Kinetic traveling waves : swimming bacteria and cane toads

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1. Introduction : Reaction-diffusion fronts (KPP equation).

2. Traveling waves in kinetic equations.
   - Motivation for kinetic equations
   - Traveling waves when V is bounded
   - Front acceleration when V is unbounded

3. Cane toads invasion in Australia
   - Presentation of the ecological problem
   - "Kinetic" modelling
   - Study of the propagation

Propagation phenomena.

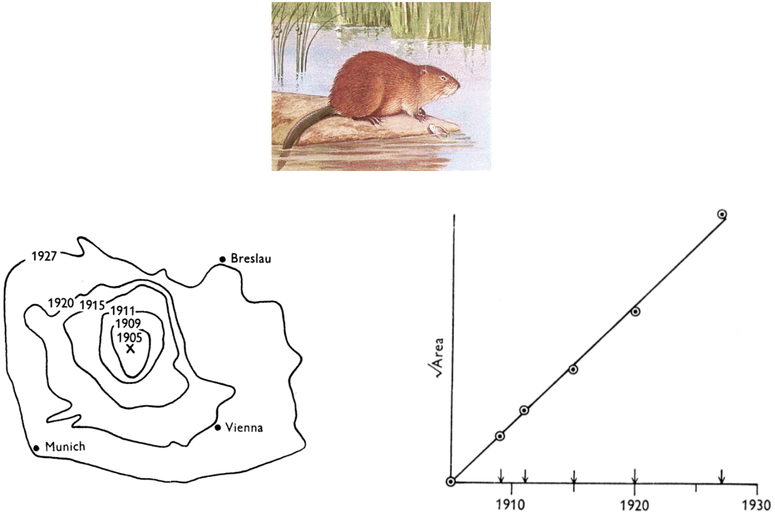


Figure : Spread of muskrats around Prague after Skellam and Elton (1951 & 1958).

The Fisher-KPP equation (1937)

$$\partial_t \rho = \underbrace{D\partial_{xx}\rho}_{\text{unbiaised movement} \,=\, \text{diffusion}} + \underbrace{r\rho(1-\rho)}_{\text{Reproduction + saturation effect} \,=\, \text{logistic growth}} \qquad \text{(KPP)}$$

A traveling wave solution of speed c is a translated profile U,

$$\rho(t,x) = U(x - ct)\,,$$

with the natural limit conditions

$$\begin{cases} U(-\infty) = 1 & \text{stable equilibrium,} \\ U(+\infty) = 0 & \text{unstable equilibrium.} \end{cases}$$

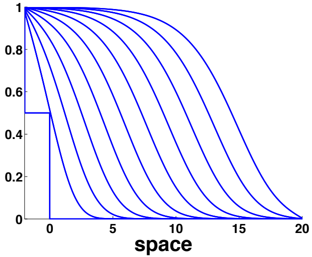


Figure : KPP fronts.

The possible speeds for the fronts

Theorem (Kolmogorov, Petrovsky, Piskunov, 1937)

There exists a minimal speed $c^* := 2\sqrt{rD}$ such that for all speed $c \geq c^*$, there exists a traveling wave solution of speed c. If the initial data has compact support then the front propagates with the minimal speed c^*.

Heuristic (pulled front). The speed of the front is given by the linearized equation at the edge of the front $(\rho \ll 1)$.

$$\partial_t \rho = D \partial_{xx} \rho + r\rho \,,$$

Exponential decay : $\rho(t,x) = \exp(-\lambda(x - ct))$ $(\lambda > 0)$.

We obtain **the dispersion relation**,

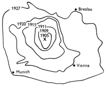
$$c\lambda = D\lambda^2 + r$$

giving **the minimal speed**

$$c(\lambda) = D\lambda + \frac{r}{\lambda} \geq 2\sqrt{rD} := c^* \,.$$

Geometric point of view - The WKB approach for the front propagation (1)

Hyperbolic scaling: $(t,x) \to \left(\frac{t}{\varepsilon}, \frac{x}{\varepsilon}\right)$



$$\varepsilon \partial_t \rho^\varepsilon = \varepsilon^2 D \partial_{xx} \rho^\varepsilon + r \rho^\varepsilon (1 - \rho^\varepsilon) \, .$$

Equivalent to $\theta \to \varepsilon\theta$ (small diffusion) et $r \to r/\varepsilon$ (large reaction).

