Speed and shape of population fronts with density-dependent diffusion

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Motivation

Understanding the movement of animals is essential to a wide range of processes of importance in ecology, evolution and conservation, such as population dispersal and species invasion.

How?

Positive

Negative

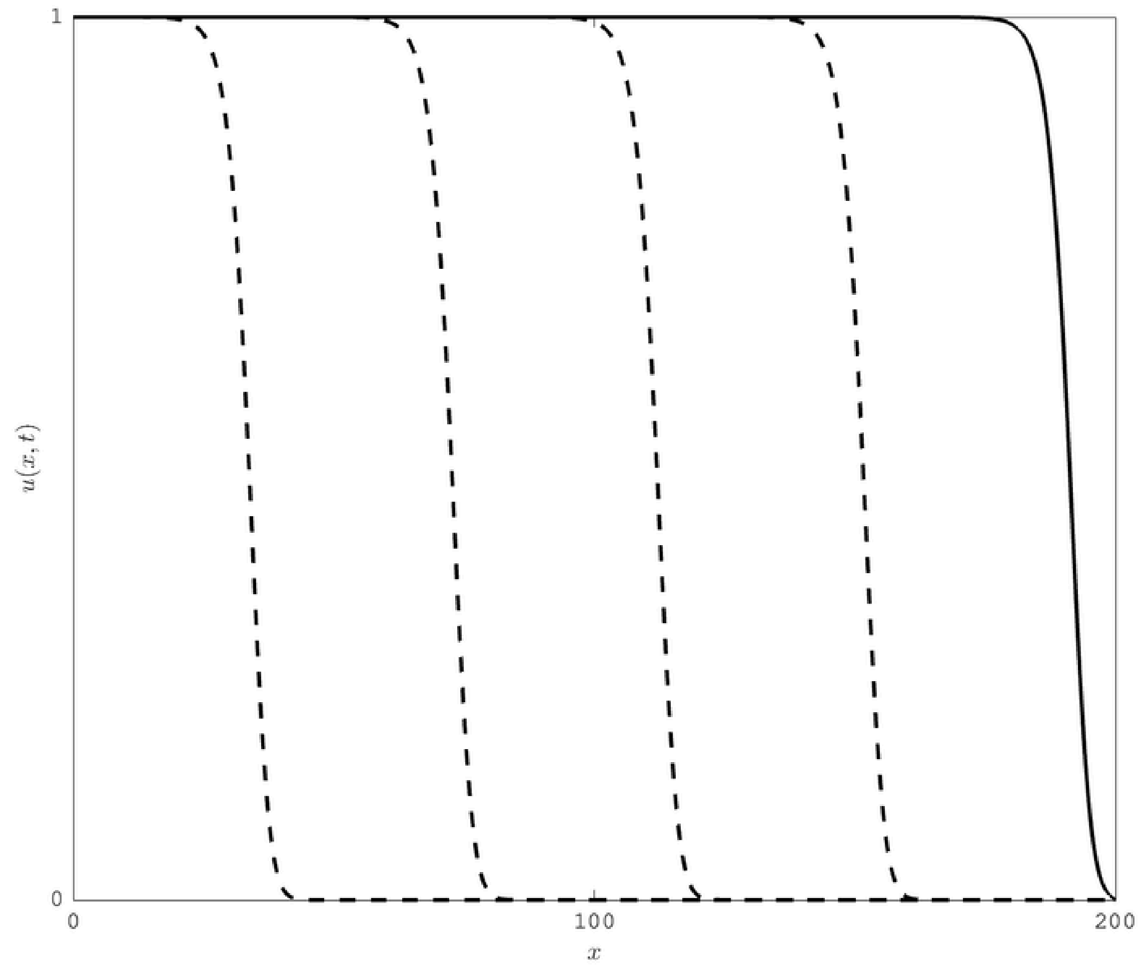
Why?

Density dependent reaction-diffusion models capture behavioural aspects of the dispersal of animal populations into new territory.

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[D(u)\frac{\partial u}{\partial x}\right] + f(u) \Rightarrow c = ?$$

Introduction

The FKPP equation admits travelling wave solutions of the pulled type, moving at constant speed and of fixed profile.



$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru(1-u) \implies c \geq 2\sqrt{rD} = 2$$

$$D(u) = u^m$$

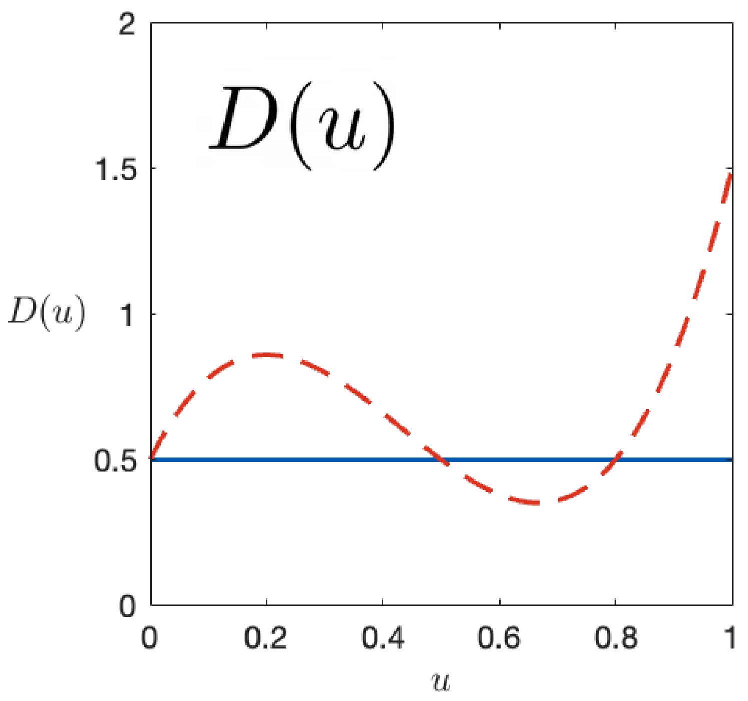
$m < 0$

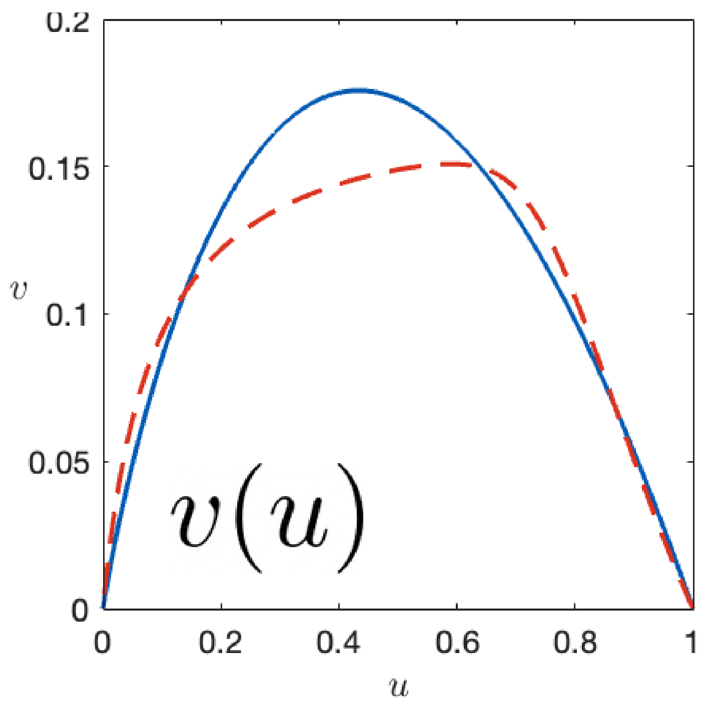
Example of negative density dependent diffusion. Leads to *accelerating* wavefronts, not permanent form solutions.

$m = 1$

Example of positive density dependent diffusion. Exactly solvable. Leads to sharp-fronted travelling wave solutions with speed $c = \frac{1}{\sqrt{2}}$.

