#### Spread in 2-allele genetic systems

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 $\rho_1$  is the density of the *aa* homozygotes,  $\rho_2$  is the density of the *aA* heterozygotes,  $\rho_3$  is the density of the *AA* homozygotes,  $\sigma_a$  is the density of the *a* gametes, and  $\sigma_A$  is the density of the *A* gametes. (1)
 (2)
 (3)
 (4)
 (5)

#### Slide 1a

One space dimension.

HFW Siam J. Math. Anal. 13 (1982) Bistable Fisher-KPP equation:

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} + u[1-u]$$

Define a spreading speed  $c^*$  and its properties. Replace the PDE by an integral equation of Volterra type, then discretize the time variable to turn the integral equation into an integro-difference equation. Defines spreading speed  $c^*$ . Missing: the symmetry  $u(x, t) \rightarrow u(-x, t)$ , which implies that  $-c^*$ 

is also a spreading speed.

Roger Lui, J. of Math. Biol. 13 (1982-3).

$$u(x,t) = \int_0^t \int_0^t \mathbf{K}(x) * u(\cdot,s) ds + \mathbf{K}(x,0) * u(\cdot,0),$$

 $\ensuremath{\mathcal{I}}$  smooth, positive.

Integral equation of Volterra type. Discretize time to get an integro-difference equation. Produces a speed  $c^*$ .

Missing: If u(x, t) is a solution, so is u(-x, t).  $-c^*$  is also a spreading speed.

$$\left\{\frac{\partial}{\partial t} - \delta_d \frac{\partial^2}{\partial x^2}\right\} \rho_1 = -D_1(\rho_1 + \rho_2 + \rho_3)\rho_1 + \beta \sigma_a^2 \tag{6}$$

$$\left\{\frac{\partial}{\partial t} - \delta_d \frac{\partial^2}{\partial x^2}\right\} \rho_2 = -D_2(\rho_1 + \rho_2 + \rho_3)\rho_2 + 2\beta\sigma_a\sigma_A \qquad (7)$$

$$\left\{\frac{\partial}{\partial t} - \delta_d \frac{\partial^2}{\partial x^2}\right\} \rho_3 = -D_3(\rho_1 + \rho_2 + \rho_3)\rho_3 + \beta \sigma_A^2 \tag{8}$$

$$\left\{\frac{\partial}{\partial t} - \delta_g \frac{\partial^2}{\partial x^2}\right\} \sigma_a = G[\rho_1 + \frac{1}{2}\rho_2] - 2\beta[\sigma_a + \sigma_A]\sigma_a \tag{9}$$

$$\left\{\frac{\partial}{\partial t} - \delta_g \frac{\partial^2}{\partial x^2}\right\} \sigma_A = G[\frac{1}{2}\rho_2 + \rho_3] - 2\beta[\sigma_a + \sigma_A]\sigma_A.$$
(10)

#### Define

$$\rho := \rho_1 + \rho_2 + \rho_3, \ \sigma := \sigma_a + \sigma_A.$$

$$\left\{ \frac{\partial}{\partial t} - \delta_d \frac{\partial^2}{\partial x^2} \right\} \sigma \beta = -\beta \sigma^2 + G\rho \tag{11}$$

$$\left\{ \frac{\partial}{\partial t} - \delta_g \frac{\partial^2}{\partial x^2} \right\} \rho \ge -\min_i \{ D_i(\rho) \} \rho + [2\beta\sigma + \tau]\sigma \tag{12}$$

#### Assume:

1.  $D'_i > 0$ . 2.  $\min_i \{D_i\}(k_1) = \max_i \{D_i\}(K_3) = G$ ,  $[2\beta\ell_1 + \tau]\ell_1 = \beta k_1^2$ ,  $[2\beta L_3 + \tau]L_3 = G$ 3.  $D_3(k_3) = D_3(K_3) = G$ ,  $\beta \ell_3^2 = Gk_3$ ,  $[2\beta L_3 + \tau]L_3 = GK_3$ **Theorem:** The set

$$\{\rho_1, \textit{rho}_2, \rho_3\sigma_a, \sigma_a, \sigma_A\} : k_1 \le \rho \le K_3, \ \textit{ell}_1 \le \sigma \le L_3\}$$

is a positive invariant set of the full system of equations. Moreover, the function  $(\rho(x, t), \sigma(x, t))$  is invertible at the interior points of this set, and either *a* or *A* is absent at each boundary point.

Conclusion: no nontrivial solution has an extremal point. (Strong maximum principle.) The integral kernel which corresponds to a nonextremal point is of Volterra type, and its support is the whole line.

A steady state solution with one of the alleles missing is a solution of a pair of integral equations whose kernel has support on the whole line.

The heat operators are very special. To apply the ideas to more general integral operators of the kind treated at this conference, we replace the convolutions with two Gaussian kernels by the applications of integral operators of the kind being discussed at this conference. That is, convolutions by Gauss kernels with diffusivities  $\delta_d$  and  $\delta_g$  are to be replaced by convolutions with two integral kernels  $\mathbf{K}^{(d)}$  and  $\mathbf{K}^{(g)}$ . Assume that each of the kernels is everywhere positive. Then the analog of the above Theorem is valid. That is, the solution of the integral equations has no extreme points. In particular, any nontrivial solution of the integral equation has an infinitely long tail where  $\rho$  and  $\sigma$  are positive.

Conclusion: A solution of the integral equation cannot be confined to a half-line, but must have a tail all the way to  $x = \pm \infty$ . If there is a colony with a peak of the variable  $\rho_3$  upstream, the corresponding  $\rho_3$  has a tail all the way to  $\pm \infty$ . This tail will interact with and outcompete any *a*-only colony downstream. Correct theorem: There are two speeds  $c^{(+)}$  and  $c^{(-)}$  such that the regions where  $\rho(x) \sim K_3$  and  $\sigma(x, t) \sim L_3$  spread at no speed above  $c^{(+)}$  and at no speed below  $c^{(-)}$ .

Note that  $\mathbf{K}(x)$  now takes 2-vectors  $(\rho, \sigma)$  into 2-vectors, so that it is a 2 × 2 matrix. If there are *n* gene loci involved, one must deal with  $\rho$  and *sigma* at the *n* sites, so **K** becomes a  $2n \times 2n$  matrix. Compare with the talk of Mark Kot.