The fondamental solution of the linearized equation is

$$K_\varepsilon(t,x) = \frac{1}{(4\pi\varepsilon D t)^{1/2}} \exp\left(\frac{rt}{\varepsilon} - \frac{x^2}{4\varepsilon D t} \right) \, .$$

This says that we should perform the following WKB / Hopf-Cole transformation

$$\rho^\varepsilon = \exp(-u^\varepsilon/\varepsilon) \, .$$

Hamilton - Jacobi limit - The WKB approach for the front propagation (2)

Equation for u^ε :

$$\partial_t u^\varepsilon + D|\partial_x u^\varepsilon|^2 + r(1-\rho^\varepsilon) = \varepsilon D \partial_{xx} u^\varepsilon\,, \quad \rho^\varepsilon = \exp(-u^\varepsilon/\varepsilon)\,. \tag{1}$$

In the limit $\varepsilon \to 0$, the solution is the **viscosity solution** of the following **constrained Hamilton-Jacobi equation**

$$\min\left(\partial_t u^0 + D|\partial_x u^0|^2 + r\,,\; u^0\right) = 0\,. \tag{2}$$

To study the front propagation, one should study the **nullset** of u^0.

REF. M.I. Freidlin, *Geometric optics approach to reaction-diffusion equations*, SIAM J. Appl. Math. (1986)

L.C. Evans et P.E. Souganidis, *A PDE approach to geometric optics for. . .* , Indiana Univ. Math. J. (1989)

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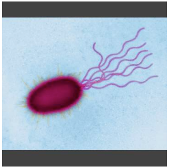
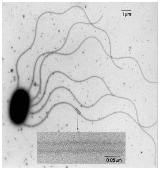
With **Vincent Calvez** (ENS Lyon), **Grégoire Nadin** (Paris 6).

How do bacteria move ...

The bacteria E. Coli moves thanks to flagella :





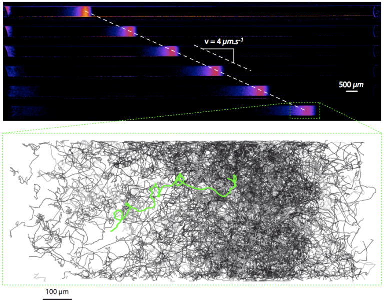
From Howard Berg's lab

and with a so-called *run and tumble* process :
straight swimming for $1s$
and
change of direction for $0.1s$.

Collective migration (1/2)

Collective migration (2/2)

Bacterial traveling pulses:



The kinetic point of view is the most relevant for this situation.

J. Saragosti, V. Calvez, N. Bournaveas, B. Perthame, A. Buguin and P. Silberzan, Directional persistence of chemotactic bacteria in a traveling concentration wave, PNAS (2011).

Kinetic equations

- Probability density of bacteria $f(t,x,v)$ at time t, position x and speed v. Total density $\rho := \int_V f(v)dv$.
- The velocity set V : symmetric, bounded or unbounded ; $v_{max} \leq +\infty$.

The model (Schmeiser, Cuesta, Hittmeir, 2010):

$$\underbrace{\partial_t f + v\partial_x f}_{\text{Free run}} = \underbrace{(M(v)\rho - f)}_{\textit{Tumbling}} + \underbrace{r\rho\left(M(v) - f\right)}_{\text{Growth with saturation}} \tag{3}$$

where the Maxwellian M on the space V satisfies

$$\int_V M(v)dv = 1, \qquad \int_V vM(v)dv = 0, \qquad \int_V v^2 M(v)dv = D. \tag{4}$$

We assume here that $v_{max} < +\infty$.

Definition

We say that a function $f(t, x, v)$ is a traveling front solution of speed $c \in \mathbb{R}^+$ of equation (3) if it can be written $f(t, x, v) = \mu\left(\xi = x - ct, v\right)$, where *the profile* $\mu \in \mathcal{C}^2\left(\mathbb{R} \times V\right)$ is nonnegative, satisfies $\mu\left(-\infty, \cdot\right) = M$, $\mu\left(+\infty, \cdot\right) = 0$, and μ solves

$$(v - c)\partial_\xi \mu = \left(M(v)\nu - \mu\right) + r\nu\left(M(v) - \mu\right), \qquad \xi \in \mathbb{R},\ v \in V. \tag{5}$$

where ν is the macroscopic density associated to μ, that is $\nu\left(\xi\right) = \int_V \mu\left(\xi, v\right) dv$.