Methods - Linear Analysis





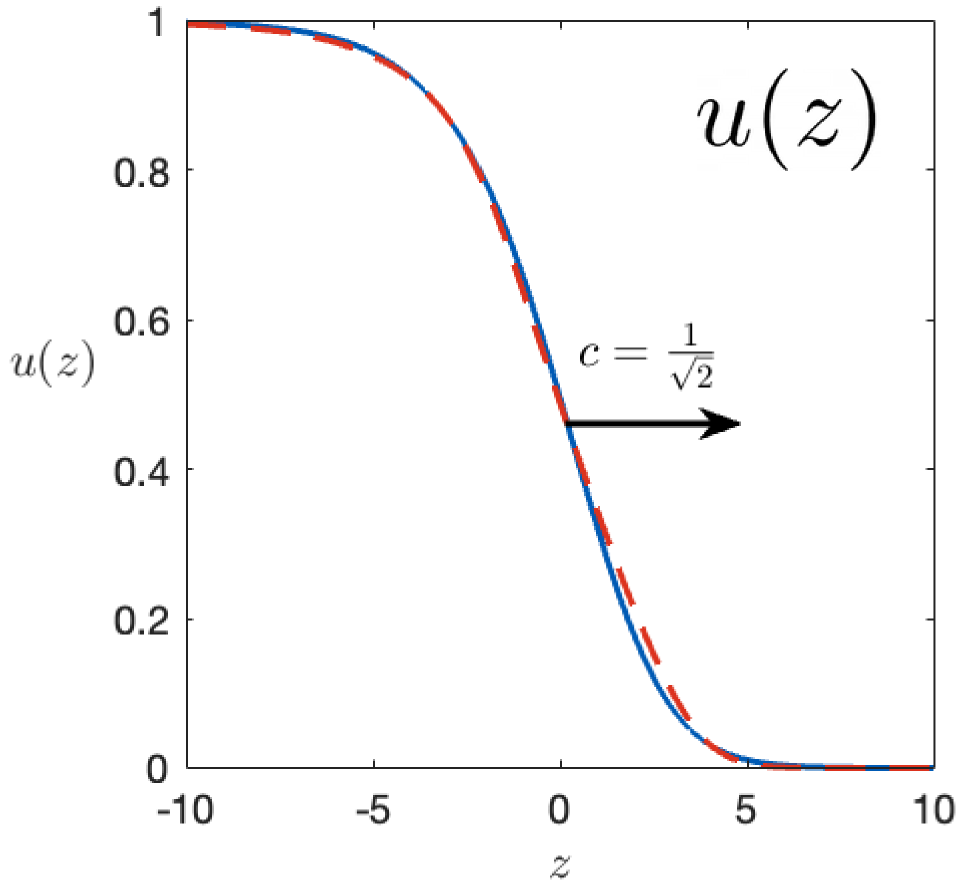
Seeking a travelling wave solution of the form $u(z) = u(x - ct)$,

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[D(u)\frac{\partial u}{\partial x}\right] + f(u) \Longrightarrow \quad \frac{\mathrm{d}u}{\mathrm{d}z} = -v, \quad \frac{\mathrm{d}v}{\mathrm{d}z} = \frac{v^2 D'(u) - cv + f(u)}{D(u)}$$

In the neighbourhood of zero, the system linearises as

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{D(0)}\begin{pmatrix} 0 & -D(0) \\ f'(0) & -c \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix}$$

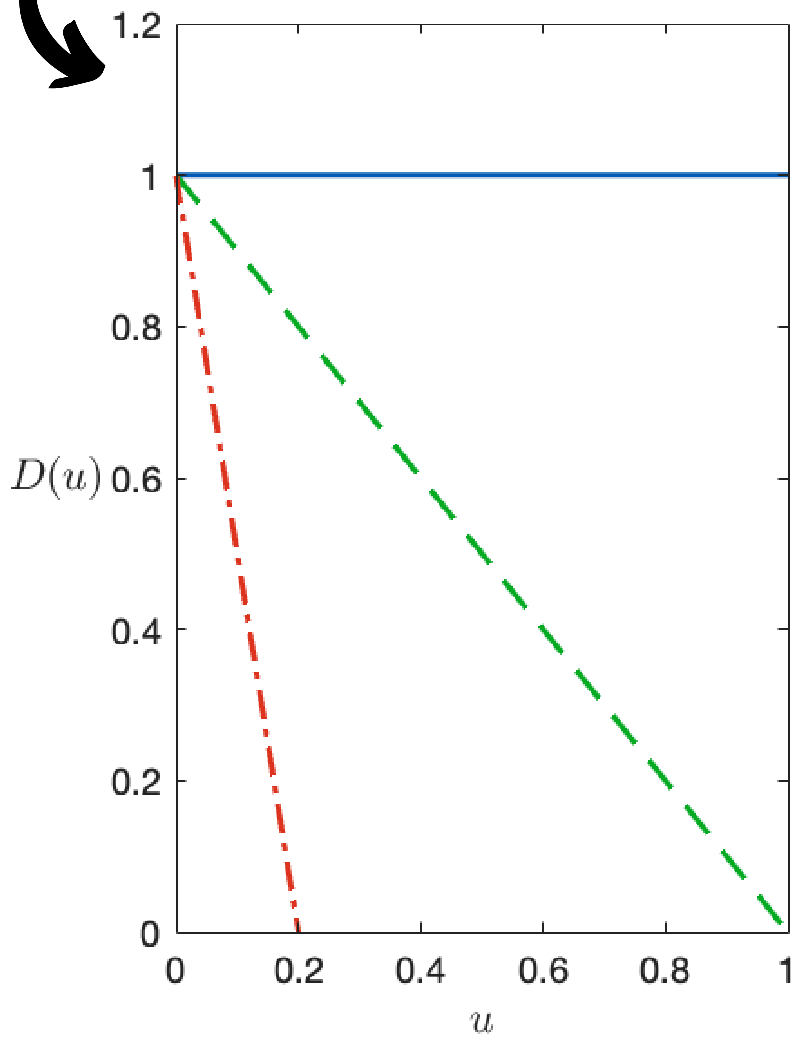
$$\Longrightarrow \boxed{c_L \geq 2\sqrt{f'(0)D(0)}}$$

