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Math 308

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Project

# Theoretical Evolutionary Ecology

Abstract:

In this application of Linear Algebra, the idea of growth of population based on Theoretical Evolutionary Ecology is presented. The topic is based on the mathematical principle in Biology, how growth of population of species can be determined and calculated. This procedure can be done by several means – using exponential function or matrix representations. In the assignment, growth of population will be shown in the matrix form.

## Main (Explanatory part with Examples)

Theoretical Evolutionary Ecology covers the topics of major interest in contemporary research-life-history evolution, optimal foraging, kin selection and inclusive fitness, the evolution of sex, the sex ratio, sexual selection, and the application of game theory to evolutionary problems. It provides a clear and systematic account of theoretical models underpinning our understanding of evolutionary adaptation.

Let's take a small group of living beings. There are two sexes, but only the females are of interest, as in them rests the procreative potential of the species (many mothers = many children; the same is not true for fathers). Let $n_x(t)$ be the number of females of age x in year t, so x and t are integers, and things are arranged  so that they're both positive (x of course is positive anyway). The females are assumed to start breeding from age x = 1, and to continue breeding each year of subsequent life up to and including age x = w (so from age x = w+1 onward they drop out of this mathematical model and we'll just assume they retire).

Let $P_x$ = probability that a female of age x survives to age x+1. $P_x$ is the fraction of x year olds likely to survive, so that means $n_{x+1}(t+1) = P_x\, n_x(t)$.

Let observe $n_x(t)$ x year olds in some year t, then in the next year (t+1) only a certain fraction will still be around, not x+1 year old. Each of the $n_x(t)$ females of age x is assumed in the beginning give birth to a certain number of females, but they're of little interest unless they survive to be 1 year old, at which point they start breeding. Let $f_x$ be average number of females born of x year olds that survive to age 1 (this may be a fraction). Therefore, if we start with $n_x(t)$ females of age x in year t, then in the next year (t+1) we assume there will be about $f_x\, n_x(t)$ of their daughters of age 1 still around. So the total number of 1 years olds in year t+1 would be $n_1(t+1) = f_1\, n_1(t) + f_2\, n_2(t) + \ldots + f_w\, n_w(t)$.

This is our final recursion relation (meaning it relates a new value of a variable to some old values). Note that $n_{x+1}(t+1) = P_x\, n_x(t)$ starts with x = 1, not x = 0, so we have w recursion relations in all. The w recursion relations can be expressed as a single matrix relation:

$$\begin{vmatrix} n_1\ (t+1) \\ n_2\ (t+1) \\ n_3\ (t+1) \\ n_4\ (t+1) \\ \ldots \\ n_w\ (t+1) \end{vmatrix} = \begin{vmatrix} f_1 & f_2 & f_3 & \ldots & f_{w-1} & f_w \\ P_1 & 0 & 0 & \ldots & 0 & 0 \\ 0 & P_2 & 0 & \ldots & 0 & 0 \\ 0 & 0 & P_2 & \ldots & 0 & 0 \\ . & . & . & & . & . \\ 0 & 0 & 0 & \ldots & P_{w-1} & 0 \end{vmatrix} \begin{vmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \\ .. \\ n_w(t) \end{vmatrix}$$

This can be even more written: $\mathbf{n}(t+1) = \mathbf{L}\,\mathbf{n}(t)$ where $\mathbf{n}(t+1)$ and $\mathbf{n}(t)$ are the columns of population values, and $\mathbf{L}$ is the square matrix defining the recursion. Finally, $\mathbf{n}(t) = \mathbf{L}\,\mathbf{n}(t-1) = \mathbf{L}^2\,\mathbf{n}(t-2) = ... = \mathbf{L}^t\,\mathbf{n}(0)$, which gives a nice way of determining the populations at any time t in terms of a set of starting populations at time t = 0.

For example, if we take $f_1 = 1/3$, $f_2 = 2/3$, $f_3 = 2/3$, $P_1 = 0.5$ and $P_2 = 1.0$. These values are seen in their appropriate slots in the 3x3 matrix (which is the matrix $\mathbf{L}$). The initial populations of the 1, 2 and 3 year olds at t = 0 (they do not influence the powers of $\mathbf{L}$). So in this case w = 3, and all females over 3 years old have given up on breeding. But on average each season the 1, 2 and 3 year old females give birth to 1/3, 2/3 and 2/3 female spawn, respectively, that survive at least one year. Also, half of 1 year olds survive to 2, and all of 2 year olds survive to 3 (unrealistic, survival rates should be expected to increase with age and experience at least to some extent).

The outputs are the matrices $\mathbf{L}^{t+1}$ and $\mathbf{L}^{t+2}$, and the columns of populations $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ (these will depend on the 3 inputs).

