An Analysis of the Usage of Turing System in Species Competition Problems

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Introduction

One important use of differential equations in life sciences is to model population densities [10, 11]. In this paper, we analyze Okubo's [14] application of diffusion-competition model that describes the interaction between two squirrel populations in Britain.

The rest of the paper is organized as follows: first, we introduce the problem by providing context for the squirrel population density problem, as well as the history of related works on diffusion-competition models. Then, we formulate the problem in concise mathematical notations following the work of Okubo et al. Next, we provide the analysis and results of the differential equation problem formulated, aiming to analyze the steady states and stability, as well as the analytical solution to the partial differential equation (PDE) problem. We also provide some interpretation of the results, and expand on the applications of Turing System in other fields. Finally, we conclude with a short summary of the main points.

a. Squirrel Population Problem

Okubo et al's [14] work aims to answer the question of how the population two the two squirrel species interacts and changes. Around 1900, some North American grey squirrels were released in some parts of Britain, and has successfully taken habitat there and spread through most of England, Wales, and Scottland. This posed a new threat to the population of the indigenous red squirrels, which is said to have declined in population and nearly disappeared. The goal of Okubo et al was to present a simple mathematical framework of competition and diffusion of the two species and obtain solutions to the differential-equation model to explain the population changes observed in the red and grey squirrel cohorts.

In their work, Okubo et al makes two important assumptions. First, the interaction between the two species includes indirect competition for food, habitat, and resources as well as direct competition through physical contact. Second, they assumed the population number is big enough that a continuous differential equations model makes sense for discrete animal population.

A big part of their work was also dedicated to estimate the parameters of the PDE problem using available data. This paper, however, focuses entirely on the PDE problem itself and therefore assumes that all constant in the PDE system in known and given.

b. Related Work

There have been a lot of work studying the population of squirrels in Britain. Many of the work in the field, unsurprisingly, are by well-known ecologists. Middleton [8] have argued that the decline of red squirrels is not induced by the introduction of its competitors, while Elton [2] and others have argues for the opposite side.

On the more mathematical side, many have also made use of systems of differential equations to study the spread of animal populations. For example, Murray et al [10] have modeled the spread of rabies among foxes using a simple logistic law. Murray [11] have also studied the spatial dispersal of species using differential equations.

The main mathematical foundations for this work is the Turing Systems. The Turing System is first introduced by Alan Turing [18] in 1990 studying patterns found in nature. Turing examined a system where two diffusable substances interact with each other and tried to identify the diffusion pattern. He found that such a system eventually lead to a spatially periodic pattern, even if the initial distribution is random or uniform. In honor of his amazing discovery, the system is named "Turing System" and the pattern "Turing pattern". Two decades after Turing's discovery, Barrio [1] have also studied Turing Systems and pointed out that they are "suitable to model a wide variety of phenomenons found in nature". Logan [7] has presented a generic form for Turing Systems:

$$u_t = \alpha u_{xx} + f(u, v)$$
$$v_t = \beta v_{xx} + g(u, v)$$

This system describes a reaction-diffusion process on the spatial domain $0 < x < L$. More recently, many have used this system of equations for applications in the life sciences. Okubo et al [14] mirrored the two squirrel populations as the two "diffusable substances", and investigated the diffusion pattern. Zincenko et al [19] have used Turing systems to investigate the human population density diffusing between urban and rural areas. Karig et al [4] have used the system to study the population of bacterial under more relaxed mathematical conditions.

Problem formulation

In this section, we formulate the population density problem as a system of partial differential equations.