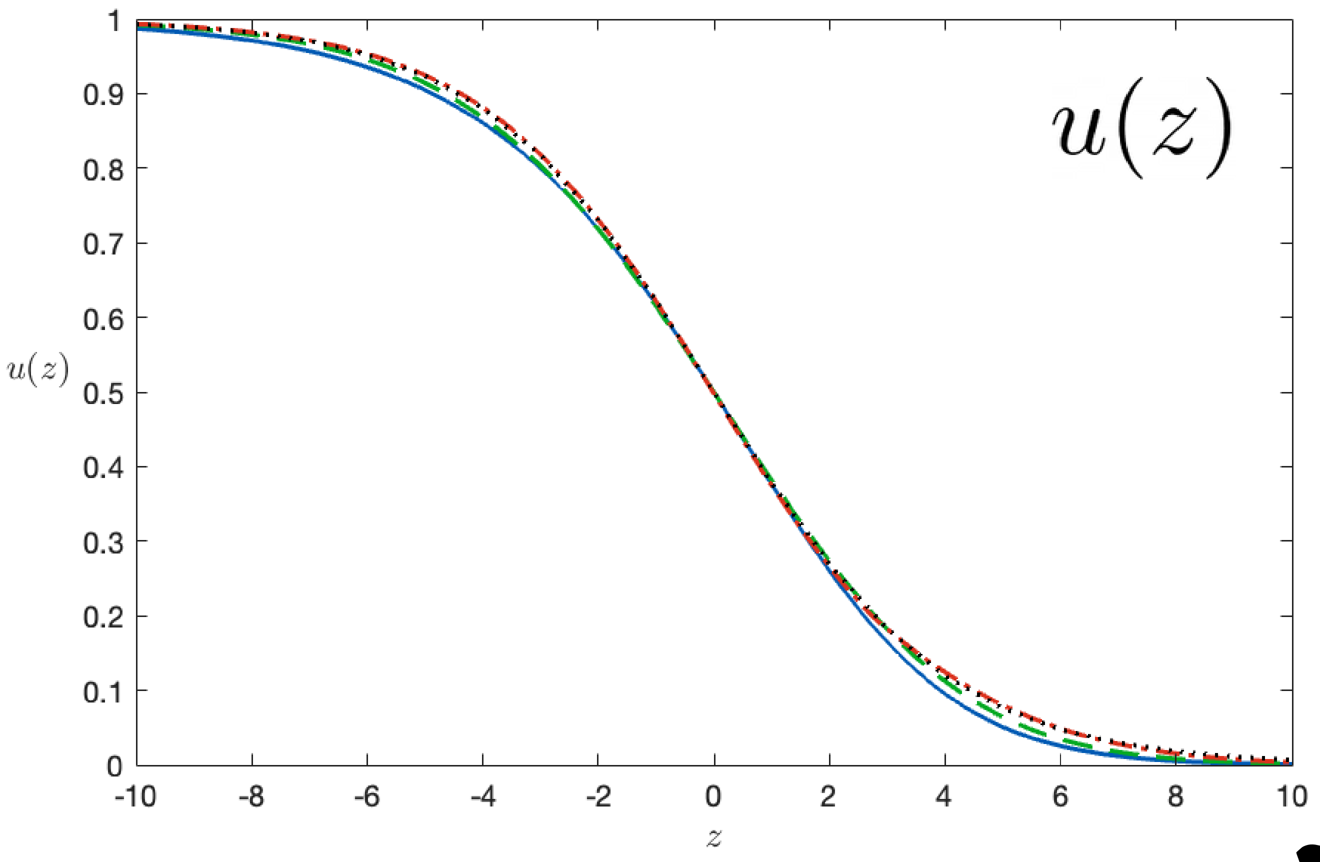


Case Study 1

eg. Crowding, Mate Searching

$$D(u) = 1 - \alpha u, \alpha > 0$$

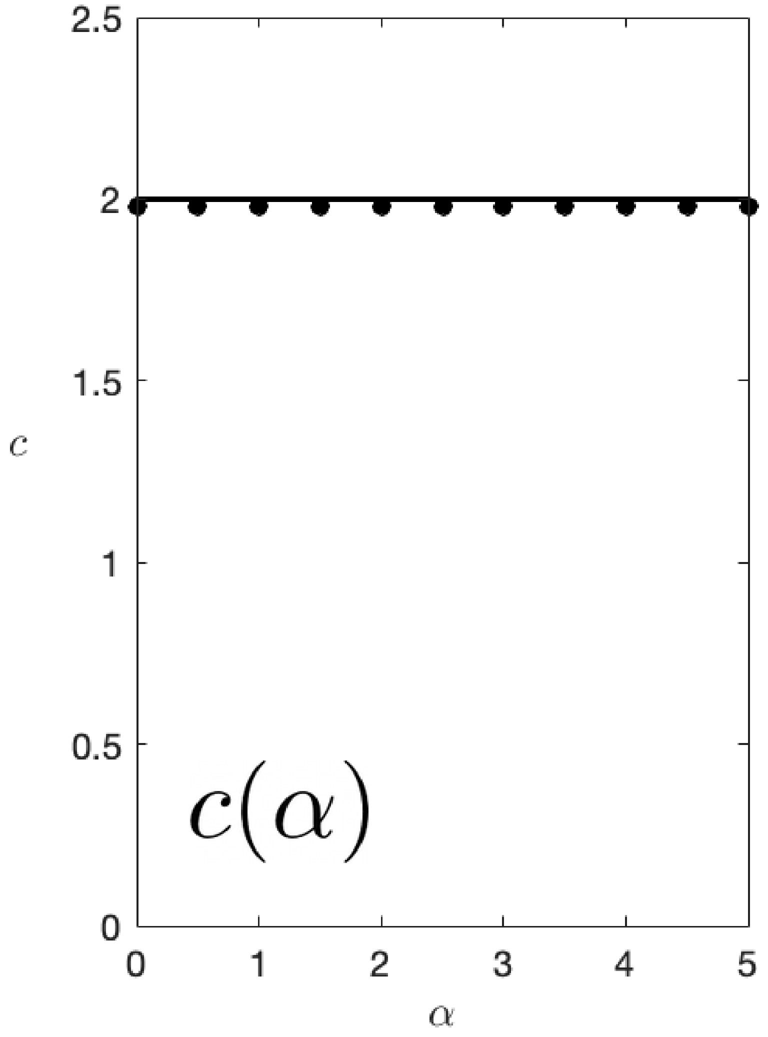




The shape of the wavefront hardly varies with α, and is always close to the analytic result for $\alpha \to \infty$:

$$u(z) = \frac{1}{2}\left(1 - \tanh\left(\frac{z}{4}\right)\right)$$

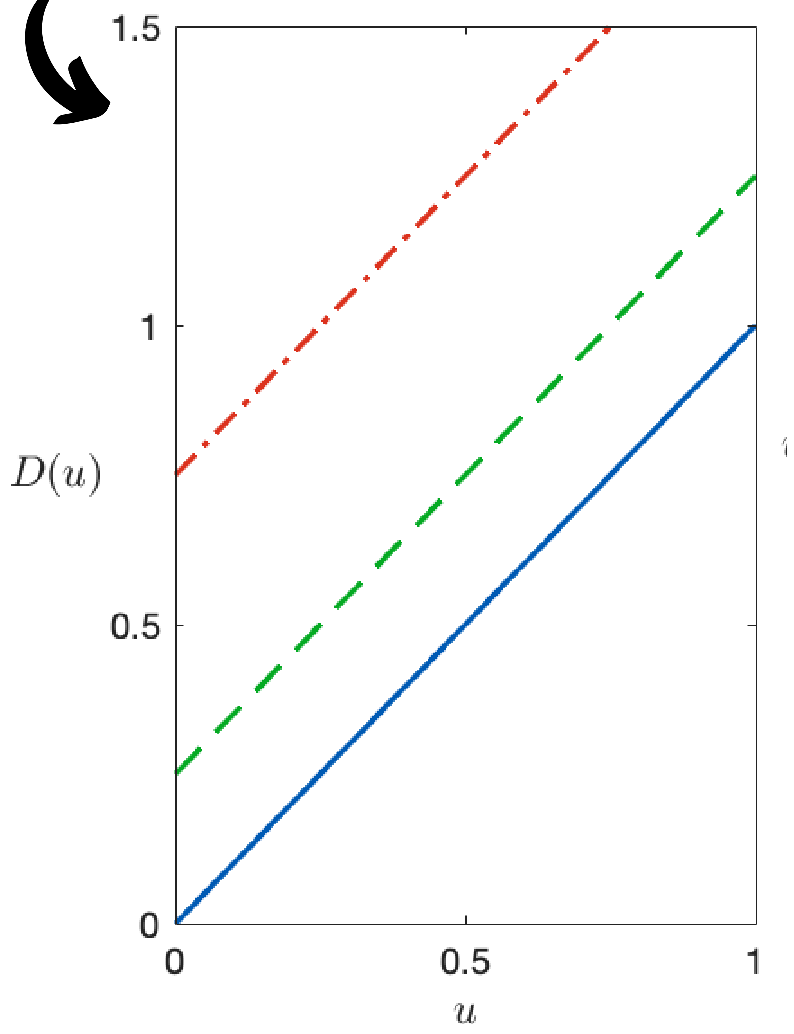
With $D(0)$ sufficiently large, waves propagate at the linear speed $c_L = 2$.

