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LM Advanced Mathematical Biology 31128

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Part 4: Travelling waves

In this part of the course we will look at several different models that are described using special cases of the reaction-advection-diffusion equation and admit solutions that describe traveling waves.

4.1 Fisher-Kolmogorov-Petrovsky-Piskunov equation

In this section, we will study an equation that was used in 1937 by the statistician and biologist Ronald Fisher to describe the spread of an advantageous mutation through a spatially-organised population (imagine a population aligned along a coastline for the one-dimensional case). Although this equation typically bears his name, a general form was also used by Kolmogorov, Petrovsky and Piskunov in their 1937 paper entitled "A study of the diffusion equation with increase in the amount of substance", and so we once again attempt to do justice to everyone involved at that time.

4.1.1 FKPP equation for population growth

Fisher was specifically concerned with using a reaction-diffusion equation for $c(\mathbf{x}, t)$, which for him represented the frequency of an advantageous mutant allele at time t and spatial position $\mathbf{x}$ within a population. However, we can instead interpret $c(\mathbf{x}, t)$ as the population density of a particular species in a fashion more analogous to what we have seen before. In the simplest model for exponential growth without boundary conditions we know that c will grow infinitely large as $t \to \infty$, which is unrealistic for a population one must assume will remain finite given what we know about the real world. To counteract the problem of infinite population size, the concept of logistic growth was introduced at the start of this course. In logistic growth, the population size is assumed to be limited by one or more resources, resulting in a so-called carrying capacity, R. In the absence of spatial variation, we saw that the ordinary differential equation for logistic growth is given by

$$\frac{dc}{dt} = kc\left(1 - \frac{c}{R}\right) \tag{4.1}$$

where k still has the interpretation of growth rate as before. Fisher's equation results from extending the logistic growth model to the spatial domain, such that we have

$$\frac{\partial c}{\partial t} = \nabla \cdot (D\nabla c) + kc\left(1 - \frac{c}{R}\right), \tag{4.2}$$

which has a dimensionless version

$$\frac{\partial u}{\partial t} = \nabla \cdot (\nabla u) + u(1 - u), \tag{4.3}$$

where now $0 \le u \le 1$ for all $t > 0$. This equation was first used by Fisher to study the propagation of a wave of mutation through populations, but it has many other wide-reaching applications, from chemical reaction kinetics to nuclear reactors. A more general form, where the reaction term $u(1-u)$ is replaced by $F(u) = u(1-u^q)$ for some $q > 0$, was also used by Kolmogorov, Petrovsky and Piskunov in some further applications to population genetics.

The problem Fisher posed was to search for solutions to equation 4.3 that represent *traveling waves*. We could imagine in his application a one-dimensional shore line population with a new mutant arising at one end, and the traveling wave representing the propagation of this mutant along the shore line as it begins to dominate the population. If $u(x,t)$ represents the frequency of this mutant allele at time t and distance x from where the mutant emerged, then the extreme cases $u = 0$ (no member of the population carries the mutation) and $u = 1$ (all members of the population carry the mutation) are precisely the homogenous steady states (constant in time and space) of this system. The traveling wave is then one that "switches" between these two homogenous steady states, as it moves up (or down) the shore line: at time $t = 0$ it starts with $u(x,0) = 1$ for all $x < x_0$ and $u(x,0) = 0$ for all $x > x_0$ (x_0 being the point beyond which the mutation remains constrained at the initial time). A traveling wave solution then means one that satisfies the ansatz $u(x,t) = U(z)$ with $z \equiv x - st$ for some *wave speed* $s > 0$. If we advance one unit of time then the solution at $t = 1$ is given by $u(x-s)$, which is just the initial solution $u(x)$ advanced by s. In the next subsection we will characterise such solutions.