Following the notation of Okubo et al [14], let $S_1(R, T)$, $S_2(R, T)$ be the population densities at time T and spatial location R of grey and red squirrels respectively. With the assumption that the two squirrel species compete for the same resources, we know that S_1 and S_2 satisfy the following systems of PDEs:

$$\begin{cases} \frac{\partial S_1}{\partial T} = D_1 \nabla^2 S_1 + a_1 S_1(1 - b_1 S_1 - c_1 S_2) \\ \frac{\partial S_2}{\partial T} = D_2 \nabla^2 S_2 + a_2 S_2(1 - b_2 S_2 - c_2 S_1) \end{cases} . \tag{1}$$

where D_i are diffusion coefficients, a_i are net birth rates, $1/b_i$ are carrying capacities, c_i are competition coefficients, and $i = 1$ is for grey and 2 for red. ∇^2 is the Laplace operator. For simplicity, we limit ourselves to the case with only one spatial dimension, x, in the spatial domain $0 < x < L$. Then, we can rewrite Equation (1)into

$$\begin{cases} \frac{\partial S_1}{\partial T} = D_1 \frac{\partial^2 S_1}{\partial x^2} + a_1 S_1(1 - b_1 S_1 - c_1 S_2) \\ \frac{\partial S_2}{\partial T} = D_2 \frac{\partial^2 S_2}{\partial x^2} + a_2 S_2(1 - b_2 S_2 - c_2 S_1) \end{cases} . \tag{2}$$

In the Okubo paper, they assumed that all parameters are non-negative and that the grey squirrels out-compete the red ones. Hence

$$b_2 > c_1, \quad c_2 > b_1 \tag{3}$$

In addition, the system has zero-flux boundary conditions because we assume squirrels in Britain are going to stay in Britain with none coming in or leaving

$$\frac{\partial S_i}{\partial x} = 0, \quad x = 0, L$$

for i = 1,2. The goal is to investigate the general behavior of the above system, and the possibility of traveling waves of invasion of grey squirrels that drive out the reds.

Analysis and Results

We divide this section into three parts. In part a, we study the the steady states of the system and their corresponding stability; in part b, we conduct phase plane analysis and argue the existence of traveling wave solutions; in part c, we analytically deduce the traveling wave solutions of the Turing System in a special case where the system of equations is reducible to Fisher's Equation.

a. Steady states and stability

Firstly, we wish to find the steady states of the system. Assume that the system has constant solution $S_1 = e_1, S_2 = e_2$. With this solution, Equation (1) becomes

$$\begin{cases} a_1 e_1(1 - b_1 e_1 - c_1 e_2) = 0 \\ a_2 e_2(1 - b_2 e_2 - c_2 e_1) = 0 \end{cases} . \tag{4}$$

Since all the coefficients are non-zero, we can derive that there are 3 steady states: $(0, 0)$, $(1, 0)$ and (0,1). These correspond to three scenarios in a given environment: no squirrels, only grey squirrels with density 1 and only red squirrels with density

1, respectively.

Now consider that there are some small perturbations U, V near our equilibria, i.e.

$$\begin{cases} S_1 = e_1 + U(x,t) \\ S_2 = e_2 + V(x,t) \end{cases} \tag{5}$$

Let

$$\begin{cases} f(s_1, s_2) = a_1 e_1(1 - b_1 e_1 - c_1 e_2) \\ g(s_1, s_2) = a_2 e_2(1 - b_2 e_2 - c_2 e_1) \end{cases} \tag{6}$$

We can then rewrite Equation (2) as

$$\begin{cases} U_t = D_1 U_{xx} + f(e_1 + U, e_2 + V) \\ V_t = D_2 V_{xx} + g(e_1 + U, e_2 + V) \end{cases} . \tag{7}$$

subject to boundary conditions

$$U_x(0,t) = U_x(L,t) = V_x(0,t) = V_x(L,t) = 0 \tag{8}$$

To linearize Equation (7), consider the Taylor expansions of f and g

$$\begin{cases} f(e_1 + U, e_2 + V) = f(e_1, e_2) + f_{S_1}(e_1, e_2)U + f_{S_2}(e_1, e_2)V + f_{S_1 S_1}(e_1, e_2)U^2 + ... \\ g(e_1 + U, e_2 + V) = g(e_1, e_2) + g_{S_1}(e_1, e_2)U + g_{S_2}(e_1, e_2)V + g_{S_1 S_1}(e_1, e_2)U^2 + ... \end{cases} . \tag{9}$$

