The More the Merrier

In the Math of Population Ecology

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MATHEMATICAL FIELD

Calculus and Differential Equations.

APPLICATION FIELD

Population Dynamics and Ecology.

TARGET AUDIENCE

Students in an elementary mathematical modeling course or in a course of calculus with elementary differential equations, including numerical solutions for systems of ordinary differential equations.

ABSTRACT

We derive a mathematical model of population ecology that describes the role of dispersal in the survival of a population in danger of extinction. Students working with the module will write a computer code, using a software such as MATLAB or Mathematica, to obtain numerical solutions of the model. They will use the numerical simulations to explore the mathematical properties of the model and interpret the results in the ecological context.

PREREQUISITES

Precalculus and basic programing skills.

TECHNOLOGY

Access to a computer algebra system, such as Mathematica or MATLAB, is required for the main activities of this modulus.

AKNOWLEDGMENTS

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Introduction

This teaching module is a hands on introduction to mathematical modeling in population ecology. Population Ecology has ben defined as "the science of what makes animal and plant populations change, persist, or go extinct"[1].

A demographic tension between competition and cooperation drives the dynamics of many species. Population declines when **competition** among individuals for diminishing resources occurs at hight density levels. In this case fewer individuals benefit from more resources, but they may also suffer from a lack of support of conspecifics. Below a threshold value the death rate is higher than the birth rate because, on average, the individuals cannot reproduce successfully. This imposes a need for **cooperation** among individuals to increase the population and guarantee the survival of the species at low density.

Starting with the simplest model of exponential growth we progressively add enough features to the model in order to obtain a reasonable mathematical description of this phenomenon.

Students working with the module will write a computer code, using a software such as MATLAB or Mathematica, to obtain numerical solutions of the model. They will use the numerical simulations to explore the mathematical results in the context of this important topic of population ecology.

1 Exponential Growth (EG)

Let $u(t)$ be the average population of an species at time $t \geq 0$. The simplest mathematical model of population ecology is the one that assumes a constant relative growth rate $u'(t)/u(t)$. That is,

$$\frac{du}{dt} = ru(t), \ t \geq 0, \tag{1}$$

where $r > 0$ is the relative growth rate. Since the solutions of equation (1) grows exponentially, this model is know as *Exponential Growth* (EG). In fact, all the solutions of (1) are of the form

$$u(t) = ce^{rt}, \ t \geq 0, \tag{2}$$

where $c = u(0)$ is the initial population.

The fast and unlimited population described by (2), and illustrated in Figure 1, can only be justified under the ideal assumption that the species doesn't encounter any

[1] B.W. Brook, *The Allure of the Few*, PLoS Biol 6(5): e127 (2008). doi:10.1371/journal.pbio.0060127.

restriction to keep growing indefinitely. Nevertheless, in reality there are many factors, such as the existence of predators or the limit of resources, that will constraint the growth of the population. We will address this situation in the following section by introducing a suitable restriction to the relative grow rate of the population.

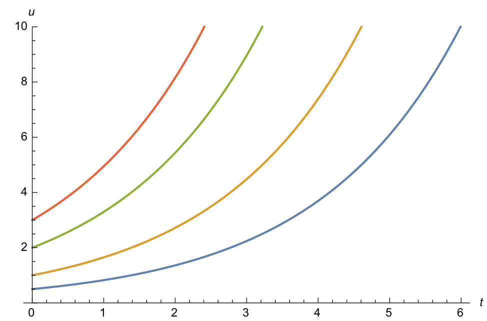

Figure 1: Graphical representation of solutions of (1) obtained with Mathematica. We use $r = .5$ and different values for the initial population $u(0)$.

2 Logistic Growth (LG)

In order to make the EG model more realistic we will assume that the relative growth rate $u'(t)/u(t)$ decreases as the population increases, and becomes negative after a limit value $K > 0$ known as the environmental carrying capacity. The mathematical formulation of this assumption, know as *Logistic Model* (LG), is given by

$$\frac{du}{dt} = r\left(1 - \frac{u(t)}{K}\right) u(t),\ \ t \geq 0, \tag{3}$$

This model imposes a constrain for the population to grow beyond the level K where diverse environmental and demographic factors create adverse conditions for survival. As such, this is a model of competition that embraces a logic of *"the fewer the better"*.

The explicit solution of (3), obtained by the method of separation of variables, is given by

$$u(t) = \frac{cK}{c + (K - c)e^{-rt}},\ \ t \geq 0, \tag{4}$$

where $c = u(0)$ is the initial population.

As described by equation (4), and illustrated in Figure 2, the solutions converge to the carrying capacity K as $t \to \infty$. In other words, the population will always grow, or decay, to the maximum of its capacity.