4.1.2 Phase-plane method for traveling waves

Substituting $u(x,t) = U(x-st) \equiv U(z)$ into the one-dimensional version of equation 4.3 and using the chain rule yields a second-order ODE

$$\frac{d^2U}{dz^2} + s\frac{dU}{dz} + U(1-U) = 0, \tag{4.4}$$

which we can transform to a coupled system of first-order ODEs by taking $V = U'$ (we now use primes to denote differentiation with respect to z) so that

$$U' = V, \quad V' = -sV - U(1-U). \tag{4.5}$$

In what follows, it is important to recall that $U = u$ with $0 \leq u \leq 1$ and argument $z = x - st$ so that, when x is fixed, taking $t \to \infty$ is equivalent to $z \to -\infty$. Thus, the steady states of the above system 4.5 are $(U, V) = (0, 0)$ and $(U, V) = (1, 0)$ that correspond, respectively, to the extreme solutions $u = 0$ and $u = 1$ we discussed previously.

To evaluate the stability of these critical points we first calculate the Jacobian matrix

$$\mathbf{J}(U, V) = \begin{pmatrix} 0 & 1 \\ -1 + 2U & -s \end{pmatrix} \tag{4.6}$$

and determine its eigenvalues at $(0, 0)$ and $(1, 0)$. The characteristic equation for eigenvalues of $\mathbf{J}(0, 0)$ is

$$\det(\mathbf{J}(0,0) - \lambda\mathbf{I}) = \begin{vmatrix} -\lambda & 1 \\ -1 & -s - \lambda \end{vmatrix} = \lambda(s + \lambda) + 1 = \lambda^2 + s\lambda + 1 = 0 \tag{4.7}$$

and therefore eigenvalues are

$$\lambda_{\pm} = \frac{-s \pm \sqrt{s^2 - 4}}{2}. \tag{4.8}$$

Thus, when $s \geq 2$ then both eigenvalues are real and negative, meaning in this case the first steady state $(U, V) = (0, 0)$ is stable. We can also use the identification of U with u to make the argument that the case $s < 2$ (eigenvalues are complex conjugates with negative real part) can be excluded as non-physical: a spiral (stable focus) about the origin implies $U < 0$ at some point arbitrarily close to the origin, which we note implies $u < 0$. The characteristic equation for eigenvalues of $\mathbf{J}(1,0)$ is

$$\det(\mathbf{J}(1,0)-\lambda\mathbf{I}) = \begin{vmatrix} -\lambda & 1 \\ 1 & -s-\lambda \end{vmatrix} = \lambda(s+\lambda)-1 = \lambda^2+s\lambda-1 = 0 \tag{4.9}$$

and therefore eigenvalues are

$$\lambda_{\pm} = \frac{-s \pm \sqrt{s^2+4}}{2}. \tag{4.10}$$

For all cases of $s > 0$ both eigenvalues are real with one positive and one negative, so $(U,V) = (1,0)$ is therefore a saddle point.

Finally, we complete the phase-plane analysis by studying the nullclines of the system 4.5 (lines along which either U' or V' are zero). For $U' = 0$ there is a nullcline given by $V = 0$, which is the U-axis itself. On this nullcline, we have three scenarios

$$V' = -U + U^2 \begin{cases} > 0, & \text{if} \quad U < 0 \\ < 0, & \text{if} \quad 0 < U < 1 \\ > 0, & \text{if} \quad U > 1 \end{cases} \tag{4.11}$$

and therefore arrows along the phase-plane U-axis point vertically upwards in the regions $U < 0$ and $U > 1$, and vertically downwards in the region $0 < U < 1$. For $V' = 0$, we have the nullcline given by $sV + U(1-U) = 0$, which is the parabola given by

$$V = \frac{1}{s}\left(U - \frac{1}{2}\right)^2 - \frac{1}{4s} \tag{4.12}$$

whose vertex is at the point $(1/2, -1/4s)$ and which passes through the points $(0,0)$ and

$(1, 0)$. On this nullcline, we have two scenarios

$$U' = V \begin{cases} < 0, & \text{if} \quad V < 0 \\ > 0, & \text{if} \quad V > 0 \end{cases} \tag{4.13}$$

and therefore arrows along parabola point horizontally left in the region $V < 0$ and horizontally right in the region $V > 0$. We can combine these results with the known stability of the point $(0, 0)$ in the case $s \geq 2$ to obtain a phase-plane portrait that illustrates the existence of a unique solution that joins the two critical points and satisfies

$$\lim_{z\to\infty} U(z) = 0, \quad \lim_{z\to-\infty} U(z) = 1, \quad 0 < U(z) < 1 \quad \text{for} \quad -\infty < z < \infty. \tag{4.14}$$

Recalling once more that $U(z) = u(x-st)$, we can identify the nature of this unique traveling wave for each $s \geq 2$.

