirecting hatchlings as they try to find their way to the sea, and beach trash ensnaring hatchlings as they move across the beach. Clearly many of these dangers are driven by human occupation of beaches. Alternatively, older turtles run the risk of getting snared by shrimp trawling nets and drowning.

What does people do

In the 1980s, conversation efforts targeted one life stage of the turtles, the eggs on the nesting beach. This life stage was targeted as it was easily accessed, protected, and monitored. However, as the turtle population dynamics were poorly understood, the question remained, are these egg protection efforts sufficient prevent extinction? Or should efforts be directed toward older life stages? For instance, should Turtle Excluder Devices (i.e. devices the minimize adult mortality due to trawling nets) be used? This later option was very unpopular with the fishing industry as discussed in the following quote found on the web:
"TEDs are panels of large mesh webbing or metal grids inserted into the funnel shaped shrimp nets. As the nets are dragged along the bottom, shrimp and other small animals pass through the TED and into the cod end of the net, the narrow bag at the end of the funnel where the catch is collected. Sea turtles, sharks, and sh too large to get through the panel are defected out an escape hatch. Fishermen, who believe that the device causes their nets to dump 20 percent or more of the shrimp as well, call them 'trawler eliminator devices.' Sea turtles breathe air just as land animals do and must come to the surface every hour or so. Without a TED, they are trapped in a net for as long as it is towed underwater and sometimes drown before being brought aboard. The problem is analogous to the seining of tuna fish, in which thousands of dolphins are drowned every year. The government's requirement for the use of TEDs has become one of the most bitterly fought regulations in the history of fisheries management."

TED



Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Number of stages: It is known that turtles live up to 54 years. However, a few stages (eggs, hatchlings, mature/nesting adults) are biologically distinct and researchers often use size as an index of age.
size/stage structured model
Seven stages: eggs/hatchlings (<1 year), small juveniles ($1-7$ years), large juveniles ($8-15$ years), subadults ($16-21$ years), novice breeders (22 years), remigrants (23 years), and mature breeders ($24-54$ years).

Matrix model without TEDs

$$L = \begin{pmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747 & 0.737 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6610 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8091 & 0.8089 \end{pmatrix}$$

Matlab: dominant eigenvalue $\lambda_1 = 0.9450$ (so total population declines by 6% per year, a slow extinction)

stable stage distribution:

$(0.2065, 0.6698, 0.1146, 0.0066, 0.0004, 0.0003, 0.0018)$

Ways of protection: which number to improve?

Matrix model with improved protecting hatchlings

$$L = \begin{pmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747a & 0.737 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6610 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8091 & 0.8089 \end{pmatrix}$$

For $a > 1$, but still $\lambda_1 < 1$ even if $0.6747a = 1$

atrix model with TEDs

$$L = \begin{pmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.6747 & 0.737 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.0486 & 0.6610 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.0147 & 0.6907a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.0518a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.8091a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8091a & 0.8089a \end{pmatrix}$$

For $a > 1$ but $0.8091a < 1$, $\lambda_1 > 1$ if $a > 1.11$. TEDs help the survival and recovery of the loggerhead turtles!

This analysis provides a strong argument for the potential effectiveness of turtle excluder devices and the potential limitations of beach based conservation efforts. Based in large part on this type of analysis, the National Academy of Sciences recommended requiring TEDs, and in 1992 the National Marine Fisheries Service (NMFS) expanded seasonal TED requirements to encompass all shrimp southeastern trawls starting in December 1994. By 1998, NMFS found that loggerhead populations were stable or increasing on most monitored nesting beaches.