Existence results

Parabolic limit result : (parabolic scaling) + ($r \to r\varepsilon^2$) :

Theorem (Cuesta, Hittmeir, Schmeiser)

Let the wave speed satisfy $s \geq 2\sqrt{rD}$*. For* ε *small enough, there exists a traveling wave solution of speed* s*.*

Existence result in the kinetic regime:

Theorem (B., Calvez, Nadin)

Assume that $v_{max} < +\infty$*. There exists a* ***minimal speed*** $c^* \in (0, v_{max})$ *such that* ***there exists a traveling wave solution of*** (3) ***of speed*** c ***for*** $c \in [c^*, v_{max}]$*. Moreover, this traveling wave is* ***nonincreasing*** *with respect to* ξ*.*

(Extending an earlier result by Schwetlick (2000)).

Finding the speed : Dispersion relation

We look for solutions of the linearized problem of type $e^{-\lambda\xi}Q(v)$. Yields the following ***spectral problem*** :

For all λ, find $c(\lambda)$ such that there exists a Maxwellian Q_λ such that

$$\forall v \in V, \quad (1+\lambda\,(c(\lambda)-v))\,Q_\lambda(v) = (1+r)\int_V M(v)Q_\lambda(v)dv. \tag{6}$$

Proposition

The minimal speed c^* is given by $c^* = \min_{\lambda>0} c(\lambda)$ where $c(\lambda)$ is for all λ a solution of the following **dispersion relation**:

$$(1+r)\int_V \frac{M(v)}{1+\lambda(c(\lambda)-v)}\,dv = 1\,. \tag{7}$$

It is not possible to solve the spectral problem when V is unbounded ($v_{max} = +\infty$).

Remarks on the results

1. The existence result is proved using a sub- and super-solutions technique (see e.g. Berestycki and Hamel).
2. One can recover the Fisher-KPP equation :

$$\text{(parabolic scaling)} + (r \to r\varepsilon^2).$$

Proposition

Assume that $v_{max} < +\infty$, then $c^* \xrightarrow[\varepsilon\to 0]{} 2\sqrt{rD} := c_{\text{KPP}}$.

Approximation of $v_{max} = +\infty$: Numerical simulations

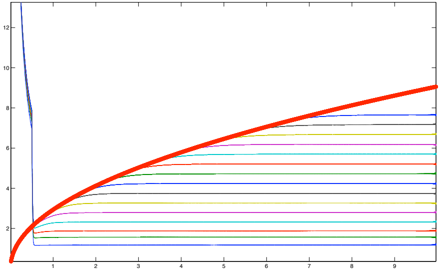


Figure : Evolution of the speed of the front for different values of the maximal speed. The Maxwellian here is a Gaussian : $M(v) = C\left(V_{max}\right)\exp\left(-\frac{v^2}{2}\right)$. "Bell" initial condition.

Theoretical approach

Theorem (B., Calvez, Nadin)

Assume that u is a solution of the Cauchy problem with a nonnegative initial datum u_0 such that there exists $b > 1$ such that

$$u_0(x,v) \leq M(x/b)M(v).$$

Then

$$\sup_{x \geq \sigma\sqrt{2r}t^{3/2}} u(t,x) \to 0 \quad \text{as } t \to +\infty.$$

and the following domination holds true

$$\forall (t,x) \in \mathbb{R}^+ \times \mathbb{R}, \quad \rho(t,x) \leq M\left(\frac{x}{t+a}\right) e^{r(t+a)}. \tag{8}$$

Sharp front limit (1/3)

When there is no growth term ($r = 0$), we obtain in the hyperbolic scaling $(t, x) \to (\frac{t}{\varepsilon}, \frac{x}{\varepsilon})$,

$$\partial_t f + v\partial_x f = \frac{1}{\varepsilon}\left(\rho M(v) - f\right)$$

The density of particles "relaxes" when $\varepsilon \to 0$ towards $M(v)$. We make a adapted kinetic WKB ansatz:

$$f^\varepsilon(t, x, v) = exp\left(-\frac{u^\varepsilon(t, x, v)}{\varepsilon}\right) M(v)$$

Theorem (B. & Calvez)

The phase $u^\varepsilon(t, x, v)$ converges locally uniformly to $u^0(t, x)$, the unique viscosity solution of the following Hamilton-Jacobi equation:

$$\int_V \frac{M(v)}{1 - \partial_t u^0(t, x) - v\partial_x u^0(t, x)} dv = 1\,.$$

