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Gene–culture shock waves

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ABSTRACT

A hyperbolic model is presented which generalises Aoki's parabolic system for the combined propagation of a mutant gene together with a cultural innovation. It is shown that this model allows for the propagation of a shock wave and the shock amplitude is calculated numerically. Particular attention is paid to the case where the shock moves into a region where the frequencies of the mutant gene and of the individuals adopting the innovation are zero.

1. Introduction

In an inspiring piece of work Jordan [20] developed a complete analysis for the evolutionary behaviour of a shock wave for a hyperbolic version of the Fisher equation

$$\frac{\partial \rho}{\partial t} - \nu \frac{\partial^2 \rho}{\partial x^2} = \gamma \rho \left(1 - \frac{\rho}{\rho_s}\right) \tag{1}$$

where $\rho(x,t)$ is a density with ν, γ and ρ_s positive constants. This equation was proposed by Fisher [13] as a model for the spread of an advantageous gene, and was simultaneously discovered and analysed by Kolmogoroff et al. [22]. In fact Jordan [20] and Jordan and Puri [21] refer to Eq. (1) as the Fisher–KPP equation. As Jordan [20] points out Eq. (1) has been studied in various contexts in the biological, physical and social sciences.

Jordan [20], in fact, uses Green and Naghdi [15] thermodynamics (cf. also Jaisaardsuetrong and Straughan [18]) to argue that in many situations Eq. (1) ought to be replaced by a pair of equations which convert it to a hyperbolic system, namely

$$\begin{aligned} \frac{\partial \rho}{\partial t} &= -\frac{\partial q}{\partial x} + \gamma \rho \left(1 - \frac{\rho}{\rho_s}\right), \\ \frac{\partial q}{\partial t} &= -V^2 \frac{\partial \rho}{\partial x}, \end{aligned} \tag{2}$$

where V is a constant which turns out to be the shock speed and q is a flux. It has been noted recently that many diffusion problems ought really to be represented by hyperbolic systems, in the spirit of (2). For example, Herrera and Falcón [16] argue this for a type of thermosolutal convection in a stellar zone, Jordan [19] eloquently argues for this in traffic flow, Mendez and Camacho [23] show that it is useful in population dynamics, and several other applications are described in detail in Christov and Jordan [9], Christov and Jordan [10–12], and in chapter 9 of the monograph by Straughan [29], including nanoscale heat transport, fish migration, propagation of the hantavirus, chemotaxis, skin burns, and radio frequency heating in a medical context. A key to this development is the realisation that in many real life processes the relaxation time involved is not necessarily small and disturbances propagate with a finite speed. Relatively large relaxation times have been observed in biological tissues by Mitra et al. [24], and by Saidane et al. [27]. It is worth mentioning that while Jordan [20] uses Green and Naghdi [15] thermodynamics to derive a hyperbolic version of Eq. (1) one could employ a derivation along the lines of Cattaneo [7]. The work of Cattaneo [7] is described in detail in Section 1.2 in Straughan [29], where he also notes that a Cattaneo-like derivation was developed earlier by Graffi [14], although for a dielectric rather than in the context of heat transport. The key aspect of the work of Jordan [20], is that he is able to obtain analytically a solution for the amplitude of a shock solution to (2), and, therefore, completely understand the shock behaviour. Such a solution is not possible in typical mechanics contexts such as in gas dynamics, or elasticity, cf. Whitham [30], unless one is analysing some linearised form and is investigating a weak shock.

While Eq. (1) is proposed for the evolution of an advantageous gene, the recent anthropological literature usually links the theory for the evolution of a gene to that of the evolution of a cultural trait. Riede and Bentley [26] note that, … "*the wave of advance model was originally developed by Fisher* [13] *to represent the spread of advantageous genes* … *it provides mathematically detailed predictions about demographic spread over time, with equations that unambiguously characterise the hypothesised migratory activity*". O'Brien and Bentley [25] write, … "*theoretical modelling of cultural transmission is based on the premise that genes and culture provide separate, though linked, systems of inheritance, variation, and evolutionary*

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change". The fact that genes and culture are intimately linked is further emphasised by Bentley and O'Brien [2] who write, ... "*it is becoming increasingly clear that the interactions of genes and culture – literally, their coevolution – offer a faster and stronger mode of human evolution than either does by itself*". They also write that, ... "*gene–culture theory is a branch of theoretical population genetics that incorporates cultural traits into models of differential transmission of genes from one generation to the next*", and they further write, ... "*the two inheritance systems cannot always be treated independently*". Further evidence for linking cultural and gene evolution is provided by Bentley et al. [5], Bentley and Ormerod [4], Bentley and O'Brien [3], Bentley et al. [6], and the many references therein. In fact, Aoki [1] developed a partial differential equation model for the propagation of a mutant gene and a cultural innovation. He derives what he calls a logistic attraction–repulsion model, in terms of $y(x,t)$, the frequency of the mutant gene, and $p(x,t)$, the frequency of the individuals adopting the innovation (frequency in this case refers to the number of genes or individuals, normalised in an appropriate way). Aoki's [1] system of equations is

$$\frac{\partial y}{\partial t} = \frac{\partial^2 y}{\partial x^2} + y(1-y)\big\{(\gamma+2\sigma)p+\delta\big\},$$
$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} + p(1-p)(\sigma y+\rho), \tag{3}$$

where γ, σ, δ and ρ are constants, and $x \in \mathbb{R}$. It should be noted that Eqs. (3) are non-dimensionalised so the diffusion coefficient is 1 and y and p lie in $[0,1]$.