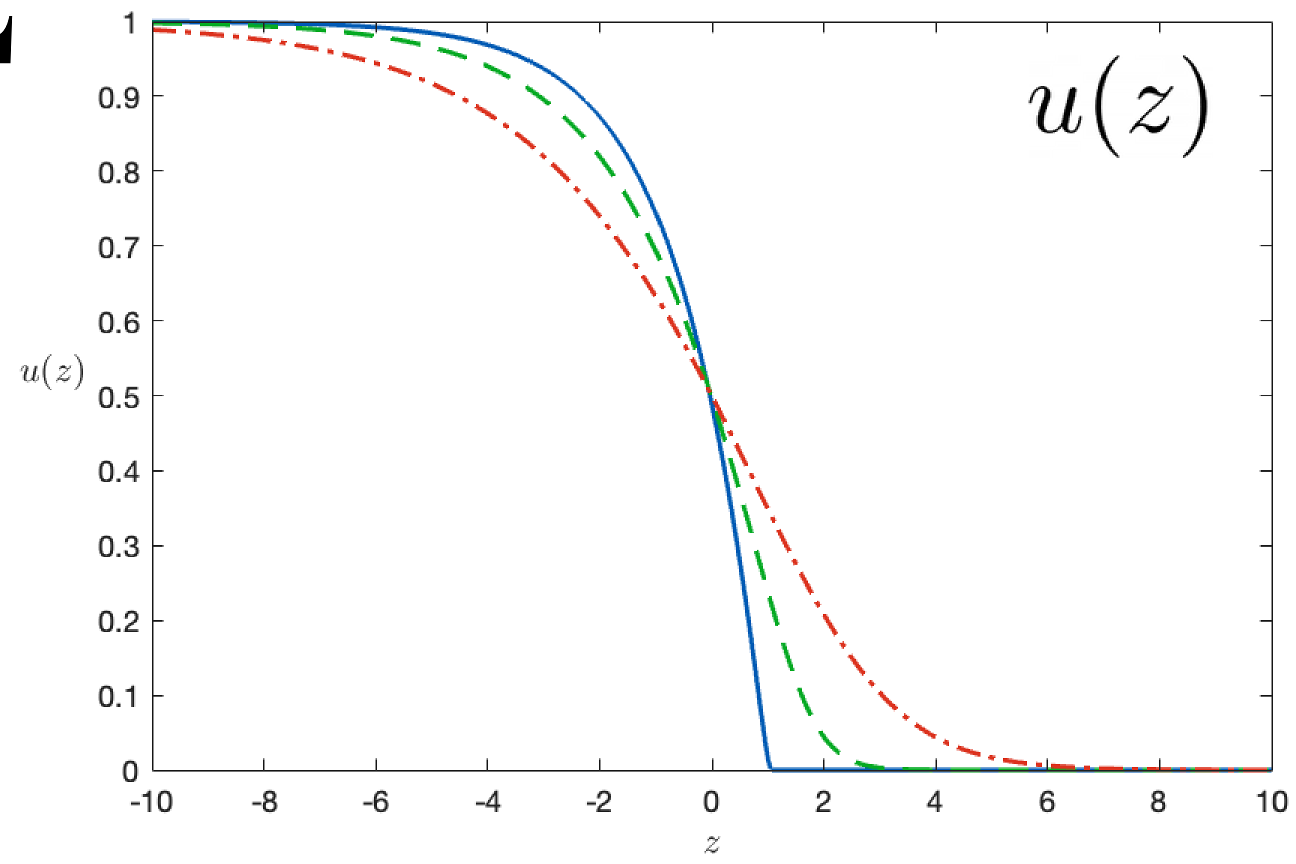


Case Study 2

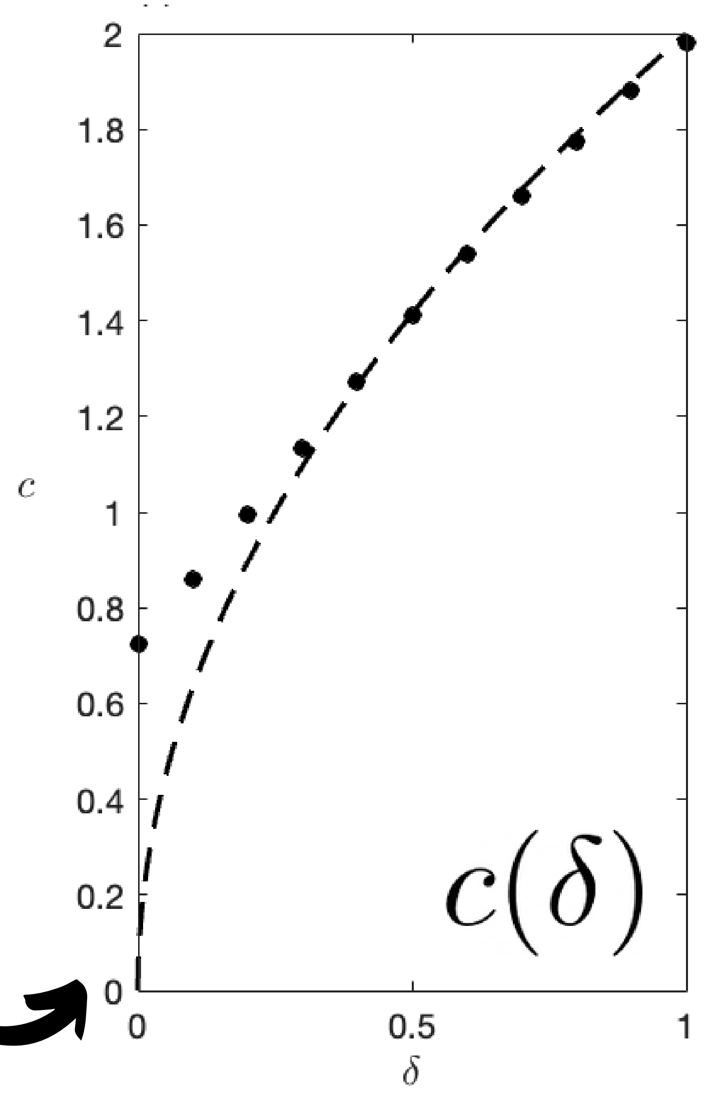
eg. Competition

$$D(u) = u + \delta, \delta \geq 0$$





Steepness of the travelling wave decreases as the value of δ increases.



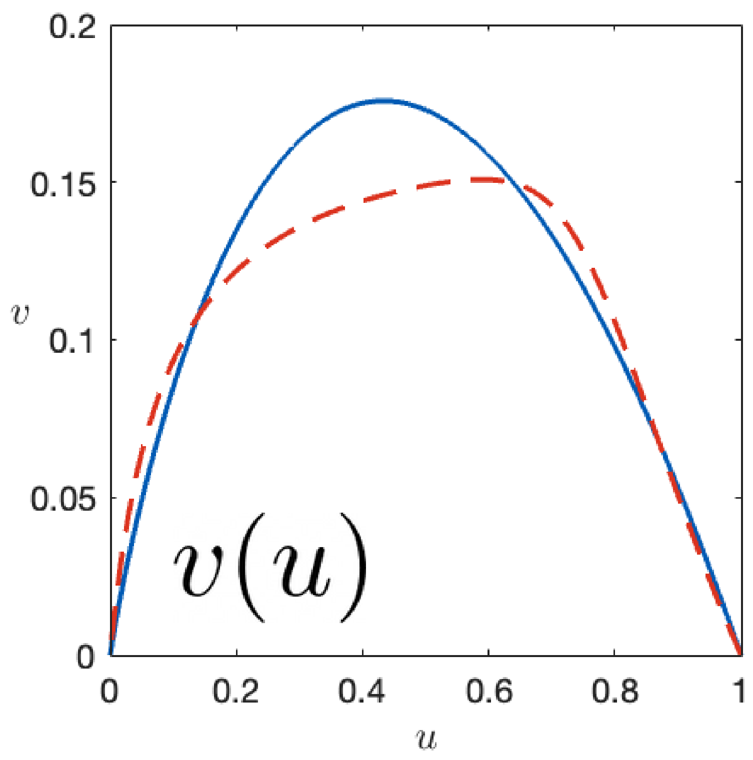
The linear analysis can be performed for $\delta > 0$ and predicts the speed of the travelling wave to be $c_L = 2\sqrt{\delta}$.

So how can we resolve the discrepancy observed in numerical solutions?

Methods - Variational Principles

To apply the method of variational principles, we first eliminate the explicit dependence on z:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[D(u)\frac{\partial u}{\partial x}\right] + f(u) \implies v\frac{\mathrm{d}}{\mathrm{d}u}\left[D(u)v\right] - cv + f(u) = 0\,.$$



Manipulation of the ODE derives a new lower bound on the wave speed:

$$c^2 \geq 2\frac{\int_0^1 (fD/s)du}{\int_0^1 (1/s')du}$$

where $s(u)$ is a trial function such that $s(0) = 0$ and $s(u) \to \infty$ as $u \to 1\,.$

Finding $s(u)$ that maximises the bound allows us to find the *exact* wavespeed. This can be done in two ways.

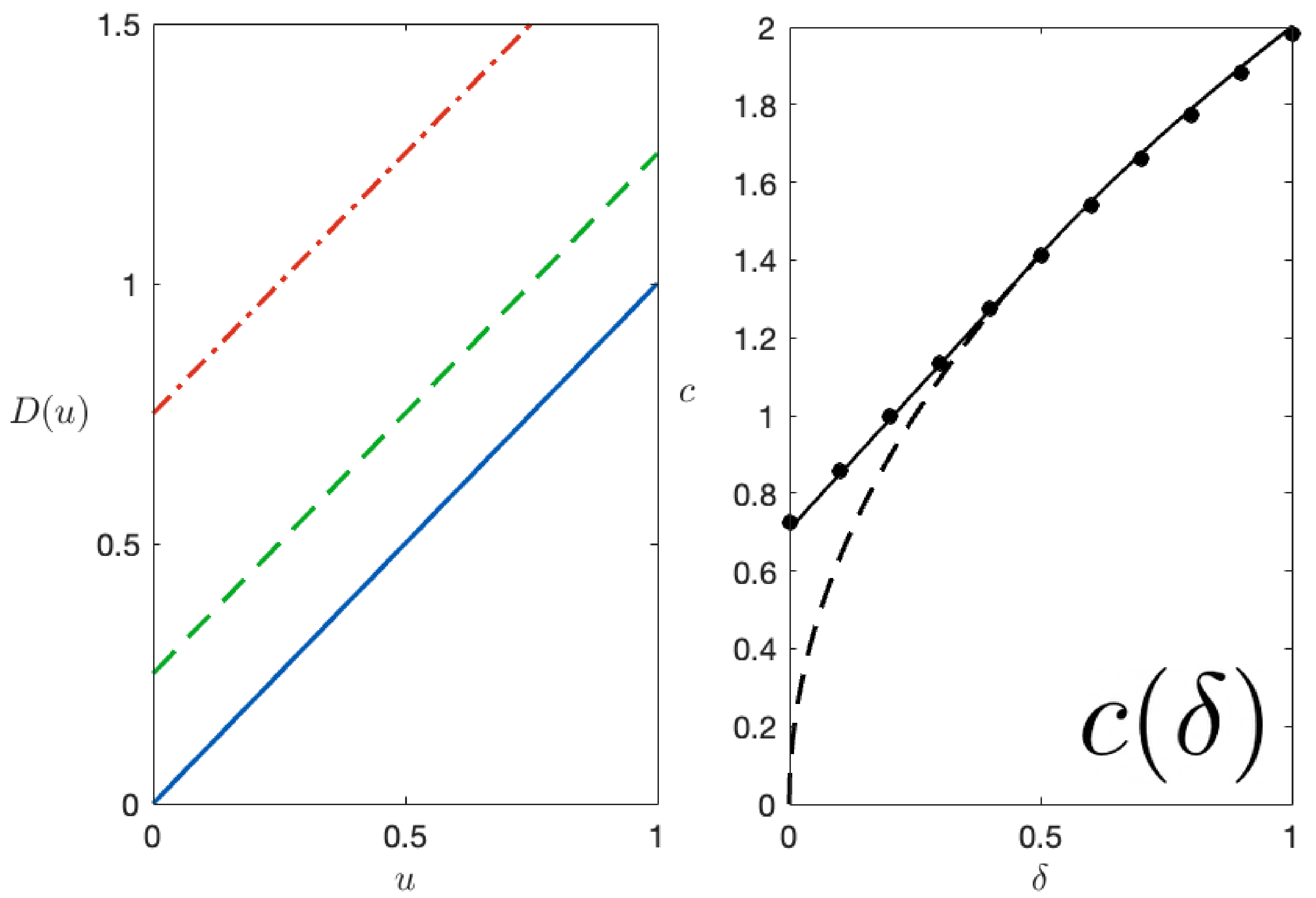
Case Study 2

Making use of the solution to the Nagumo equation, we explore the family of trial functions:

$$s(u) = \left(\frac{u}{1-u}\right)^{\beta}, \quad \beta \in [0,2).$$

Substituting this, along with the appropriate forms of $D(u)$ and $f(u)$ into the variational principle and computing the integrals, we derive the bound on wave speed to be:

$D(u) = u + \delta, \delta \geq 0$

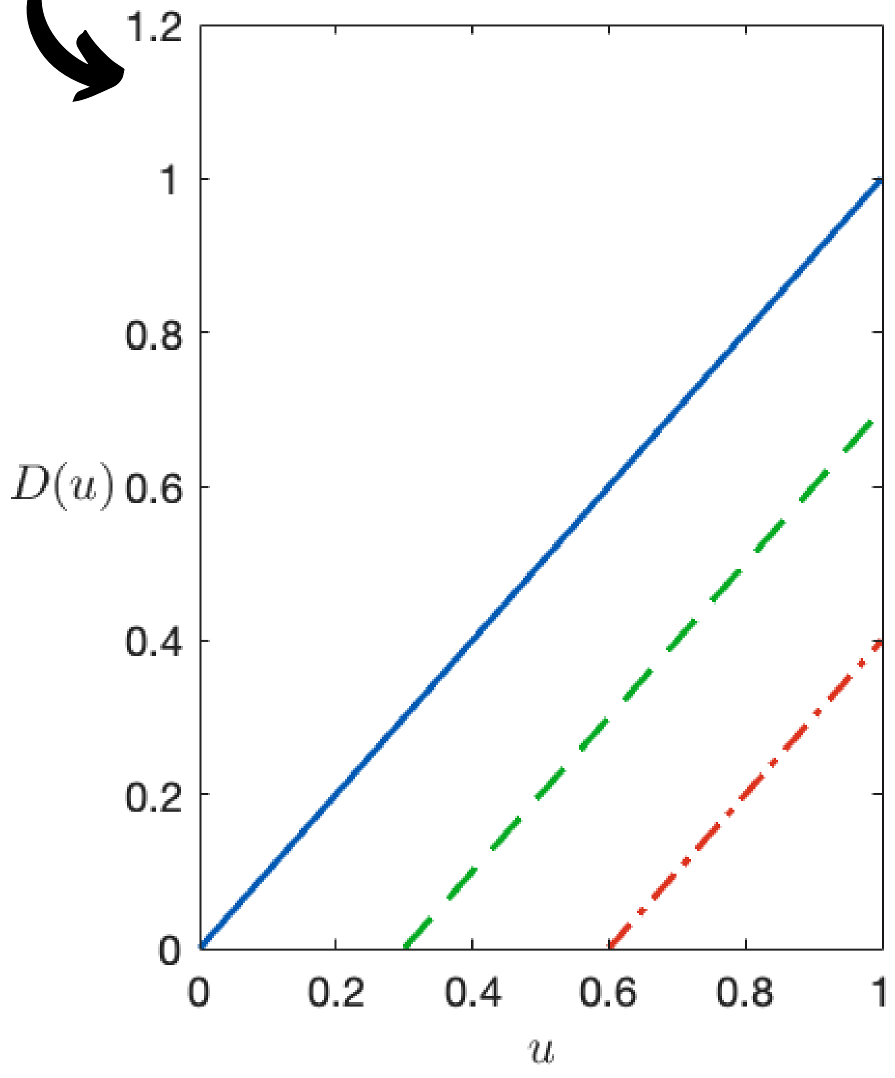


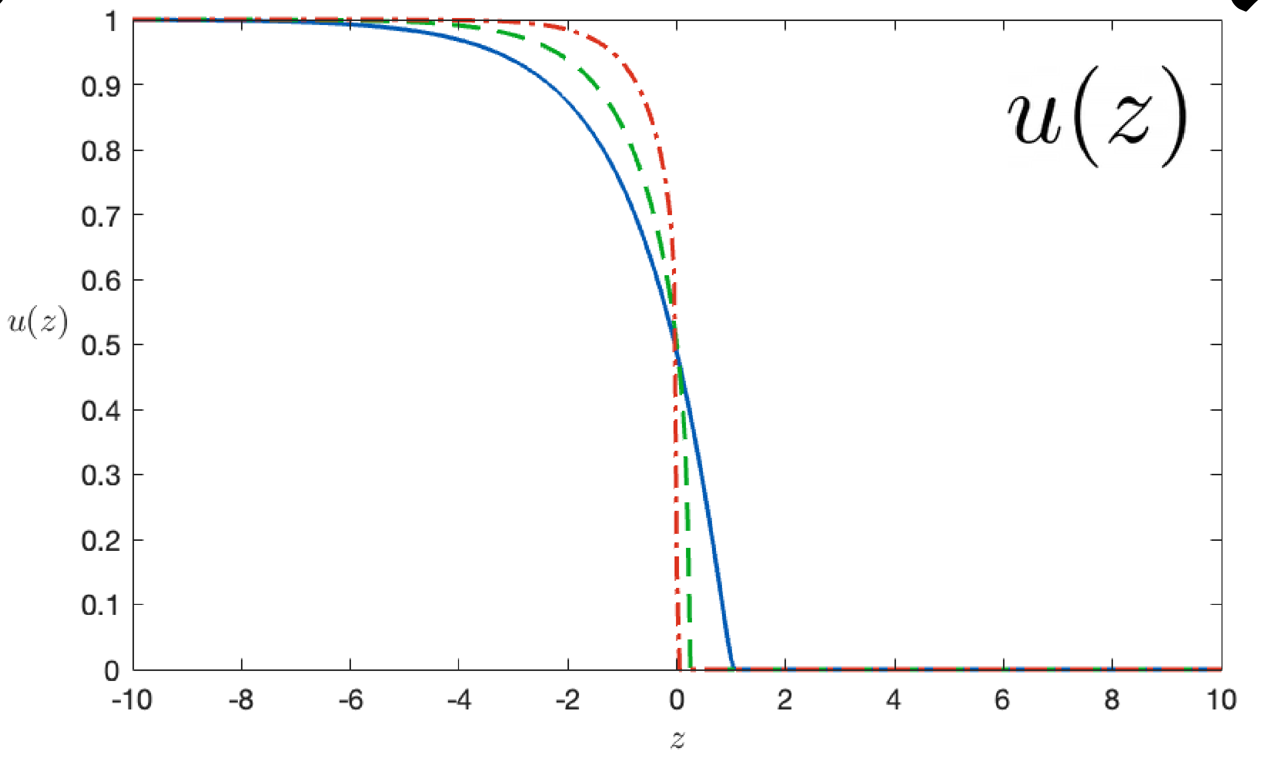
$$\frac{1}{2}c^2 \geq \sup_{\beta\in[0,2)} \frac{1}{4}\beta(2-\beta+4\delta) = \begin{cases} \frac{(1+2\delta)^2}{4} & \text{if} \quad \delta < 1/2, \\ 2\delta & \text{otherwise.} \end{cases}$$

Case Study 3

eg. Overcrowding

$$D(u) = \max\{0, u - \theta\}$$

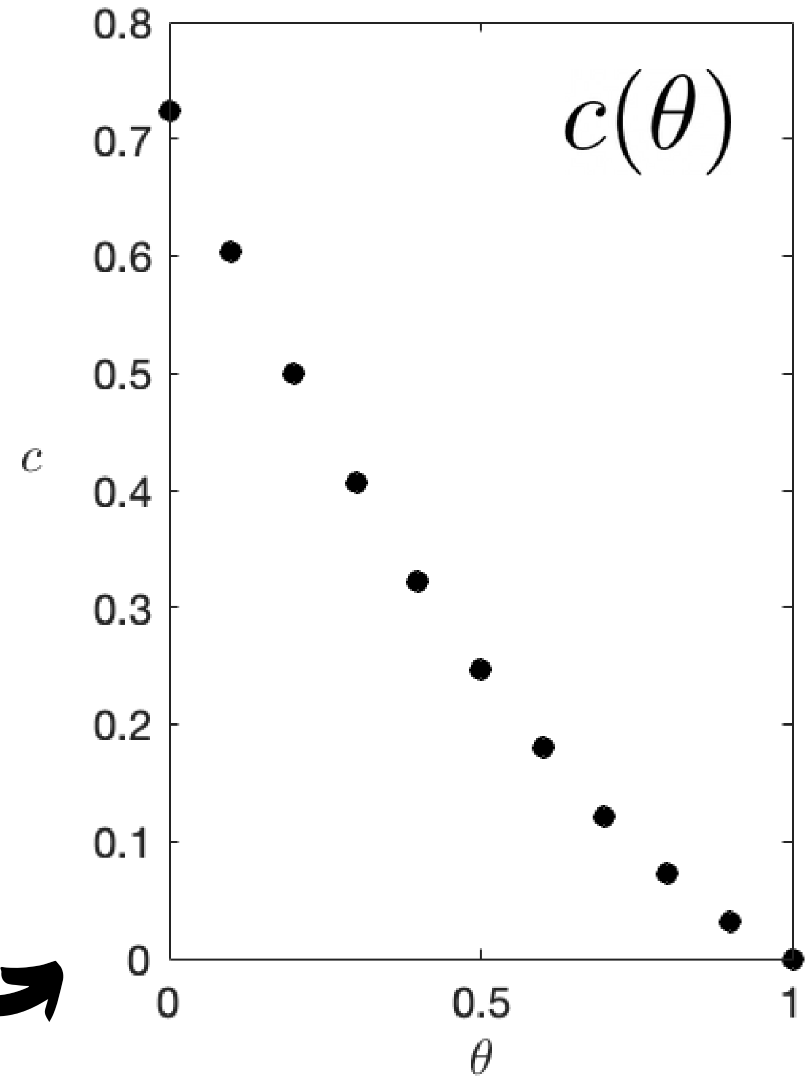




Sharp-fronted travelling wave solutions are produced when $\theta > 0$.