4.1.3 Initial conditions and minimum wave speed at the front

By studying the eigenvalues of the linearised system obtained after assuming a traveling wave solution to the FKPP equation 4.3, we used a physical argument to justify that we must have a minimum wave speed, $s \geq 2$. Fisher and Kolmogrov actually argued something slightly stronger, proving that, for the initial conditions presented in the first subsection, $u(x, t)$ tends to a travelling wave solution with wave speed $s = 2$. Recall these initial conditions are such that at time $t = 0$ the solution satisfies $u(x, 0) = 0$ for all $x > x_0$ for some x_0, and $u(x, 0) = 0$ for all $x > x_0$. We will not be able to go through the entire proof here, but use some intuition to illustrate.

At the leading front of the wave we have that u is very small, meaning that the linear equation

$$\frac{\partial \hat{u}}{\partial t} = \frac{\partial^2 \hat{u}}{\partial x^2} + \hat{u} \tag{4.15}$$

is a good approximation in this region. We can also construct an initial condition for the linear solution such that $\hat{u}(x, 0) \geq u(x, 0)$ for all x by taking $\hat{u}(x, 0) = Ae^{-ax}$ with $a > 0$ and A sufficiently large enough (e.g. take $A = e^{ax_0}$ since then $\hat{u}(x, 0) = e^{a(x_0 - x)} \geq e^0 = 1 \geq u(x, 0)$ for all $x < x_0$). We define $\delta u = \hat{u} - u$ as the difference between the linear and nonlinear solutions, and find that is must satisfy $\delta u \geq 0$ for all $t > 0$ since

$$\frac{\partial}{\partial t}\delta u = \left(\frac{\partial^2 \hat{u}}{\partial x^2} + \hat{u}\right) - \left(\frac{\partial^2 u}{\partial x^2} + u - u^2\right) = \frac{\partial^2}{\partial x^2}\delta u + \delta u + u^2 > \frac{\partial^2}{\partial x^2}\delta u + \delta u \tag{4.16}$$

and by construction we have $\delta u \geq 0$ at $t = 0$. Thus, u is bounded by $\hat{u}$ for all time.

We next look for a traveling wave solution to the linear equation and substitute $\hat{u}(x, t) = Ae^{-a(x - \hat{s}t)}$ into 4.15 to obtain the condition

$$a\hat{s} = a^2 + 1 \Rightarrow \hat{s} = a + \frac{1}{a} \geq 2 \tag{4.17}$$

where the lower bound is met when $a = 1$. Thus, because u is bounded by $\hat{u}$ its wave speed can not be greater than $\hat{s}$ and, since this must hold for all $\hat{s}$ including $\hat{s} = 2$, the nonlinear wave speed must be 2.

4.2 Geographic spread of epidemics

Traveling waves can also be used to model the spread of an infectious disease through a population, i.e. an epidemic. In this section, we shall first introduce the Kermack-McKendrick model for spread of an infectious disease in a well-mixed population. This will enable us to consider the basic aspects of epidemiological modelling of disease transmission and the time development of epidemics. The model will then be extended to a population distributed in a spatial domain, where we will study spread of the disease in space via traveling waves.

4.2.1 Kermack-McKendrick epidemic model

Consider an infectious disease that, after recovery, confers immunity (we only model complete immunity, not immunity that is slowly lost over time). The total population, P_T, can be divided into three sub-populations whose compositions vary in time: 1) the susceptible sub-population, P_S, who can catch the disease; 2) the infectious sub-population, P_I, who have the disease and can transmit it; and 3) the removed sub-population, P_R, who have had the disease and either recovered or died. The progress of disease is schematically described by $P_S \to P_I \to P_R$ and these models are often also called SIR models.