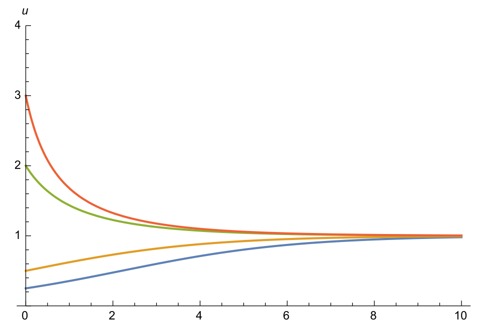

Figure 2: Graphical representation of solutions of (3) obtained with Mathematica. We use $r = .5$, $K = 1$, and different values for the initial population $u(0)$. Notice that the adoption of $K = 1$ is equivalent to rescaling equation (3) by replacing u with u/K, and considering $u(t)$ as a density with respect to the carrying capacity K.

3 LG with Diffussion

In this section we introduce spatial distribution to the LG model. For simplicity we assume that the population inhabits in a one dimensional array of n locations $i = 1, 2, \ldots, n$, with $u_i(t)$ representing the population of an species in the location i at time $t \geq 0$.

Following the logic of *"the fewer the better"* embedded in the LG model, we assume that individuals disperse to to avoid crows. This is obtained by a process, know as *diffusion*, that assumes that individuals in a location i disperse to their neighbor locations $i - 1$ and $i + 1$ affecting their local grow rate by a factor of the form $d(u_{i-1} - u_i)$ and $d(u_{i+1} - u_i)$ respectively, where the dispersal rate d is a positive constant. In the absence of grow rate, this leads the model

$$\frac{du_i}{dt} = d(u_{i-1} - u_i) + d(u_{i+1} - u_i), \; i = 1, 2, \ldots n, \; t \geq 0, \tag{5}$$

where we assume that $u_0 = u_1$ and $u_{n+1} = u_n$.

Notice that the dispersal mechanism described by equation (5) produces a local increase of the population, $u_i' > 0$, if the population u_i is smaller than the populations u_{i-1} and u_{i+1} at it's neighbors. Similar, it produces a local reduction of the population, $u_i' < 0$, if the population u_i is larger than the populations u_{i-1} and u_{i+1} at it's neighbors. Notice the similarity of (5) with Newton's law of cooling that states that heat flows from hot to cooler locations, Combining (3) with (5) we obtain the following LG model with diffusion

$$\frac{du_i}{dt} = du_{i-1} - 2du_i + du_{i+1} + r\left(1 - \frac{u_i}{K}\right)u_i,\ i = 1, 2, \ldots n,\ t \geq 0, \tag{6}$$

where $u_0 = u_1$, $u_{n+1} = u_n$, and d is a positive constant.

Figure 3 shows the time evolution of a solution to equation (6) with random initial distribution $u_i(0)$, $i = 1, 2, \ldots, n$. It is observed that at any location the population grows, or decay, to the carrying capacity K. This is essentially a replication of the behavior observed for the LG model (3), and confirms that diffusion is the right dispersal mechanisms for the logistic model with spatial population distribution.

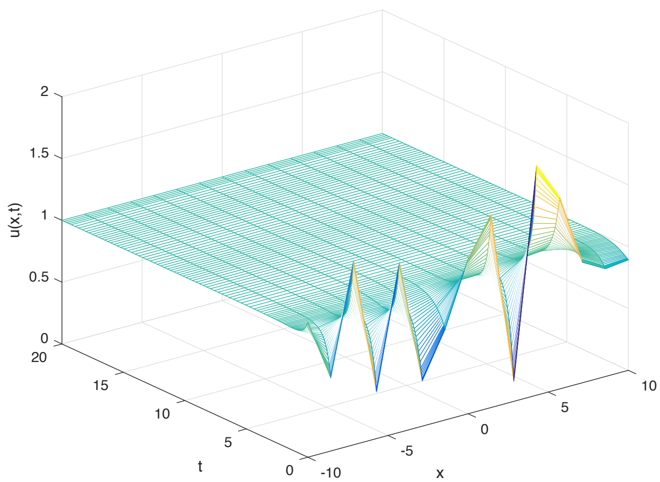

Figure 3: Graphical representation of a solution of (6) obtained with MATLAB. We use $n = 15$, $r = 1$, $K = 1$, $d = 0.5$, and a random distribution of the initial population $u_i(0)$, $i = 1, 2 \ldots, n$. Notice that the adoption of $K = 1$ is equivalent to rescaling equation (6) by replacing u_i with u_i/K, and considering $u_i(t)$ as a density distribution with respect to the carrying capacity K.