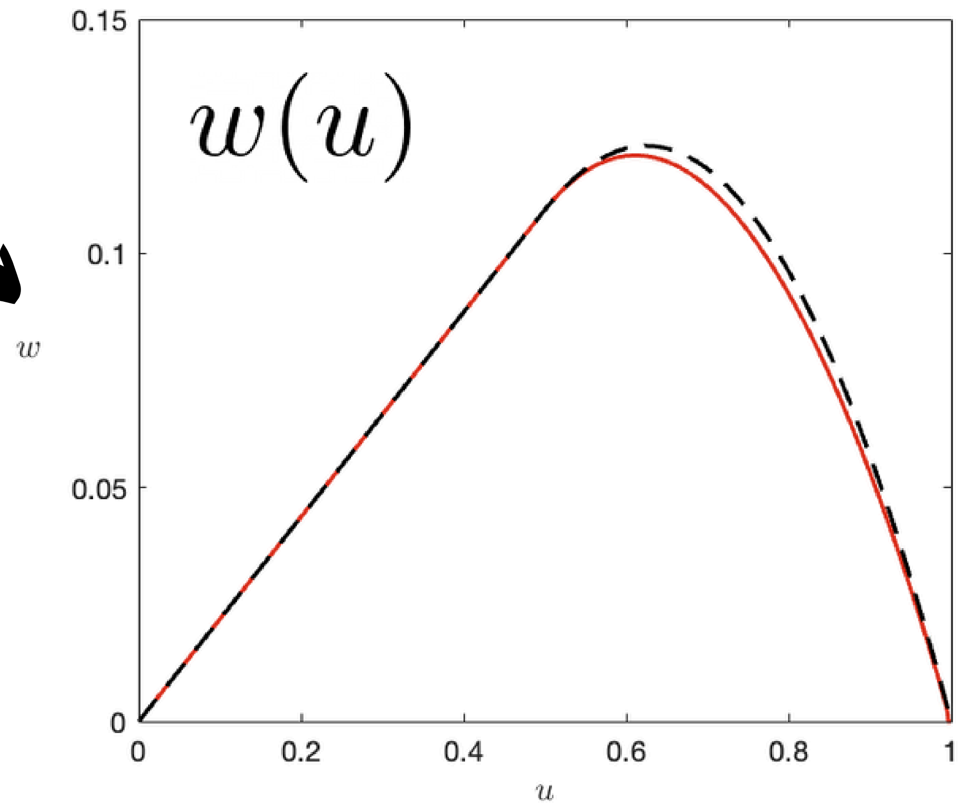
Prohibiting diffusion at small u precludes pulled wavefronts propagating at linear speed c_L.

So how do we calculate the wavespeed?

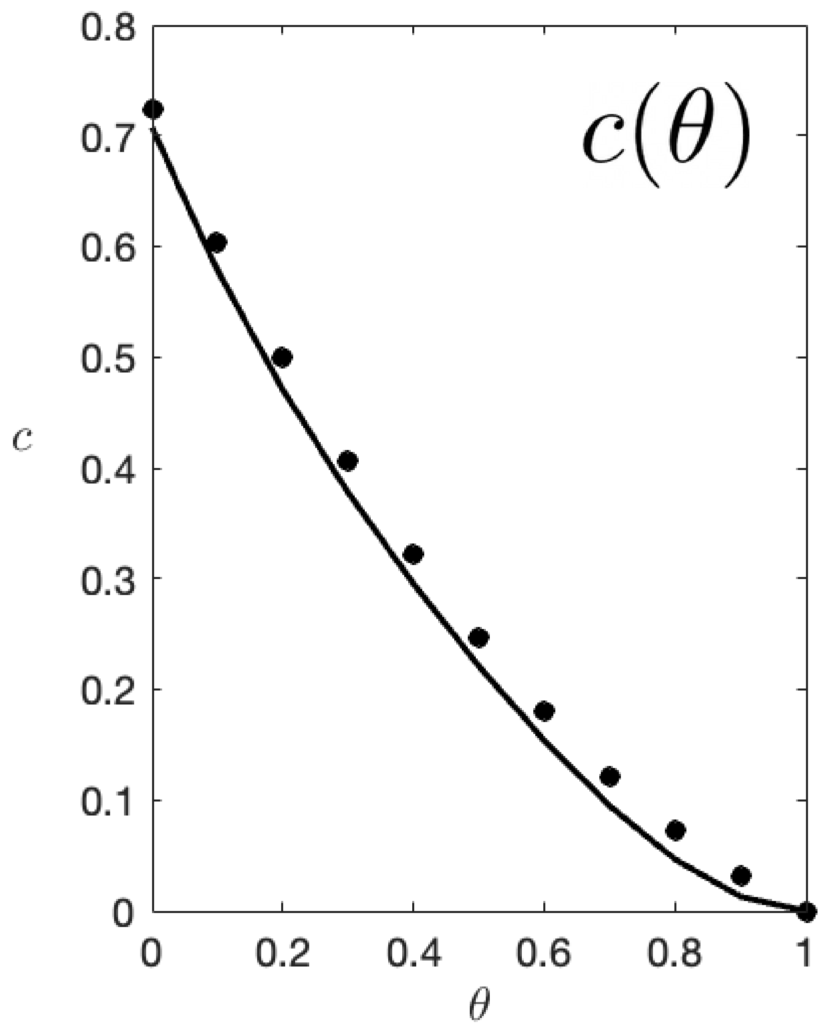


Case Study 3

Let $w = D(u)v(u)$, then we can approximate the solution trajectory w and use this to approximate the trial function by calculating:



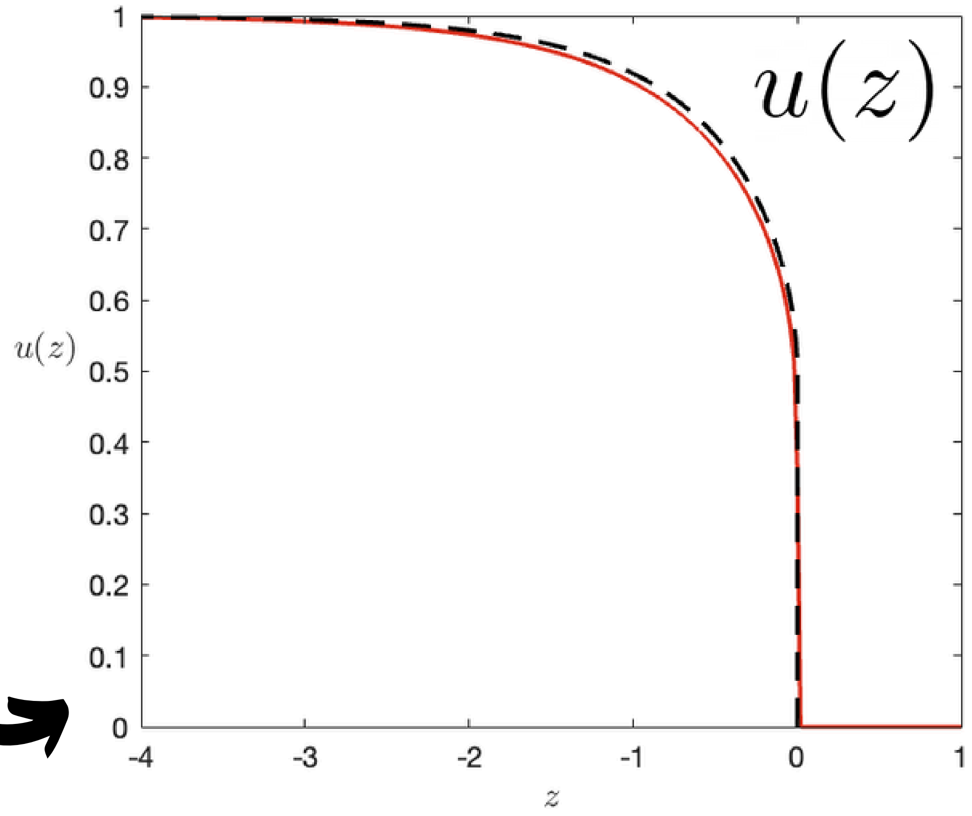
$$\tilde{s}(u) = \exp \int \frac{c}{w} du \, .$$



The bound derived from the variational principle can then be further approximated as:

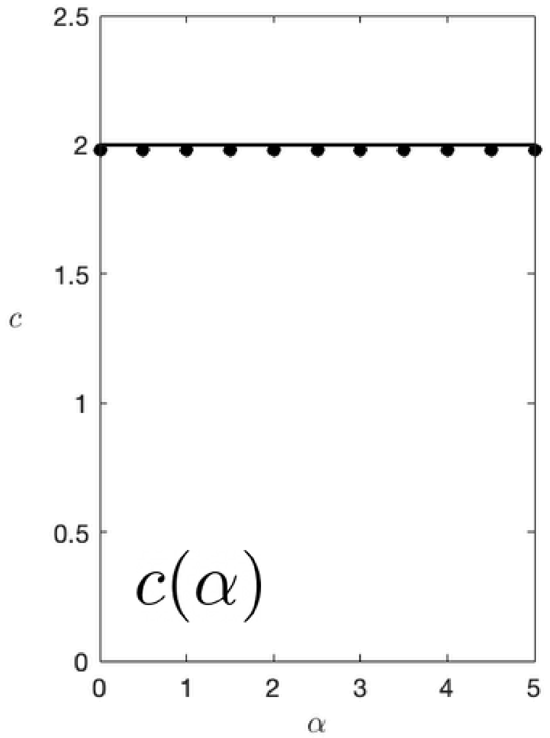
$$c \approx \frac{1}{\sqrt{2}}(1+\theta^2)(1-\theta)^2$$

The approximation also gives good agreement with the shape of the wavefront.