To derive the Kermack-McKendrick model we make a number of additional simplifying assumptions:

(a) The total population remains at constant size and is "well-mixed" such that the spatial distributions of sub-populations are not considered

(b) The rate of increase in the infectious sub-population is proportional to the number of infectious and susceptible members of the population at any given time

(c) The rate of removal (via death or recovery) of the infectious sub-population is proportional to the number of infectious members of the population at any given time

(d) The incubation period of the disease is short enough to be considered negligible (any member who contracts the disease is infectious right away).

With these assumptions we arrive at the ODE system

$$\frac{dP_S}{dt} = -k_I P_S P_I \tag{4.18}$$

$$\frac{dP_I}{dt} = k_I P_S P_I - k_R P_I \tag{4.19}$$

$$\frac{dP_R}{dt} = -k_R P_I \tag{4.20}$$

where $k_I > 0$ and $k_R > 0$ are the rate constants of infection and removal, respectively, and the total population size is conserved for all time, i.e. $P_T(t) = P_S(t) + P_I(t) + P_R(t) \Rightarrow dP_T/dt = 0$. As initial conditions we take

$$P_S(0) = S_0 > 0, \quad P_I(0) = I_0 > 0, \quad P_R(0) = 0. \tag{4.21}$$

Given the above model, a central question is whether or not the infection will spread or, in other words, whether or not there will be an epidemic. Since

$$\frac{dP_I}{dt}(0) = k_I P_S(0) P_I(0) - k_R P_I(0) = k_I S_0 I_0 - k_R I_0 = I_0(k_I S_0 - k_R) \tag{4.22}$$

and

$$\frac{dP_S}{dt} \leq 0, \quad \text{for all} \quad t \geq 0 \tag{4.23}$$

we find that the parameter

$$\rho = \frac{k_I S_0}{k_R} \tag{4.24}$$

determines whether or not there will be an epidemic. Specifically, $\rho < 1$ implies $k_I S_0 > k_R$ so we have $dP_I/dt \leq 0$ for all $t \geq 0$ and therefore $P_I(t) \to 0$ as $t \to \infty$, meaning the infection dies out (i.e., no epidemic occurs). On the other hand, if $\rho > 1$, then P_I will initially increase and we will have an epidemic. The parameter ρ is often called the *reproduction rate* of the infection: it is the number of secondary infections produced by one primary infection in a wholly susceptible population. If more that one secondary infection is produced from one primary infection ($\rho > 1$), then an epidemic ensues.

4.2.2 Epidemic model with spatial spread

The first assumption (a) of the Kermack-McKendrick model is that the population is well-mixed. Recall from the introduction how this assumption enables us to model the system with a system of ODEs. Here we relax this assumption by allowing individuals within the population to travel in space, such that P_S, P_I, P_R are now functions of both space and time. For simplicity, we consider only one spatial dimension and drop our consideration of P_R, since its dynamics are entirely determined by knowledge of $P_S(x,t)$ and $P_I(x,t)$. We furthermore assume that the spatial dispersal of individuals within the population is governed by simple diffusion (both susceptible and infectious individuals have the same diffusion coefficient, D) and, at every point in space, individuals interact according to the dynamics of the Kermack-McKendrick model. The model therefore takes the form

$$\frac{\partial P_S}{\partial t} = -k_I P_S P_I + D\frac{\partial^2 P_S}{\partial x^2} \tag{4.25}$$

$$\frac{\partial P_I}{\partial t} = k_I P_S P_I - k_R P_I + D\frac{\partial^2 P_I}{\partial x^2} \tag{4.26}$$

and we impose an initial homogenous susceptible population density $P_S(x,0) = S_0$. The problem is then to characterise the conditions for spatial spread of the disease.

