Stat 534: formulae referenced in lecture, week 9: Population modeling

Change over time: focus on B_t and D_t

- Discrete time: $N_{t+1} = N_t + B_t - D_t + I_t - E_t$
  - $N_{t+1} = N_t + B_t - D_t$
- Continuous time:

$$
\begin{aligned}
\frac{d\,N(t)}{d\,t} &= N(t)(b(t) - d(t)) \\
\frac{1}{N(t)}\frac{d\,N(t)}{d\,t} &= b(t) - d(t) \\
\frac{d\,\log N(t)}{d\,t} &= b(t) - d(t)
\end{aligned}
$$

Exponential growth:

- $b(t) - d(t)$ constant, $= r$
- $N_t = N(0)e^{rt}$

Density dependence:

- Example: density-dependent death rate
  - $b(t) = r$
  - $d(t) = \frac{r}{K}N(t)$

$$\frac{1}{N(t)}\frac{d\,N(t)}{d\,t} = r\left(\frac{K - N(t)}{K}\right)$$

$$N(t) = \frac{K}{1 + \left[\frac{K - N(0)}{N(0)}\right]\,\exp(-r\,t)}$$

$$\pi = \frac{1}{(1 + \exp\left[-(\beta_0 + \beta_1\,t)\right])}$$

Song sparrows:

- 20 adult individuals introduced to an island in San Fransisco Bay

- 10 years later, how large do we expect the population to be?
- requires a population model and vital rates
- Population model:
  - Assume no density dependence (exponential growth)
  - Customary to consider females only
  - Well known that juveniles (age 0 = 1st year of life) are different from adults
  - Can not just count birds
  - Need to account for at least two ages
  - Decide to use 3 stages (will revisit later)
    * newborn = 1st year of life, age 0
    * adults1 = 2nd year of life, age 1
    * adults2 = 3rd year of life, age 2
    * Then any survivors die
- Vital rates
  - Multiple years of data from populations elsewhere in SF Bay
  - Fecundity:
    * f_i = # female fledge per female per yr
    * $f_0 = 0$, $f_1 = 2.6$, $f_2 = 2.6$
  - Mortality:
    * ϕ_i = P[survive from age i to age $i+1$]
    * $\phi_0 = 0.2$, $\phi_1 = 0.57$, $\phi_2 = 0$

Note about vital rates:

- Each rate, a_{ij} is the expected # of age i individuals from one age j individual after one year
- e.g., a_{32} is the expected # of adults2 from 1 adult1, i.e. survival
- Complication: when does the year start?
- Pre-breeding census:

  - Year starts just before breeding
  - So age 1 fecundity is # female eggs laid × P[fledge] × P[age 0 survives]

- Post-breeding census:
  - Year starts just after breeding
  - So age 1 fecundity is P[age 1 survives] × # female eggs laid × P[fledge]

- When compiling data,
  - keep track of the annual cycle
  - and when census occurs
  - especially important when combining multiple sources of data

Matrix population models:

$$\boldsymbol{N}_{t+1} = \boldsymbol{A}\,\boldsymbol{N}_t$$

- For 3 age song sparrow population

$$\boldsymbol{N}_t = \begin{bmatrix} N_t(0) \\ N_t(1) \\ N_t(2) \end{bmatrix}$$

$$\boldsymbol{A} = \begin{bmatrix} 0 & f_1 & f_2 \\ \phi_0 & 0 & 0 \\ 0 & \phi_1 & 0 \end{bmatrix}$$

$$\begin{aligned} N_{t+1}(0) &= f_1\,N_t(1) + f_2\,N_t(2) \\ N_{t+1}(1) &= \phi_0\,N_t(0) \\ N_{t+1}(2) &= \phi_1\,N_t(1) \end{aligned}$$

- Define N_t scalar, no (age) as $N_t = \sum_{age} N_t(age)$, total population size

- Projecting the population forward in time:
  - $\boldsymbol{N}_{t+1} = \boldsymbol{A}\,\boldsymbol{N}_t$
  - $\boldsymbol{N}_{t+2} = \boldsymbol{A}\,\boldsymbol{N}_{t+1} = \boldsymbol{A}\,\boldsymbol{A}\,\boldsymbol{N}_t$
  - $\boldsymbol{N}_{t+3} = \boldsymbol{A}\,\boldsymbol{N}_{t+3} = \boldsymbol{A}\,\boldsymbol{A}\,\boldsymbol{A}\,\boldsymbol{N}_t$