4 LG with Threshold (LGT)

In the LG model (3) population declines when competition among individuals for diminishing resources, or other demographic pressures, occur at high level density, the fewer the better. When there are too few individuals it may be that they will each benefit from more resources, but in many cases they will also suffer from a lack of conspecifics.

Too few may not be necessarily the better. This is a very common situation in nature and it is know as the Allee effect. The main feature of the Allee effect is that below a threshold value the death rate is higher than the birth rate because, on average, the individuals cannot reproduce successfully. This, in turn, imposes a threat to the survival of the species at low densities. It is the *"the more the merrier"* of population ecology.

The following model, know as Logistic Growth with Threshold (LGT), incorporates into the LG model an Allee effect with threshold value $T < K$,

$$\frac{du}{dt} = r\left(\frac{u(t)}{T} - 1\right)\left(1 - \frac{u(t)}{K}\right)u(t),\ t \geq 0. \tag{7}$$

Figure 4 illustrate the main features of the LGT model. If the initial population $u(0)$ is located above the threshold level T the solution behaves like the LG model converging to the carrying capacity as $t \to \infty$. Nevertheless, if $u(0) < T$ the population goes extinct.

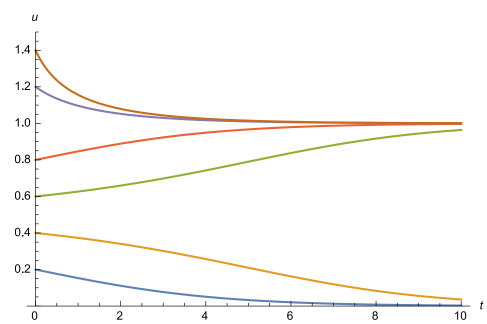

Figure 4: Graphical representation of solutions of (3) obtained with Mathematica. We use $r = .5$, $T = .5$, $K = 1$, and different values for the initial population $u(0)$. Notice that the adoption of $K = 1$ is equivalent to rescaling equation (7) by replacing u with u/K, T with T/K, and considering $u(t)$ as a density with respect to the carrying capacity K.

A natural question arises, does a population menaced by extinction due to the Allee effect contains mechanisms for its survival? One may infer that a selective migration mechanism may allow a population located in a neighborhood of low density, to cluster together in an attempt to raise their local population above the threshold at which the birth rate begins to exceed the death rate. We give the name of **permanent recovery** to this kind of behavior. In the following sections we will investigate migration patterns that promotes this type of response.

5 LGT with Diffusion

In this section we will explore whether the diffusive migration mechanisms described in Section 3 will allow the permanent recovery of a population in danger of extinction. Accordingly, we consider the following LGT model with diffusion

$$\frac{du_i}{dt} = du_{i-1} - 2du_i + du_{i+1} + r\left(\frac{u_i}{T} - 1\right)\left(1 - \frac{u_i}{K}\right)u_i, \ i = 1, 2, \ldots n, \ t \geq 0, \tag{8}$$

where $u_0 = u_1$, $u_{n+1} = u_n$, and d is a positive constant.

The following theorem asserts that the diffusive dispersal mechanism of equation (8) doesn't allow recovery. For the proof of a more general version of this theorem see [1, Theorem 1].

Theorem 1. *Let $u_i(t)$, $i = 1, 2, \ldots, n$, be a solution of* (8) *such that* $0 \leq u_i(0) < T$, $i = 1, 2, \ldots, n$. *Then*

$$0 \leq u_i(t) < T, \, i = 1, 2, \ldots, n,$$

for all $t > 0$.

Assignment 1. *Write a computer code to solve system* (8) *numerically. We recommend the MATLAB solver* **ode45***, or the Mathematica function* **NDSolve***, to obtain an accurate solution.*

Assignment 2. *Use the code obtained in Assignment 1 to illustrate and verify the conclusion of Theorem 1.*

6 LGT with Advection–Diffusion

In this section we consider the following LGT model with a more general dispersal mechanisms compose of variable dispersal rates.

$$\frac{du_i}{dt} = d_{i-1}u_{i-1} - 2d_iu_i + d_{i+1}u_{i+1} + r\left(\frac{u_i}{T} - 1\right)\left(1 - \frac{u_i}{K}\right)u_i, \ i = 1, 2, \ldots n, \ t \geq 0, \tag{9}$$

where $u_0 = u_1$, $u_{n+1} = u_n$, and d_i, $i = 1, 2, \ldots, n$, are positive constants.

The following theorem shows that (9) does exhibit a migration mechanism that allows the permanent recovery of a population in danger of extinction. For the proof of a more general version of this theorem see [1, Theorem 2].