Since U and V are assumed to be small perturbations, we can drop the non-linear terms. Also note that $f(e_1, e_2) = g(e_1, e_2) = 0$. Hence, the linearized form of Equation (7) is

$$\begin{cases} U_t = D_1 U_{xx} + f_{S_1}(e_1, e_2)U + f_{S_2}(e_1, e_2)V \\ V_t = D_2 V_{xx} + g_{S_1}(e_1, e_2)U + g_{S_2}(e_1, e_2)V \end{cases} . \tag{10}$$

which can be rewritten in the matrix form

$$\overrightarrow{W_t} = D\overrightarrow{W_{xx}} + J\overrightarrow{W} \tag{11}$$

where

$$\overrightarrow{W} = \begin{pmatrix} U \\ V \end{pmatrix}, \ D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}, \ J = \begin{pmatrix} f_{S_1}(e_1, e_2) & f_{S_2}(e_1, e_2) \\ g_{S_1}(e_1, e_2) & g_{S_2}(e_1, e_2) \end{pmatrix}.$$

The solutions to Equation (11), a standard diffusion equation with a source term, take the form

$$\overrightarrow{W} = \overrightarrow{C} e^{\lambda_n t} cos(\frac{n}{L}), \ \overrightarrow{C} = \begin{pmatrix} c_{1n} \\ c_{2n} \end{pmatrix}, \ n = 0,1,2,...$$

Plug this solution into Equation (11), we obtain

$$(\lambda_n I + \frac{Dn^2\pi^2}{L^2} - J)\overrightarrow{W} = 0 \tag{12}$$

Note that

$$J = \begin{pmatrix} a_1 - 2a_1b_1e_1 - a_1c_1e_2 & -a_1c_1e_1 \\ -a_2c_2e_2 & a_2 - 2a_2b_2e_2 - a_2c_2e_1 \end{pmatrix} \tag{13}$$

In order for Equation (12) to have non-trivial solutions, we need

$$det(\lambda_n I + \frac{Dn^2\pi^2}{L^2} - J) = 0, \tag{14}$$

thus eigenvalues λ_n can be solved. In addition, the stability of each equilibrium point can be concluded by studying the signs of the eigenvalues. Our results have shown that $(0,0)$ is an unstable node, $(1,0)$ is a stable node, and (0,1) is a saddle point. The knowledge of the stability of each steady state can be useful in the phase plane analysis in the following section, and can facilitate our understanding of the dynamics of the system.