  - $\boldsymbol{N}_{t+k} = \boldsymbol{A}^k \, \boldsymbol{N}_t$
- Vocabulary:
  - Leslie matrix: age-structured population
  - Lefkovitch matrix: stage/size-structured population

Applied to song sparrows:

- The data:

$$\boldsymbol{N}_0 = \begin{bmatrix} 0 \\ 10 \\ 10 \end{bmatrix}$$

$$\boldsymbol{A} = \begin{bmatrix} 0 & 2.6 & 2.6 \\ 0.2 & 0 & 0 \\ 0 & 0.57 & 0 \end{bmatrix}$$

- After 1 year:

$$\boldsymbol{N}_1 = \boldsymbol{A} \, \boldsymbol{N}_0 = \begin{bmatrix} 52 \\ 0 \\ 5.7 \end{bmatrix}$$

- 10 year transition matrix:

$$\boldsymbol{A}^{10} = \begin{bmatrix} 0.181 & 0.813 & 0.501 \\ 0.039 & 0.181 & 0.109 \\ 0.024 & 0.110 & 0.071 \end{bmatrix}$$

- After 10 years:

$$\boldsymbol{N}_{10} = \boldsymbol{A}^{10} \, \boldsymbol{N}_0 = \begin{bmatrix} 13.14 \\ 2.90 \\ 1.81 \end{bmatrix}$$

  total #: 17.85

Long-term behaviour of the population:

- Properties, when $\boldsymbol{A}$ is constant
- Numerical example, demonstrating:
  - Change in total population: $\frac{N_{t+1}}{N_t} \to \lambda$

- Change in each age: $\frac{N_{t+1}(age)}{N_t(age)} \rightarrow \lambda$
- Age distribution: $\frac{N_t(age)}{N_t} \rightarrow u(age)$
- Age as vector: $\frac{\boldsymbol{N}_t}{N_t} \rightarrow \boldsymbol{u}$

- Given $\boldsymbol{A}$, can compute λ and u without simulation
  - solutions to $\boldsymbol{A}\,\boldsymbol{u} = \lambda\,\boldsymbol{u}$
  - $\boldsymbol{A}\,\boldsymbol{u}_t = \boldsymbol{u}_{t+1} = \lambda\,\boldsymbol{u}$
  - So satisfy constant change in pop. size and constant age distribution
- λ is the largest eigenvalue of $\boldsymbol{A}$
- and $\boldsymbol{u}$ is the associated eigenvector

Eigen decomposition of $\boldsymbol{A}$

- In this section, $\boldsymbol{A}$ is a square, symmetric matrix
- End result is that $\boldsymbol{A}$ can be expressed as a product of 2 matrices with useful properties

$$\boldsymbol{A} = \boldsymbol{U}\boldsymbol{D}\boldsymbol{U}^{'}$$

  - Consequence of square symmetric is that all matrices have real numbers
- Actual population transition matrices
  - lead to some complex numbers
  - and complex conjugate operations
  - Concepts the same, just more-involved math
- If $\boldsymbol{A}$ is a $k \times k$ matrix,
  - Many solutions $(\lambda,\, \boldsymbol{u})$ to $\boldsymbol{A}\,\boldsymbol{u} = \lambda\,\boldsymbol{u}$
  - For any vector, require that $\boldsymbol{u}^{'}\boldsymbol{u} = 1$
    * i.e., $\sum_i \boldsymbol{u}(i)^2 = 1$
  - For any pair, $\boldsymbol{u}^1$ & $\boldsymbol{u}^2$, require that $(\boldsymbol{u}^1)^{'}\boldsymbol{u}^2 = 0$
    * i.e., $\sum_i \boldsymbol{u}^1(i) \times \boldsymbol{u}^2(i) = 0$
    * i.e., the two vectors make a right angle

- Then there are only k possible $\boldsymbol{u}$ vectors, each with an associated λ

- Collect the $\boldsymbol{u}$ into a matrix, $\boldsymbol{U}$

$$\boldsymbol{U} = \begin{bmatrix} \boldsymbol{u}^1 & \boldsymbol{u}^2 & \boldsymbol{u}^3 \end{bmatrix}$$

  - Requirements for $\boldsymbol{u}$'s $\Rightarrow \boldsymbol{U}\boldsymbol{U}' = \boldsymbol{U}'\boldsymbol{U} = \boldsymbol{I}$

- and the associated λ into a diagonal matrix

$$\boldsymbol{D} = \begin{bmatrix} \lambda^1 & 0 & 0 \\ 0 & \lambda^2 & 0 \\ 0 & 0 & \lambda^3 \end{bmatrix}$$