Sharp front limit (2/3) - A kinetic eikonal equation

The Hamilton-Jacobi equation can be written

$$\partial_t u^0(t,x) + H(\partial_x u^0(t,x)) = 0\,,$$

with a convex Hamiltonien $H(p)$ tel que :

$$\|\nabla H\|_\infty \leq v_{\max}\,.$$

This generalizes the eikonal equation obtained for the heat equation:

$$\partial_t u^0(t,x) + |\partial_x u^0(t,x)|^2 = 0\,.$$

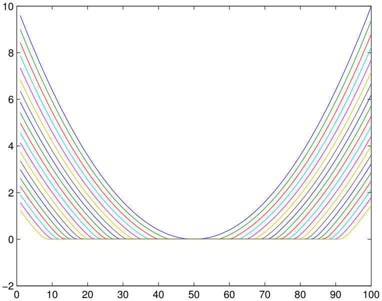
This is **not expected** from a standard Chapman-Enskog expansion on the BGK equation.

Sharp front limit (3/3) - Kinetic traveling fronts

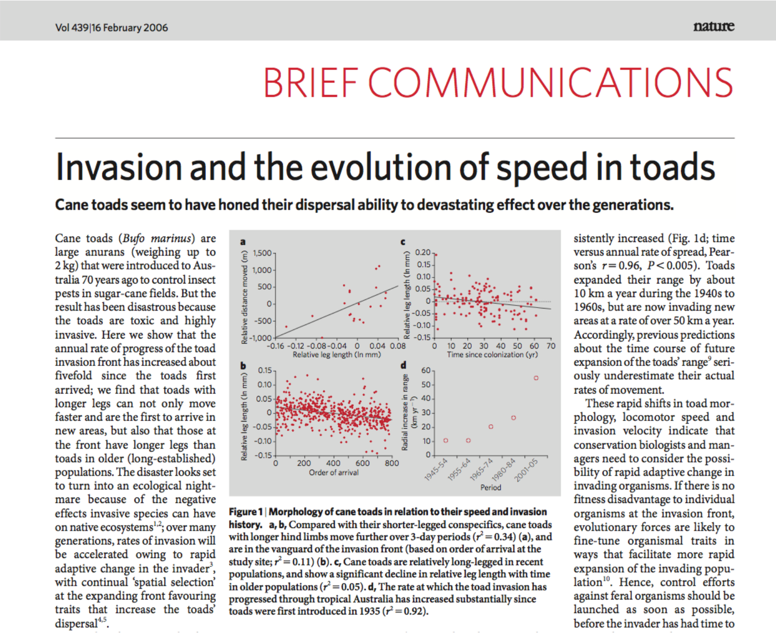
When we add growth $r > 0$, we obtain the following variational Hamilton-Jacobi equation

$$\min\left(\partial_t u^0 + H(\partial_x u^0), u^0\right) = 0$$

Where the Hamiltonian $H(p)$ is implicitly given by $\int_V \frac{(1+r)M(v)}{1+H(p)-vp} dv = 1\,.$



With **Vincent Calvez** (ENS Lyon), **Nicolas Meunier** (Paris 5), **Sepideh Mirrahimi** (Inst. Math. Toulouse), **Benoît Perthame** (Paris 6), **Gaël Raoul** (CEFE, Montpellier) et **Raphaël Voituriez** (Paris 6)



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BRIEF COMMUNICATIONS

Invasion and the evolution of speed in toads

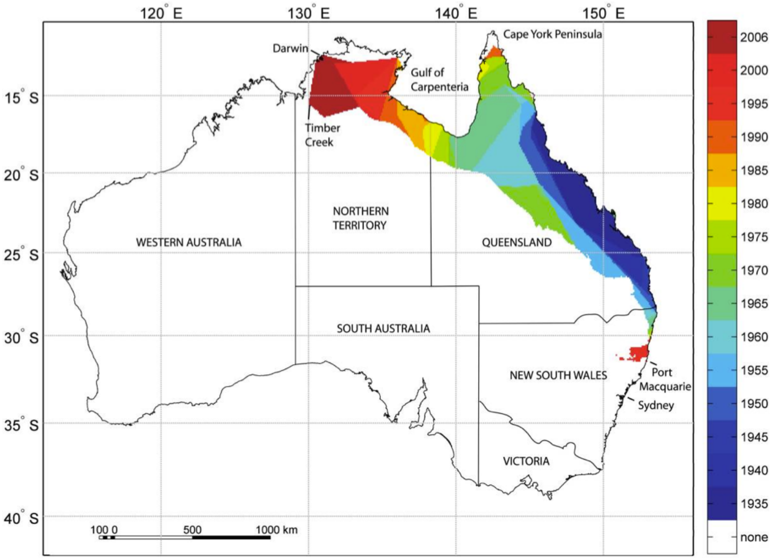
Cane toads seem to have honed their dispersal ability to devastating effect over the generations.