b. Phase plane analysis

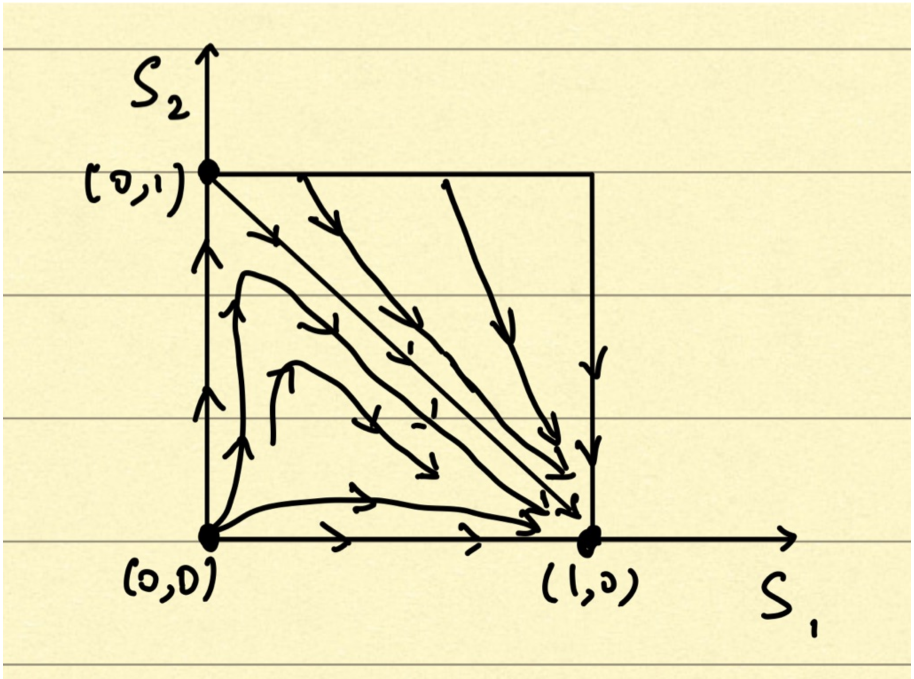

Figure 1: Phase plane

Figure (1) is the phase plane of the system inferred from the node type of each equilibrium point, where S_1 and S_2 are the two axes. The phase plane suggests the existence of a solution from (0,1) to (1,0), and that when diffusion is included, there is a possible traveling wave solution connecting these two points [12]. This particular solution corresponds to the event that invading grey squirrels out-competes red ones to extinction. The following section will expand on the calculations of the traveling wave solution.

c. Traveling wave solutions

In this section, we consider the traveling wave solutions to the simplified 1-dimensional Turing System in Equation (2). Following Okubo's work, we attempt to re-write this system in a non-dimensional form with dimensionless time t and dimensionless spatial coordinate x:

$$t = a_1 * T$$

$$x = X(a_1/D_1)^{0.5}$$

Then, the dimensionless population densities at space x and time t is $\theta_i = \theta_i(x,t), i =$ 1,2:

$$\theta_1 = b_1 * S_1$$

$$\theta_2 = b_2 * S_2$$

Also define constants:

$$\begin{cases} \kappa = D_2/D_1 \\ \alpha = a_2/a_1 \\ \gamma_1 = c_1/b_2, \quad \gamma_2 = c_2/b_1 \end{cases} \tag{15}$$

where κ represents the ratio of diffusion of red squirrel to grey squirrel and α is the ratio of growth rates. Using these constants and non-dimensional variables, we can write down the non-dimensional Turing System:

$$\begin{cases} \frac{\partial\theta_1}{\partial t} = \frac{\partial^2\theta_1}{\partial x^2} + \theta_1(1-\theta_1-\gamma_1\theta_2) \\ \frac{\partial\theta_2}{\partial t} = \kappa\frac{\partial^2\theta_2}{\partial x^2} + \alpha\theta_2(1-\theta_2-\gamma_2\theta_1) \end{cases} \tag{16}$$

And the constraints assumed in formula (3) becomes:

$$\gamma_1 < 1, \quad \gamma_2 > 1 \tag{17}$$

From the analysis of the phase plane and stationary points, we already know that the system (16) along with constraints (17) has three steady states: unstable state at $(0,0)$, stable state at $(1,0)$, and saddle point at $(0,1)$. The phase plane indicates that a travelling wave solution will start from point $(0,1)$ to $(1,0)$. In the remainder of this section we will derive this solution that corresponds to the grey squirrels (θ_1) drives the red (θ_2) to near extinction.

We aim to find traveling wave solutions to Equation (16) where θ_1, θ_2 are wave solutions to constant shape travelling to the $+x$ direction with velocity V:

$$\begin{cases} \theta_i = \theta_i(z), \quad i = 1,2 \\ z = x - Vt, \quad V > 0 \end{cases} \tag{18}$$

Solutions of this form is also proposed by Logan [7]. So now our job is to determine the value of the wave velocity V. Using this solution form, we simplify system (16) to:

$$\begin{cases} -V\frac{d\theta_1}{dz} = \frac{d^2\theta_1}{dz^2} + \theta_1(1-\theta_1-\gamma_1\theta_2) \\ -V\frac{d\theta_2}{dz} = \kappa\frac{d^2\theta_2}{dz^2} + \alpha\theta_2(1-\theta_2-\gamma_2\theta_1) \end{cases} \tag{19}$$

Based on the phase plane, the boundary conditions for $(1,0)$ and $(0,1)$ are:

$$\begin{cases} \theta_1 = 1, \quad \theta_2 = 0, \quad z = -\infty \\ \theta_1 = 0, \quad \theta_2 = 1, \quad , z = +\infty \end{cases} \tag{20}$$