- $\boldsymbol{A}\,\boldsymbol{u} = \lambda\,\boldsymbol{u}$ applies to each column of $\boldsymbol{U}$

- so $\boldsymbol{A}\,\boldsymbol{U} = \boldsymbol{U}\,\boldsymbol{D}$

- Post multiply by $\boldsymbol{U}'$: $\boldsymbol{A}\,\boldsymbol{U}\,\boldsymbol{U}' = \boldsymbol{U}\,\boldsymbol{D}\,\boldsymbol{U}'$

  - $\boldsymbol{A}\,\boldsymbol{U}\,\boldsymbol{U}' = \boldsymbol{A}\,\boldsymbol{I} = \boldsymbol{A}$

- Vocabulary:

  - eigenvalues: λ's
  - eigenvectors or right eigenvectors: u's
  - (λ, u) are pairs: each λ has an associated u

What are some useful consequences of $\boldsymbol{A} = \boldsymbol{U}\,\boldsymbol{D}\,\boldsymbol{U}'$?

- When $\boldsymbol{A}$ is a variance-covariance or correlation matrix:

  - $\boldsymbol{D}$ and $\boldsymbol{U}$ provide a principal components analysis
  - Use a smaller number of variables to summarize the variability in the data set that created $\boldsymbol{A}$
  - Focus on the largest 1, 2 or 3 (rarely more) values of λ
  - and their associated eigenvectors

- For any matrix:

  - $\boldsymbol{A}^k = \boldsymbol{U}\,\boldsymbol{D}^k\,\boldsymbol{U}'$

- $\boldsymbol{D}^k = \begin{bmatrix} (\lambda^1)^k & 0 & 0 \\ 0 & (\lambda^2)^k & 0 \\ 0 & 0 & (\lambda^3)^k \end{bmatrix}$

- When $\boldsymbol{A}$ is a transition matrix
  - largest λ is the "long-term" population growth rate
  - associated u is the steady-state age/stage category distribution
  - 2nd and 3rd largest λ tell you about how and how quickly population converges to the "long-term" characteristics

Reproductive values:

- RA Fisher 1930, *Genetical Theory of Natural Selection*
- Different value for each age/stage category
- Loosely: average # of future offspring from a stage i individual
- When two sexes, consider only female offspring from a female individual
- What if a population is growing? i.e., $\lambda > 1$
  - Consider annual reproduction
  - A child now is "worth" more than a child born 5 years from now
  - "now" can reproduce and contribute to the population for 5 years
  - "later" doesn't
  - Fisher's innovation: "discount" later contributions based on λ
  - i.e., compute "present value" of each contribution
  - Just like discounting prices or salaries for inflation
- "left" eigenvectors
  - Solve $\boldsymbol{V}' \boldsymbol{A} = \boldsymbol{D} \boldsymbol{V}'$

- which are the "right" eigenvectors of $\boldsymbol{A}'$
  - To see why:
  - $\left(\boldsymbol{V}' \boldsymbol{A}\right)' = \left(\boldsymbol{D} \boldsymbol{V}'\right)'$
  - $= \boldsymbol{A}' \boldsymbol{V} = \boldsymbol{V} \boldsymbol{D}'$
  - $= \boldsymbol{A}' \boldsymbol{V} = \boldsymbol{V} \boldsymbol{D}$ because $\boldsymbol{D}$ is symmetric
- "left" and "right" have same $\boldsymbol{D}$ but $\boldsymbol{V} \neq \boldsymbol{U}$

- Find v associated with the largest λ
- Elements of the associated v are the relative reproductive value of a stage i individual

For Song sparrows:

- Largest eigenvalue = 0.918
  - < 1, so long term population trend is a decline (8.2% per year)
- Associated u: [-0.969, -0.211, -0.131]′
- For age distribution, standardize to sum to 100%: [73.9%, 16.1%, 10.0%]′
- Associated v: [-0.182, -0.837, -0.516]′
- I standardize to sum to 1.0: [0.12, 0.54, 0.34]′
- Interpretation of the reproductive values
  - age 0 individual (just fledged):
    low rv - high probability of dying in 1st year
  - age 1 individual
    high rv - has 1-2 breeding events
  - age 2 individual
    lower rv - has 0-1 breeding events
- 2nd and 3rd eigenvalues are:
  -0.459 + 0.335i, -0.459 - 0.335i
- a complex conjugate pair of complex numbers