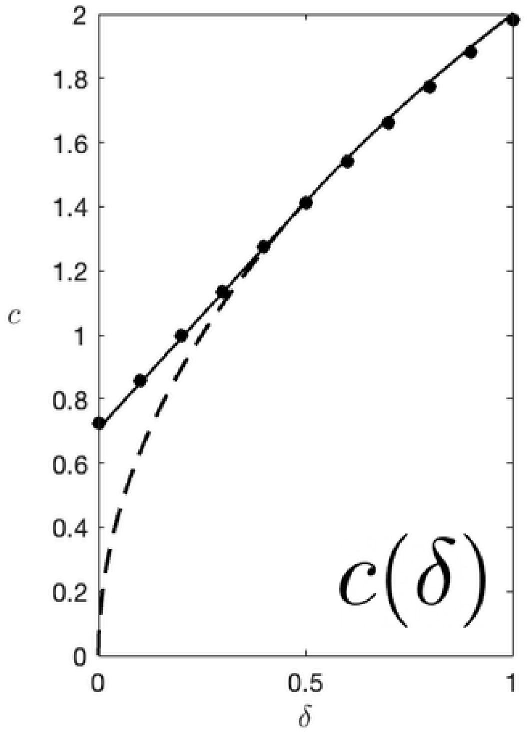
Summary

We explored the effect of different types of density dependence on travelling wave solutions, to model behavioural aspects of the dispersal of animal populations into new territory.



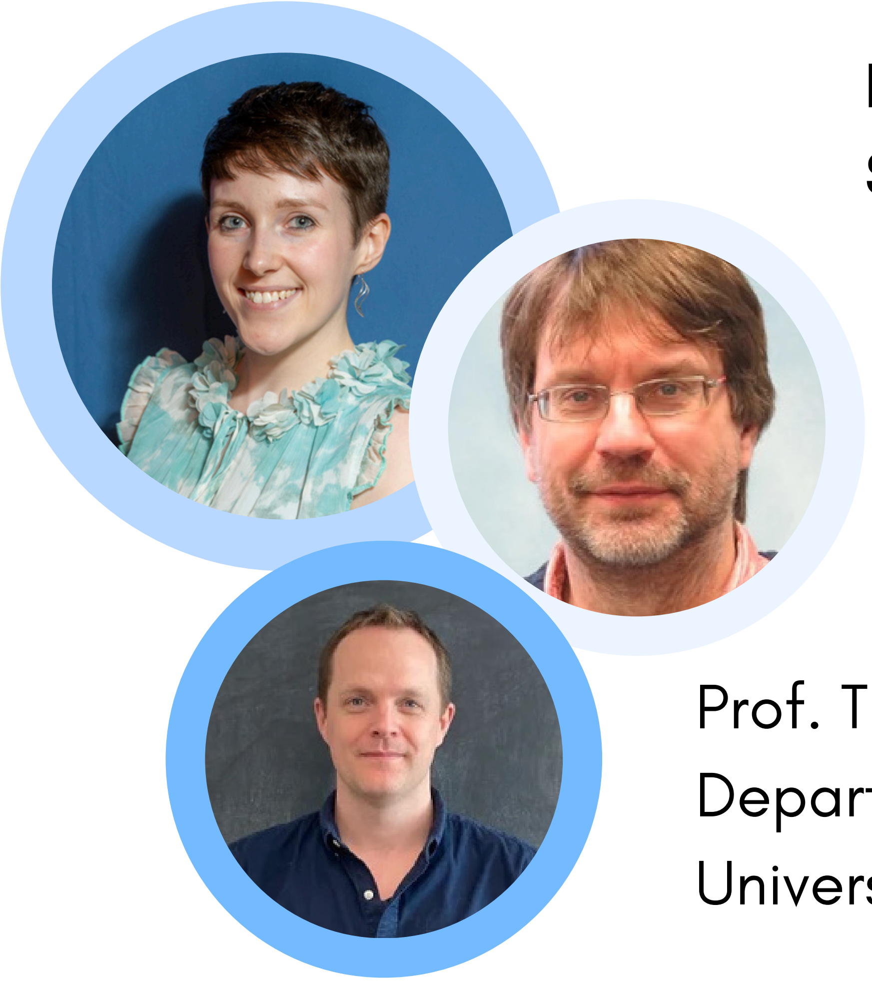
When $D(0)$ is sufficiently greater than zero, but finite, the selected speed will be the linear speed $c_L = 2\sqrt{f'(0)D(0)}$.

When $D(0)$ is small or zero, variational methods allow us to compute minimum realisable speeds for a wider range of $D(u)$, extending known results.



Findings provide greater biological insights into the dispersal of animal populations under a wider range of behaviours and in particular, the consequences of species invasions into new territory.

Thanks for listening!



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Methods - Linear Analysis

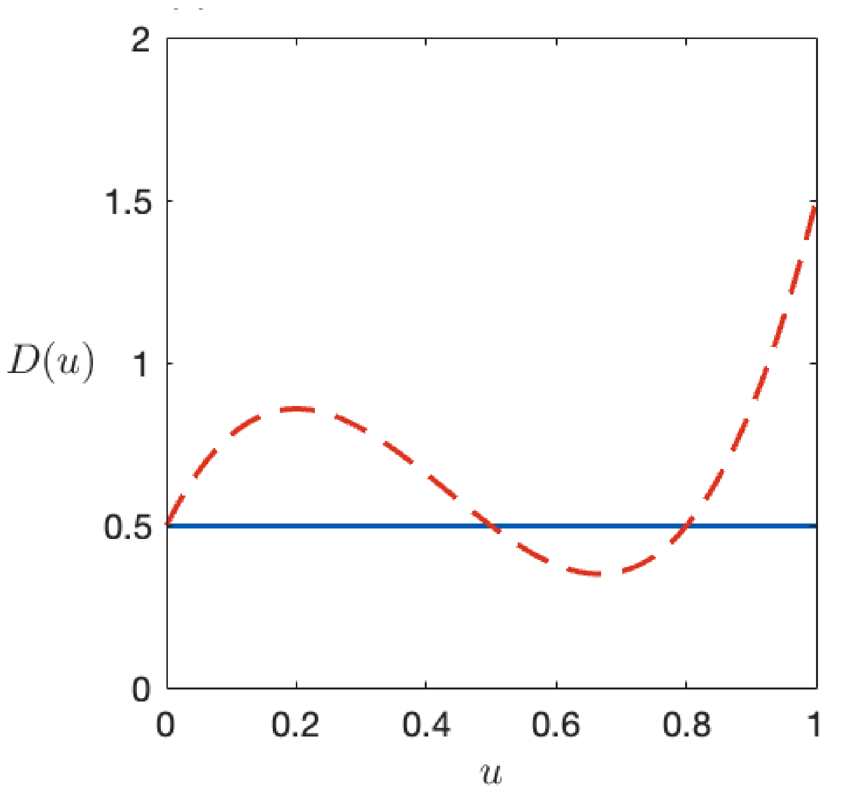
Following a standard linear stability analysis, let $u(z) = u(x - ct)$ then, substituting $v = -\frac{du}{dz}$ we arrive at the coupled ODE system:

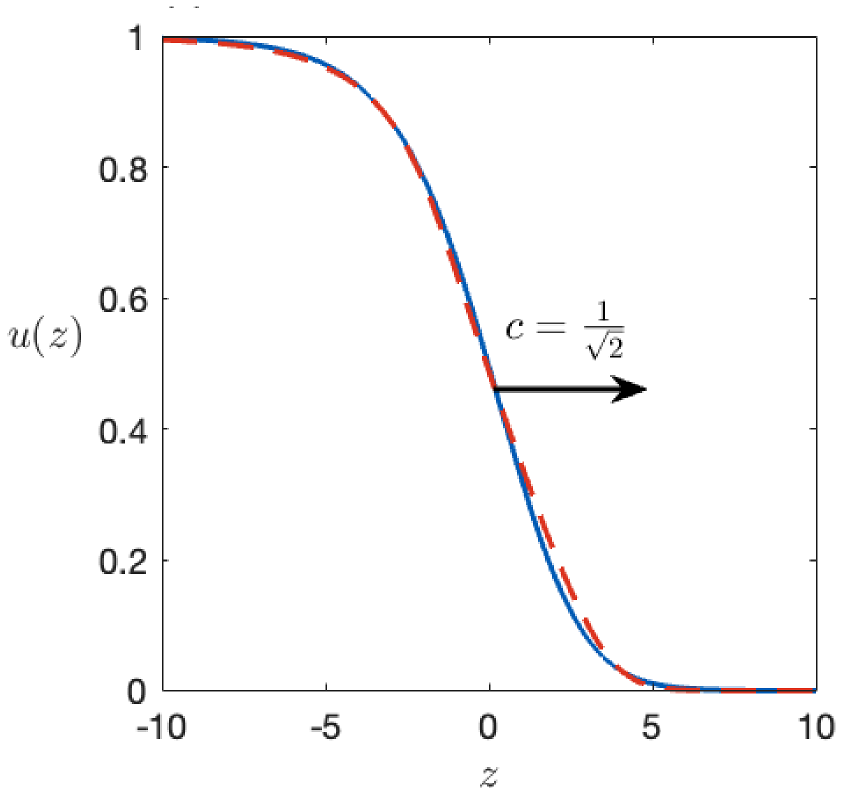
$$\frac{\mathrm{d}u}{\mathrm{d}z} = -v, \quad \frac{\mathrm{d}v}{\mathrm{d}z} = \frac{v^2 D'(u) - cv + f(u)}{D(u)}.$$

In the neighbourhood of zero, the system linearises as

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{D(0)}\begin{pmatrix} 0 & -D(0) \\ f'(0) & -c \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix} \Rightarrow \boxed{c_L \geq 2\sqrt{f'(0)D(0)}}$$

Under sufficiently steep initial conditions the travelling wave solutions will move at the *minimum realisable speed*, $c_L = 2\sqrt{f'(0)D(0)}$.





Methods - Variational Principles

To apply the method of variational principles, we first eliminate the explicit dependence on z:

$$v \frac{\mathrm{d}}{\mathrm{d}u}\left[D(u)v\right] - cv + f(u) = 0 \, .$$

Let $s(u)$ be any monotonically increasing function with $s(0) = 0$ and $s(u) \to \infty$ as $u \to 1$. Multiplying by $\frac{D(u)}{s(u)}$ and integrating by parts with respect to u we obtain:

$$\int_0^1 \frac{fD}{s} du = c \int_0^1 \frac{Dv}{s} du - \frac{1}{2} \int_0^1 \frac{s'}{s^2}(Dv)^2 du \, .$$

We then define the function

$$\phi(v) = c\frac{Dv}{s} - \frac{1}{2}\frac{s'}{s^2}(Dv)^2$$

which obtains its maximum value at

$$v_{max} = c\frac{s}{s'D} \quad \Rightarrow \quad \phi(v) \leq \frac{c^2}{2s'} \, .$$

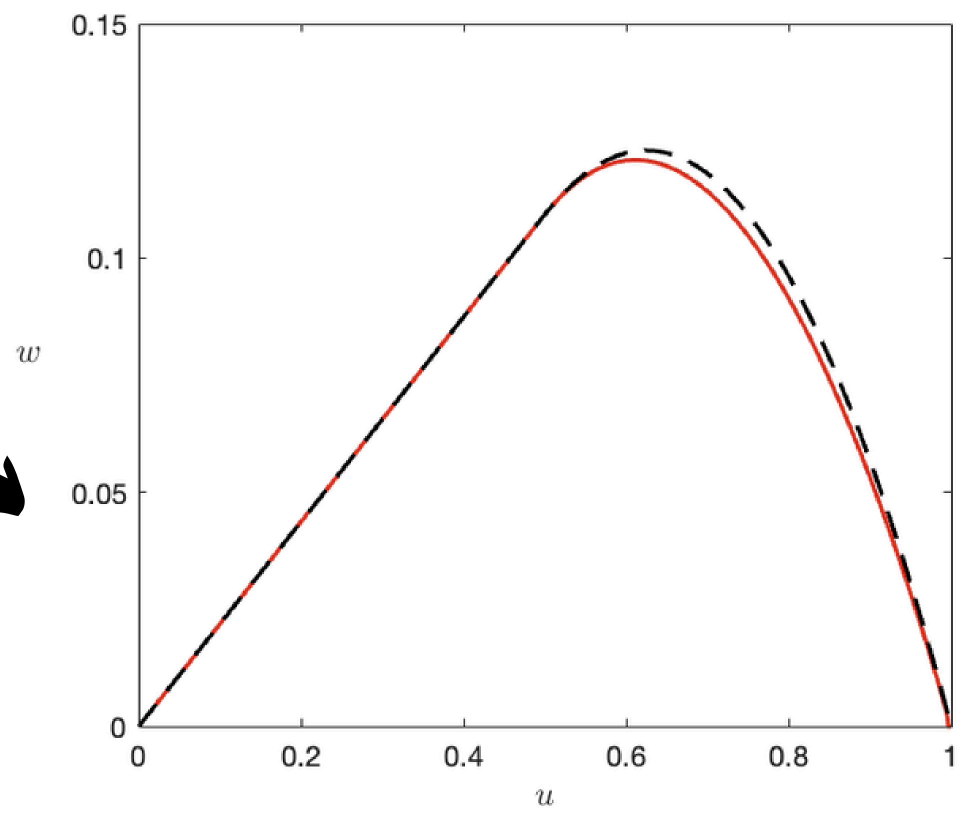
Substituting into the integral equation and rearranging, we can obtain the lower bound on wavespeed:

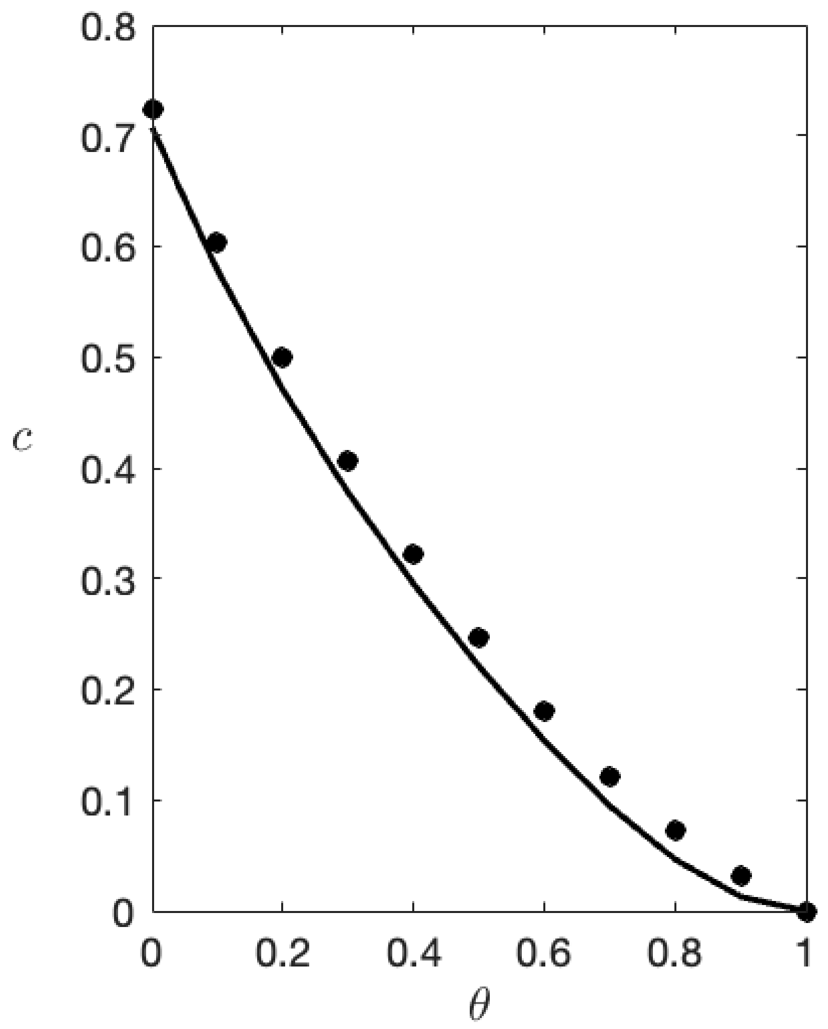
$$c^2 \geq 2\frac{\int_0^1 (fD/s)du}{\int_0^1 (1/s')du}$$

Case Study 3

Introducing $w = D(u)v(u)$ which satisfies $w(w' - c) + fD = 0$, we can approximate w to find the wavespeed.

$$w = \begin{cases} cu & \text{if } u \leq \theta \\ \frac{c(1-u)(u-\theta^2)}{(1-\theta)^2} & \text{otherwise.} \end{cases}$$





The trial function can then be approximated as:

$$\tilde{s}(u) = \exp \int \frac{c}{w} du \approx \begin{cases} u\,\theta^{\frac{1-\theta}{1+\theta}-1} & \text{if } u \leq \theta \\ \left(\frac{u-\theta^2}{1-u}\right)^{\frac{1-\theta}{1+\theta}} & \text{otherwise.} \end{cases}$$

The bound derived from the variational principle can be well approximated by:

$$c \approx \frac{1}{\sqrt{2}}(1+\theta^2)(1-\theta)^2$$