Okubo et al [14] claims in their work that Equation (19) with boundaries (20) cannot by solved analytically, only numerically. However, we can still analyze the system under the specific case that

$$\kappa = \alpha = 1, \quad \gamma_1 + \gamma_2 = 2$$

We can add the two Equations in (19) to get:

$$-V\frac{d\theta}{dz} = \frac{d^2\theta}{dz^2} + \theta(1-\theta), \quad \theta = (\theta_1 + \theta_2) \tag{21}$$

Similarly, the boundary conditions from (20) becomes:

$$\theta = 1, \quad z = \pm\infty \tag{22}$$

Since $\theta = \theta(z)$ is a function of z, a monotonic variable is terms of x, t, and θ still takes on the same boundary value at both ends, θ has to be a constant for all values of z:

$$\theta = \theta_1 + \theta_2 = 1, \quad \forall z$$

We can in turn use this relationship between θ_1 and θ_2 to solve the system (19). First, to solve the first equation in system (19), we plug in $\theta_2 = 1 - \theta_1$, and get:

$$-V\frac{d\theta_1}{dz} = \frac{d^2\theta_1}{dz^2} + \theta_1(1\gamma_1)(1-\theta_1) \tag{23}$$

Note that this is in fact in the form of Fisher's Equation. In Fisher's original paper [3], he pointed out that the wave speed has to be greater than some threshold for wave solutions to exist. In a general form of Fisher's equation

$$\frac{\partial u}{\partial t} - D\frac{\partial^2 u}{\partial x^2} = ru(1-u)$$

the minimum wave speed is

$$c \geq 2\sqrt{rD}$$

Therefore, returning to Equation (23), the solution to wave speed V must satisfy:

$$V \geq V_{min}^{(1)} = 2\sqrt{1-\gamma_1}, \quad \gamma_1 < 1 \tag{24}$$

Similarly, we can solve the second equation in system (19) by plugging in $\theta_1 = 1 = \theta_2$, and get:

$$-V\frac{d\theta_2}{dz} = \frac{d^2\theta_2}{dz^2} + \theta_2(\gamma_2 - 1)(1-\theta_2) \tag{25}$$

By the same reasoning process, we know the wave speed must also satisfy

$$V \geq V_{min}^{(2)} = 2\sqrt{\gamma_2 - 1}, \quad \gamma_2 > 1 \tag{26}$$

Since we have assumed the special case of $\gamma_1 + \gamma_2 = 1$, so $1 - \gamma_1 = \gamma_2 - 1$. This means that the two minimum wave speeds we derived in Equation (23) and (25) are exactly the same. Finally, changing the expressions back to their dimensional form using the definitions from (15), we have:

$$V_{min} = 2\sqrt{(1 - \frac{c_1}{b_2})(D_1 a_1)} \tag{27}$$

In conclusion, solution V to system 19 under the specific case $\kappa = \alpha = 1, \gamma_1 + \gamma_2 = 2$ is $V \geq V_{min}$. The wave travels from $(\theta_1, \theta_2) = (0, 1)$ to $(1, 0)$ at some speed that's bounded from below.

Interpretation

The analysis in the last section indicates that since the grey squirrels are assumed to have competitive advantage, they would drive the red squirrels to extinction in competition. This is consistent with the results in the numerical simulation by Okubo et al [14]. Although the analysis in the previous section made the simplifying assumption of limiting the spatial variable to one dimension, the two-dimensional diffusion-competition problem yields very similar results.

In the beginning, before the North American grey squirrels were introduced into Britain, there is only the indigenous red squirrels. This corresponds to the saddle point $(S_1, S_2) = (0, 1)$, which is itself an equilibrium point and will stay the same without outside interference. When the grey squirrels were introduced, the necessary forces were applied to move the system equilibrium. At the start, the state moved from $(0, 1)$ to $(\epsilon, 1 - \epsilon)$ for some small number of introduced grey squirrels, ϵ. From the phase plane analysis and traveling wave solution analysis, we know there is a traveling wave solution from $(0, 1)$ to $(1, 0)$. Therefore, the state will traverse from $(\epsilon, 1 - \epsilon)$ to $(1, 0)$ with a minimum speed of $V_{min} = 2\sqrt{(1 - \frac{c_1}{b_2})(D_1 a_1)}$. When the solution arrives at point $(1, 0)$, this corresponds to the point where there is only grey squirrels and red squirrels have been driven to extinction.