Theorem 2. *Assume that there exists a non-empty proper subset I_1 of the set $I := \{1, \ldots, n\}$ such that*

$$d_i < \frac{d_{i-1} + d_{i+1}}{2}, \tag{10}$$

for all $i \in I_1$. Then, there exists $\delta > 0$ such that if $d_i < \delta$ for all $i \in I_1$ then system (9) *exhibits permanent recovery. That is, there are solutions $u_i(t)$, $i = 1, 2, \ldots, n$ of* (9) *with $0 \leq u_i(0) < T$, $i = 1, 2, \ldots, n$, such that there exists $i_0 \in I$ and $t_0 > 0$, for which $u_{i_0}(t) > T$ for all $t > t_0$.*

Assignment 3. *Adapt the code obtained in Assignment 1 to illustrate and verify the conclusion of Theorem 2.*

Assignment 4. *Figure 6 shows a solution of* (9) *with dispersal rates d_i, $i = 1, 2, \ldots 10$, and initial population $u_i(0)$, $i = 1, 2, \ldots 10$, given in Table 1. As suggested by Figure 6 the population grow from an initial population under the threshold $T = .25$ in all the locations, with average distribution $\frac{1}{10}\sum_{i=1}^{10} u_i(0) = 0.1501$, to a distribution with two location over the threshold and average distribution $\frac{1}{10}\sum_{i=1}^{10} u_i(t) = 0.2065$ at time $t =$ 15.*

(a) Use the code implemented in Assignment 3 to replicate Figure 6.

(b) Run a simulation with initial distribution $u_i(0) = 0.2065$, $i = 1, 2, \ldots, n$, which is a redistribute of the population reached at the end of the simulation in part (a). Does the average distribution increases?

(c) Use Theorem 2 to modify some of the dispersal rates d_i, $i = 1, 2, \ldots, n$,given in Table 1, to obtain an increase of the average distribution of the population starting with initial distribution $u_i(0) = 0.2065$, $i = 1, 2, \ldots, n$, as in part (b).

(d) What conclusions can you draw, in ecological terms, from the numerical experiments done in (a), (b), and (c). Could they suggest a strategy to save a population that is in danger of extinction?. How would you proceed to apply Theorem 2 in a real situation?

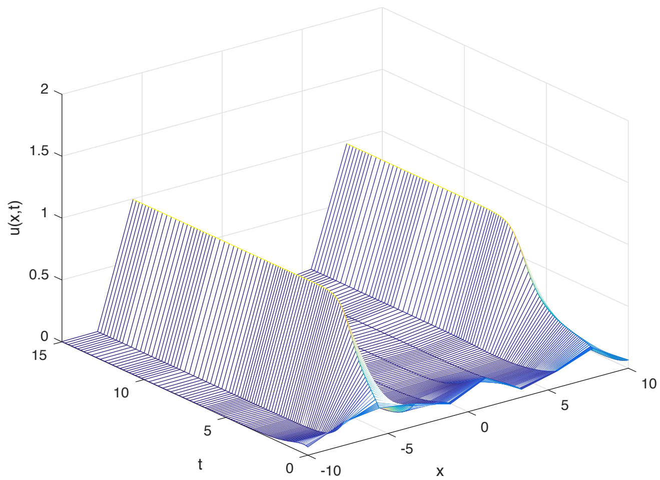

Figure 5: Graphical representation of a solution of (9) obtained with MATLAB. We use $n = 10$, $r = 1$, $T = .25$, $K = 1$. The dispersal rates d_i, $i = 1, 2, \ldots 10$ and initial population $u_i(0)$, $i = 1, 2, \ldots 10$ are given in Table 1. Notice that the adoption of $K = 1$ is equivalent to rescaling equation (9) by replacing u_i with u_i/K, T with T/K, and considering $u_i(t)$ as a density distribution with respect to the carrying capacity K

i	1	2	3	4	5	6	7	8	9	10
d_i	0.7437	0.7843	0.0112	0.8086	0.9494	0.4630	0.7316	0.3029	0.0539	0.8804
$u_i(0)$	0.0668	0.1884	0.2246	0.1821	0.1017	0.2346	0.0639	0.1333	0.2387	0.0669

Table 1: Dispersal rates d_i, $i = 1, 2, \ldots 10$ and initial population $u_i(0)$, $i = 1, 2, \ldots 10$ used for the simulation illustrated in Figure 6.

References

[1] V. Padrón, M.C. Trevisan, Effect of aggregating behaviour on population recovery on a set of habitat islands, Math. Biosc. 165 (2000) 63–78.