Cane toads (*Bufo marinus*) are large anurans (weighing up to 2 kg) that were introduced to Australia 70 years ago to control insect pests in sugar-cane fields. But the result has been disastrous because the toads are toxic and highly invasive. Here we show that the annual rate of progress of the toad invasion front has increased about fivefold since the toads first arrived; we find that toads with longer legs can not only move faster and are the first to arrive in new areas, but also that those at the front have longer legs than toads in older (long-established) populations. The disaster looks set to turn into an ecological nightmare because of the negative effects invasive species can have on native ecosystems[1,2]; over many generations, rates of invasion will be accelerated owing to rapid adaptive change in the invader[3], with continual 'spatial selection' at the expanding front favouring traits that increase the toads' dispersal[4,5].

Figure 1 | Morphology of cane toads in relation to their speed and invasion history. a, b, Compared with their shorter-legged conspecifics, cane toads with longer hind limbs move further over 3-day periods ($r^2 = 0.34$) (**a**), and are in the vanguard of the invasion front (based on order of arrival at the study site; $r^2 = 0.11$) (**b**). **c,** Cane toads are relatively long-legged in recent populations, and show a significant decline in relative leg length with time in older populations ($r^2 = 0.05$). **d,** The rate at which the toad invasion has progressed through tropical Australia has increased substantially since toads were first introduced in 1935 ($r^2 = 0.92$).

sistently increased (Fig. 1d; time versus annual rate of spread, Pearson's $r = 0.96$, $P < 0.005$). Toads expanded their range by about 10 km a year during the 1940s to 1960s, but are now invading new areas at a rate of over 50 km a year. Accordingly, previous predictions about the time course of future expansion of the toads' range[9] seriously underestimate their actual rates of movement.

These rapid shifts in toad morphology, locomotor speed and invasion velocity indicate that conservation biologists and managers need to consider the possibility of rapid adaptive change in invading organisms. If there is no fitness disadvantage to individual organisms at the invasion front, evolutionary forces are likely to fine-tune organismal traits in ways that facilitate more rapid expansion of the invading population[10]. Hence, control efforts against feral organisms should be launched as soon as possible, before the invader has had time to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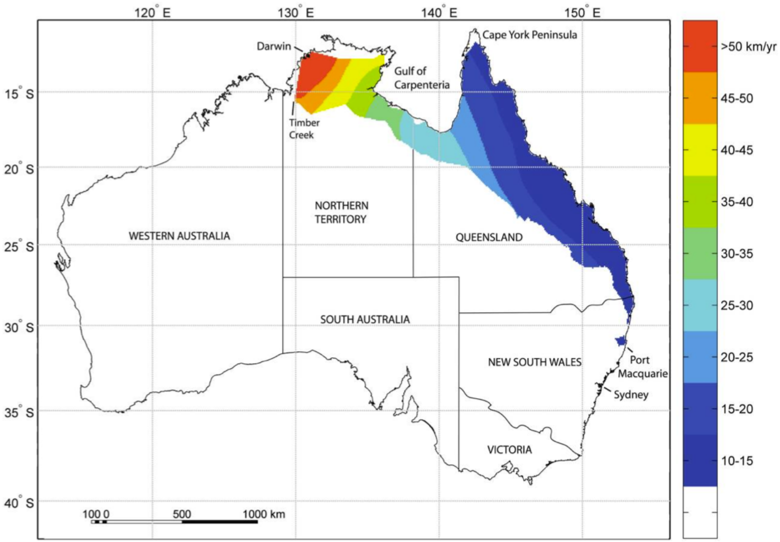
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The model

"Kinetic" type of model : density of toads $f(t,x,\theta)$.

- The motility of the toads is heterogeneous = The diffusion depends on the trait.
- Mutations = diffusion with a rate α.
- When reproducing, a toad gives his trait to his offspring.