To simplify notation, we first perform non-dimensionalisation using the scalings

$$P_S = S_0 P_S^*, \quad P_I = S_0 P_I^*, \quad x = \sqrt{\frac{D}{k_I S_0}} x^*, \quad t = \frac{1}{k_I S_0} t^*$$

to obtain

$$\frac{\partial P_S^*}{\partial t^*} = -P_S^* P_I^* + \frac{\partial^2 P_S^*}{\partial (x^*)^2} \tag{4.27}$$

$$\frac{\partial P_I^*}{\partial t} = P_S^* P_I^* - \frac{k_R}{k_I S_0} P_I^* + \frac{\partial^2 P_I^*}{\partial (x^*)^2} \tag{4.28}$$

which, after dropping the asterisks and identifying $k_R/k_I S_0 = 1/\rho$ with the inverse of the reproduction rate, becomes

$$\frac{\partial P_S}{\partial t} = -P_S P_I + \frac{\partial^2 P_S}{\partial x^2} \tag{4.29}$$

$$\frac{\partial P_I}{\partial t} = P_S P_I - \frac{1}{\rho} P_I + \frac{\partial^2 P_I}{\partial x^2}. \tag{4.30}$$

We want to characterise traveling wave solutions to these equations, and so make the ansatz $P_S(x,t) = P_S(z)$ and $P_I(x,t) = P_I(z)$ where $z = x - st$. This reduces the system to two, coupled second-order ODEs of the form

$$P_S'' + sP_S' - P_S P_I = 0, \quad P_I'' + sP_I' + P_I\left(P_S - \frac{1}{\rho}\right) = 0 \tag{4.31}$$

for some wave speed s, where the primes denote differentiation with respect to z. The existence problem for a traveling wave solution with wave speed $s > 0$ is then translated to finding a range of values for ρ such that

$$P_I(-\infty) = P_I(\infty) = 0, \quad 0 \leq P_S(-\infty) < P_S(\infty) = 1.$$

In other words, there will be a traveling wave that propagates in time t along the spatial x dimension in an initially fully-susceptible population.

While the fourth-order system is difficult to study in phase-space as we did previously for the FKPP equation, we can make use of similar arguments used at the end of the previous section to say that P_I will be very small and P_S close to one near the leading front, to justify the linear approximation

$$P_I'' + sP_I' + P_I\left(1 - \frac{1}{\rho}\right) \approx 0. \tag{4.32}$$

In this regime, we have a solution of the form $P_I(z) \propto \exp(\lambda z)$, where λ satisfies

$$\lambda^2 + s\lambda + \left(1 - \frac{1}{\rho}\right) = 0, \tag{4.33}$$

which we solve to obtain

$$\lambda_\pm = \frac{-s \pm \sqrt{s^2 - 4(1 - 1/\rho)}}{2}. \tag{4.34}$$

As for the FKPP equation, we must exclude complex conjugates that correspond to non-physical solutions that oscillate about $P_I = 0$ since that would imply $P_I(z) < 0$ for some values of z. Therefore, if a traveling wave solution is to exist, the wave speed s and reproduction rate ρ must together satisfy

$$s \geq 2\sqrt{\left(1 - \frac{1}{\rho}\right)}, \quad \rho > 1. \tag{4.35}$$

We see that the $\rho > 1$ condition is exactly the same as the condition for an infection to generate an epidemic in a well-mixed population and, assuming this to be the case, the condition on s sets the minimum wave speed at which the epidemic will travel through the population. As ρ is increased, this minimum wave speed becomes larger.

Exercise 4.1 Find a change of coordinates such that the FKPP-equation 4.2 reduces to its dimensionless form 4.3.

Exercise 4.2 Show that in the special case $s = 5/\sqrt{6}$, a traveling wave solution to the second-order ODE 4.4 is given analytically by

$$U(z) = \frac{1}{\left(1 + C\exp(z/\sqrt{6})\right)^2}$$

where $C > 0$ is an arbitrary positive constant.

Exercise 4.3 Consider the one-dimensional spatial system

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

where $0 < R < 1$ is a constant parameter.

(a) Substitute the traveling wave ansatz $u(x, t) = U(z)$ with $z = x - st$ and $s \geq 0$ to reduce this equation to a system of coupled first-order ODEs.

(b) Find the steady states of the ODE system obtained in part (a) and evaluate their stability.

(c) Determine a lower bound on s that means none of the steady states represent a spiral solution.