As we see whatever 3 values of $n_x(0)$ started with, if we go far enough into the future (t large) we'll end up approximately with

$n_1(t) \to 2a$,
$n_2(t) \to a$,
$n_3(t) \to a$,

for some limiting constant a. If in the beginning $n_1(0) = 2n_2(0) = 2n_3(0)$ (for example, the values, 200, 100 and 100), then the populations $n_x(t)$ will remain constant for all $t > 0$. As t gets large, the matrices $\mathbf{L}^t$ seem to converge to the matrix

$$\begin{matrix} 1/2 & 2/3 & 1/3 \\ 1/4 & 1/3 & 1/6 \\ 1/4 & 1/3 & 1/6 \end{matrix}$$

In fact, let's denote this limiting matrix by $\mathbf{L}^{\%}$ (which is supposed to look like **L** to the power infinity, because that's what it actually is). Since infinity + 1 = infinity, then expect $L^{\%} = \mathbf{L}\mathbf{L}^{\%} = \mathbf{L}^{\%}\mathbf{L}$.

And in fact, multiplying $\mathbf{L}^{\%}$ from the left or right by **L** yields $\mathbf{L}^{\%}$ back again.

Continuing on in this vein, recall that $\mathbf{n}(t) = \mathbf{L}^t\, \mathbf{n}(0)$, where $\mathbf{n}(t)$ is the column matrix of 3 populations $n_x(t)$. Therefore, let $\mathbf{n}(\%) = \mathbf{L}^{\%}\, \mathbf{n}(0)$, which is the column of populations after an infinite number of generations (which won't happen until the year 2089). Performing the matrix multiplication we get

$n_1(\%) = 2n_2(\%) = 2n_3(\%) = (n_1(0)/2 + 2n_2(0)/3 + n_3(0)/3)$.

(So $n_1(\%) + 2n_2(\%) + n_3(\%) = (n_1(0) + 4n_2(0)/3 + 2n_3(0)/3)$. But

$\mathbf{L}\, \mathbf{n}(\%) = \mathbf{L}\mathbf{L}^{\%}\, \mathbf{n}(0) = \mathbf{L}^{\%+1}\, \mathbf{n}(0) = \mathbf{L}^{\%}\, \mathbf{n}(0) = \mathbf{n}(\%)$,.................(eigenvector equation),

and that explains why if $n_1(t) = 2n_2(t) = 2n_3(t)$, then $\mathbf{n}(t+1) = \mathbf{L}\, \mathbf{n}(t) = \mathbf{n}(t)$.

The general form of a matrix eigenvalue equation is

$\mathbf{A}\, \mathbf{v} = \mu\, \mathbf{v}$

where **A** is an n x n matrix, **v** an n x1 matrix (vector), and μ a number. **v** is called the eigenvector, and μ its eigenvalue. If **v** is an eigenvector of some matrix **A**, then so is c**v** for any constant c; so eigenvectors determine eigen-"directions".

In the **L**-eigenvector equation written above, **n**(%) is the eigenvector, and $\mu = 1$ is the corresponding eigenvalue. (There are two other eigenvalues for **L**, but they are complex numbers with nonzero imaginary components, and they won't be of interest to us.)

The eigenvalue μ = 1 is quite special, and it is responsible for the fact that the nine components of $\mathbf{L}^{\%}$ are finite real numbers, and for the fact that whatever populations $n_x(0)$ we may start with, after a large number of generations we will settle near the stable values of $n_x(\%)$, which are finite.

For example, if $f_1 = 8/7$, $f_2 = 16/7$, $f_3 = 16/7$, $P_1 = 0.5$ and $P_2 = 1.0$.
These values divided by 2 (see below) in their appropriate slots in the 3x3 matrix (which is the matrix **L/2).**

In this case the fecundity factors $f_x$ have each been increased by a factor of 24/7. The vectors with components,

8c
2c
c

with c any number, are eigenvectors of this new matrix **L** with eigenvalue 2. Therefore the matrix $\mathbf{L}^t$ has the same eigenvectors, but eigenvalue $2^t$, an exponentially increasing function of t. That means that the components of $\mathbf{L}^t$ will also be exploding exponentially. On the other hand, the matrix **L**/2 has the same eigenvectors but the eigenvalue 1, so it is powers of this matrix (just multiply by $2^t$ to get **L** itself), as its components will remain finite as t goes to infinity. However, the values of $n_x(t)$ are given without factors, and they rapidly increase with t. The ratios of the three $n_x(t)$ are going to 8:2:1, the eigen-"direction" ratios given above. That is, even though the $n_x(t)$ do not converge to a stable fixed point in this case, their ratios converge to the eigenvector ratios 8:2:1.

Although the components of **L** will increase like $2^t$, the components of **L**/2 converge to

| | | |
|---|---|---|
| 7/11 | 12/11 | 8/11 |
| 7/44 | 3/11 | 2/11 |
| 7/88 | 3/22 | 1/11 |

Conclusion: had the $f_x$ to be decreased even slightly from their original values, we would have had an eigenvalue less than 1, and this would have resulted in exponential population decline and eventual extinction. An eigenvalue greater than 1 is most likely, and the model need to get complicated by limiting resources to prevent the unrealistic unlimited growth that was observed here.

Bibliography:

"Linear Algebra and Its Applications," David Lay

"Evolutionary Theoretical Ecology," Michael Bulmer

website: http://www.maths.ox.ac.uk/cmb/