The model writes :

$$\partial_t f = \theta \partial_{xx} f + \alpha \partial_{\theta\theta} f + r f - r\rho f \, , \quad \rho(t,x) = \int_\Theta f \, d\theta' \, .$$

with Neumann boundary conditions in $\theta \in [\theta_{min} \geq 0, \theta_{max} \leq +\infty]$.

REF. L. Desvillettes, R. Ferrière et C. Prévost, *Infinite dimensional reaction-diffusion for population dynamics*, preprint CMLA (2004)

N. Champagnat et S. Méléard, *Invasion and adaptive evolution for individual-based spatially structured populations*, J. Math. Biol. (2007)

O. Bénichou, V. Calvez, N. Meunier, and R. Voituriez, *Front acceleration by dynamic selection in Fisher population waves*, Phys. Rev. E (2012)

When $\theta_{max} < +\infty$

Linear problem at infinity :

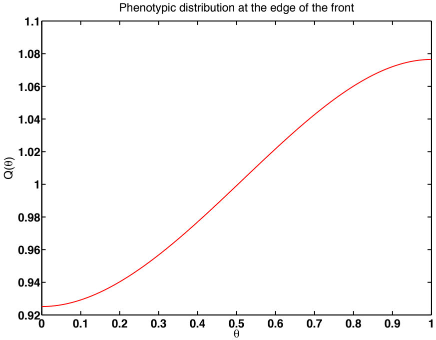
$$\text{Ansatz : } f(t,x,\theta) = \exp(-\lambda(x-ct))Q(\theta)$$

We determine the speed of the front through a **spectral problem** :

$$\begin{cases} \left(-\lambda c(\lambda) + \theta\lambda^2 + r\right) Q(\theta,\lambda) + \alpha\partial^2_{\theta\theta} Q(\theta,\lambda) = 0\,, \\ \partial_\theta Q(\theta_{\min},\lambda) = \partial_\theta Q(\theta_{\max},\lambda) = 0\,, \quad \forall\theta\ Q(\theta,\lambda) \geq 0\,. \end{cases}$$

Most motile toads on the edge of the front.

The eigenvector $Q(\theta, \lambda)$ gives the distribution of the motilities at the edge of the front.



It concentrates to $\delta_{\theta=\theta_{\text{max}}}$ when $\alpha \to 0$.

REF. R. Shine et al, *An evolutionary process that assembles phenotypes through space rather than through time*, PNAS (2011)

Sharp front limit.

The hyperbolic limit (= sharp front limit) $(t, x) \to (\frac{t}{\varepsilon}, \frac{x}{\varepsilon})$ is given by the viscosity solution of the following Hamilton-Jacobi equation:

$$\min\left(\partial_t u^0 + \partial_x u^0 \cdot c(\partial_x u^0), u^0\right) = 0\,, \tag{9}$$

where the effective speed of propagation of the front $c(p)$ is derived from the following spectral problem in the trait space:

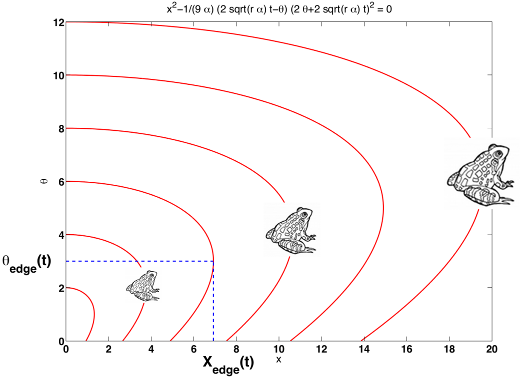
$$\begin{cases} \left(-pc(p) + \theta|p|^2 + r\right) Q(\theta, p) + \alpha\partial^2_{\theta\theta} Q(\theta, p) = 0\,, \\ \partial_\theta Q(\theta_{\min}, p) = \partial_\theta Q(\theta_{\max}, p) = 0\,, \quad \forall\theta\ Q(\theta, p) \geq 0\,. \end{cases}$$

Unbounded θ : Accelerating again.

Good scaling: $(t, x, \theta) \to (\frac{t}{\varepsilon}, \frac{x}{\varepsilon^{\frac{3}{2}}}, \frac{\theta}{\varepsilon})$

The position of the front in the sharp front limit is given by

$$X_{\mathrm{edge}}(t) = \frac{4}{3}\left(\alpha^{1/4} r^{3/4}\right) t^{3/2} .$$



Thank you for your attention !

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