Furthermore, Since $(1, 0)$ is a stable equilibrium, it is hard to return to the initial point $(0, 1)$ just by giving the system some perturbation and introducing some red squirrel populations. It seems like the North American squirrels are there to stay, calling Britain their new home.

Finally, we note that there is something particularly interesting about the results above; it indicates that a species competing and overcoming another is qualitatively very similar to one species spreading without the other. When there is no competition, a species will spread out like a wave and eventually reach a constant radial speed [17]. The only difference may be that the diffusion wave speed is slower with the presence of a competitor.

Extensions

In this section, we make provide contexts for some extended applications of the Turing System, which is the core of our analysis in this paper. Our goal here is to familiarize the readers with the applications of the Turing System.

The Turing System can be written in a generalized form

$$\begin{cases} \frac{\partial S_1}{\partial T} = D_1 \nabla^2 S_1 + f_1(S_1, S_2, ..., S_k) \\ \frac{\partial S_2}{\partial T} = D_2 \nabla^2 S_2 + f_2(S_1, S_2, ..., S_k) \\ \qquad\qquad ... \\ \frac{\partial S_k}{\partial T} = D_k \nabla^2 S_k + f_k(S_1, S_2, ..., S_k) \end{cases} . \tag{28}$$

and has wide applications in a variety of natural phenomenons where two or more diffusible substances interact. In Turing's classic paper [18] that first introduced the Turing System, he proposed a model that described how the interaction of two homogeneously distributed substances can produce ordered stable structures despite initial chaos, and hypothesized that the resulting wavelike patterns are the chemical basis of morphogenesis [6].

Besides competing species in an environment, another interesting application of the Turing system is zebra-fish skin pigmentation. The stripes of zebra-fish are composed of a mosaic-like arrangement of 3 types of pigment cells: melanophores, xanthophores, and iridophores [5]. Studies have shown that the generation of the stripe pattern is dependent on the interactions between pigment cells, instead of a prepattern mechanism [13]. The system can be characterized by the following system of equations containing 3 factors:

$$\frac{\partial u}{\partial t} = F(u, v, w) - c_u u + D_u \nabla^2 u$$

$$\frac{\partial v}{\partial t} = G(u, v, w) - c_v v + D_v \nabla^2 v$$

$$\frac{\partial w}{\partial t} = H(u, v, w) - c_w w + D_w \nabla^2 w$$

$$F(u, v, w) = \begin{cases} 0 & : \quad c_1 v + c_2 w + c_3 < 0 \\ c_1 v + c_2 w + c_3 < 0 : & 0 < c_1 v + c_2 w + c_3 < U \\ U & : \quad U < c_1 v + c_2 w + c_3 \end{cases}$$

$$G(u, v, w) = \begin{cases} 0 & : \quad c_4 v + c_5 w + c_6 < 0 \\ c_4 v + c_5 w + c_6 < 0 : & 0 < c_1 v + c_2 w + c_3 < V \\ V & : \quad V < c_4 v + c_5 w + c_6 \end{cases}$$

$$H(u, v, w) = \begin{cases} 0 & : \quad c_7 v + c_8 w + c_9 < 0 \\ c_7 v + c_8 w + c_9 < 0 : & 0 < c_7 v + c_8 w + c_9 < W \\ W & : \quad W < c_7 v + c_8 w + c_9 \end{cases}$$

where u, v represent the density of melanophores and xanthophores, respectively, and w is a long range factor. The equations cannot be solved analytically, but can be numerically simulated.

Conclusions

In this paper, we analyzed the use of Turing System in the problem of squirrel species competition in Britain. Our main contribution is analyzing the problem posed in Okubo et al's [14] work in depth, corroborating their findings, and identifying relevant related works in the usage of Turing Systems. We built on their work and provided original insights on the solution of the PDE system. Our main finding through the analysis indicates that the competitively advantageous grey squirrels will drive out the red squirrels in a diffusion-competition environment. The modeling result is corroborated by field studies of the squirrel populations [16, 9, 15].

Acknowledgements

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