Our goal is to propose and analyse a hyperbolic generalisation of system (3) and derive a coupled nonlinear system of ordinary differential equations for the shock amplitudes appropriate to y and p. We then solve this system numerically and are able to fully analyse the shock behaviour. We believe this is the first time a complete analysis has been performed for such a system.

2. The model and shock waves

In this work we adopt a hyperbolic form of the Aoki model (3) by using a Cattaneo [7] type of argument to replace Eqs. (3) by

$$\frac{\partial y}{\partial t} = -\frac{\partial J}{\partial x} + y(1-y)\big\{(\gamma+2\sigma)p+\delta\big\},$$
$$\tau\frac{\partial J}{\partial t} + J = -\frac{\partial y}{\partial x},$$
$$\frac{\partial p}{\partial t} = -\frac{\partial K}{\partial x} + p(1-p)(\sigma y+\rho),$$
$$\tau\frac{\partial K}{\partial t} + K = -\frac{\partial p}{\partial x}, \tag{4}$$

where $\tau > 0$ is a relaxation time, and J and K are fluxes for y and p, respectively. Let us observe that Eqs. (4) reduce to the standard problem of Aoki [1] when $\tau = 0$. We restrict attention to the situation when J and K in (4) have the same relaxation time. This gives rise to a shock where the mutant gene and the individuals may propagate simultaneously.

Let $\mathcal{S}$ be a singular surface for Eqs. (4), it is actually a singular point when x is in one dimension, or it may be thought of as a plane wave in three space dimensions, moving along the x-axis. Suppose $y(x,t)$ and $p(x,t)$ are C^2 everywhere except across $\mathcal{S}$ where they may suffer a finite discontinuity. Define $y^{+,-}$ and $p^{+,-}$, by

$$y^- = \lim_{x\to\mathcal{S}^-} y(x,t), \qquad y^+ = \lim_{x\to\mathcal{S}^+} y(x,t),$$
$$p^- = \lim_{x\to\mathcal{S}^-} p(x,t), \qquad p^+ = \lim_{x\to\mathcal{S}^+} p(x,t),$$

where the limits at $\mathcal{S}^+$ and $\mathcal{S}^-$ denote limits from the right and the left, respectively. We define the shock amplitudes Y and P by

$$Y(t) = [y] = y^+ - y^-, \qquad P(t) = [p] = p^+ - p^-, \tag{5}$$

where the notation for the jump $[\cdot]$ in a function is introduced. From Eqs. (4) one may derive the Rankine–Hugoniot equations

$$V[y] = [J], \qquad V\tau[J] = [y];$$
$$V[p] = [K], \qquad V\tau[K] = [p], \tag{6}$$

cf. Whitham [30], Iesan and Scalia [17]. Thus, from Eqs. (6) one shows that the shock speed V is constant and given by

$$V^2 = \frac{1}{\tau}. \tag{7}$$

(We stress that the diffusion coefficient is really involved in V. Eq. (7) arises because of Aoki's [1] non-dimensionalisation which transforms time and space. Aoki's [1] Eqs. (3) are derived from a discrete system. In his derivation the diffusion coefficient which arises is $k = \tilde{m}(\Delta x)^2/2\Delta t$ where $\tilde{m}/2$ is the probability of emigration to the left and to the right colony in a discrete model of the individuals where Δx is the distance between neighbouring colonies and Δt is the time taken for migration. The non-dimensionalisation used to remove k is involved and analyses three cases depending on the various parameters which arise. Due to this non-dimensionalisation we believe adopting the same value of τ in (4) is acceptable.)

Singular surface theory is covered in depth in Chen [8], and conveniently in chapter 4 of Straughan [29]. From this theory the Hadamard relation shows that

$$\frac{\delta Y}{\delta t} = [y_t] + V[y_x], \tag{8}$$

where y_t and y_x denote partial derivatives, where $\delta/\delta t$ is the derivative at the wavefront, and where V is the shock speed. We also require the relation for the jump of a product, namely,

$$[ab] = a^+[b] + b^+[a] - [a][b]. \tag{9}$$

We commence by taking the jump of Eqs. $(4)_{1,2}$ to find using (8),

$$\frac{\delta}{\delta t}[y] - V[y_x] = -[J_x] + (\gamma+2\sigma)\big[py(1-y)\big] + \delta\big[y(1-y)\big], \tag{10}$$

and

$$\tau\frac{\delta}{\delta t}[J] - \tau V[J_x] + [J] = -[y_x]. \tag{11}$$

Now form $(10) + V(11)$ and make repeated use of (9). One then repeats the same procedure for $(4)_{3,4}$. After some calculation one may arrive at the following system of equations for Y and P,

$$\frac{\delta Y}{\delta t} = Y\frac{1}{2}\left\{-\frac{1}{\tau} + (\gamma+2\sigma)p^+\left(1-2y^+\right) + \delta\left(1-2y^+\right)\right\}$$
$$+ P\frac{y^+}{2}(\gamma+2\sigma)\left(1-y^+\right) - PY(\gamma+2\sigma)\left(\frac{1-2y^+}{2}\right)$$
$$+ Y^2\left\{\frac{p^+(\gamma+2\sigma)+\delta}{2}\right\} - PY^2\left(\frac{\gamma+2\sigma}{2}\right),$$
$$\frac{\delta P}{\delta t} = P\frac{1}{2}\left\{-\frac{1}{\tau} + \sigma y^+\left(1-2p^+\right) + \rho\left(1-2p^+\right)\right\}$$
$$+ Y\frac{\sigma p^+(1-p^+)}{2} - YP\frac{\sigma}{2}\left(1-2p^+\right)$$
$$+ P^2\left(\frac{\sigma y^+ + \rho}{2}\right) - \frac{\sigma}{2}YP^2. \tag{12}$$