# Spatial Evolutionary Games

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# Hawks-Doves game

Maynard Smith and Price (1973), used this example in order to explain why conflicts over territory between male animals of the same species are usually of the "limited war" type and do not cause serious damage. When a confrontation occurs, Hawks escalate and continue until injured or until an opponent retreats, while Doves make a display of force but retreat at once if the opponent escalates. The payoff matrix is

| | Hawk | Dove |
|---|---|---|
| Hawk | $(V-C)/2$ | $V$ |
| Dove | $0$ | $V/2$ |

Here $V$ is the value of the resource, which two doves split, and $C$ is the cost of competition.

The payoffs are sometimes written as

| | Hawk | Dove |
|---|---|---|
| Hawk | $((V-C)/2,(V-C)/2)$ | $(V,0)$ |
| Dove | $(0,V)$ | $(V/2,V/2)$ |

to indicate the payoff to both players, but here we will write

| | Hawk | Dove |
|---|---|---|
| Hawk | $(V-C)/2$ | $V$ |
| Dove | $0$ | $V/2$ |

The entries give the payoff to player 1 when they use the row strategy and the player 2 uses the column strategy, e.g., if player o1 is a Dove and player 2 is a Hawk then the payoff to player 1 is 0.

When $V = 4$ and $C = 6$ the matrix is

| | Hawk | Dove |
|---|---|---|
| Hawk | $-1$ | 4 |
| Dove | 0 | 2 |

If $2/3$'s of the population is Hawks and $1/3$'s are Doves then

strategy H has payoff $(-1) \cdot 2/3 + 4 \cdot 1/3 = 2/3$
strategy D has payoff $0 \cdot 2/3 + 2 \cdot 1/3 = 2/3$

Both strategies have the same payoff, so this is an equilibrium. If the fraction playing $H$ increases to 0.7 then

strategy H has payoff $(-1) \cdot 0.7 + 4 \cdot 0.3 = 0.5$
strategy D has payoff $0 \cdot 0.7 + 2 \cdot 0.3 = 0.6$

so the fraction of Hawks will decrease and the **equilibrium is stable**.

# Stag Hunt

This game was mentioned by Rousseau in his 1755 book *A Discourse on Inequality*. If two hunters cooperate to hunt stag (an adult male deer) then they will bring home a lot of food, but there is practically no chance of bagging a stag by oneself. If both hunters go after rabbit they split what they kill. An example of a game of this type is:

| | Stag | Hare |
|---|---|---|
| Stag | 3 | 0 |
| Hare | 2 | 1 |

In this case if the two strategies have frequency $p = 1/2$ in the population, then the two strategies have equal payoffs. If the frequency of the stag strategy rises to $p > 1/2$ then it has the better payoff and will continue to increase so this is an **unstable equilibrium**.

# The paradox of altruism = Prisoner's dilemma

This game is sometimes formulated in terms of prisoners deciding whether to confess or not, we will talk in terms of cooperators $C$ and defectors $D$. Here $c$ is the cost that cooperators pay to provide a benefit $b$ to the other player.

$$\begin{array}{ccc} & \mathrm{C} & \mathrm{D} \\ \mathrm{C} & b-c & -c \\ \mathrm{D} & b & 0 \end{array}$$

If $b > c > 0$ then the defection dominates cooperation, and, as we will see, altruistic cooperators are destined to die out in a homogeneously mixing population. This is unfortunate since the $(D, D)$ payoff is worse than $(C, C)$ payoff.

# Homogeneously mixing environment

Frequencies of strategies follow the replicator equation

$$\frac{dx_i}{dt} = x_i(F_i - \bar{F})$$

$F_i = \sum_j G_{i,j} x_j$ is the fitness of strategy $i$, $\bar{F} = \sum_i x_i F_i$, average fitness

**If we add a constant to a column of $G$ then $F_i - \bar{F}$ is not changed.**

We will use this fact to reduce any example to one with 0's on the diagonal.

# Three types of $2 \times 2$ games

If the entire population uses one strategy, i.e., $x_1(0) = 0$ or $x_1(0) = 1$, nothing happens.

**Hawks Doves.** Stable equilibrium $(u^*, 1 - u^*)$. $x_1(t) \to u^*$

**Stag Hunt.** Unstable equilibrium $(u^*, 1 - u^*)$.
If $x_1(0) > u^*$ then $x_1(t) \to 1$. If $x_1(0) < u^*$ then $x_1(t) \to 0$.

**Altruism.** Strategy 2 dominates strategy 1. $x_1(t) \to 0$.


SPACE, THE FINAL
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# Archetti, Ferraro, and Christofori (2015)

Heterogeneity for IGF-II production maintained by public goods dynamics in neuroendocrine pancreatic cancer. PNAS 112, 1833–1838

$$\begin{array}{ccc} & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & \lambda \\ \mathbf{2} & 1 & 1 \end{array} \qquad \text{or} \qquad \begin{array}{ccc} & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & \lambda - 1 \\ \mathbf{2} & 1 & 0 \end{array}$$

2's produce Insulin-like growth factor-II while 1's free ride on that produced by other cells. Since they do not produce the growth factor $\lambda > 1$.

$(\lambda - 1)/\lambda$, $1/\lambda$ is a stable equilibrium. Replicator equation converges to it.

# Spatial Model

Space is the $d$-dimensional integer lattice, $d \geq 3$. Interaction kernel $p(x) = 1/2d$ for the nearest neighbors $x \pm e_i$, $e_i$ is the $i$th unit vector.

$\xi(x)$ is strategy used by $x$. Fitness is

$$\psi(x) = \sum_y p(y-x) G(\xi(x), \xi(y)).$$

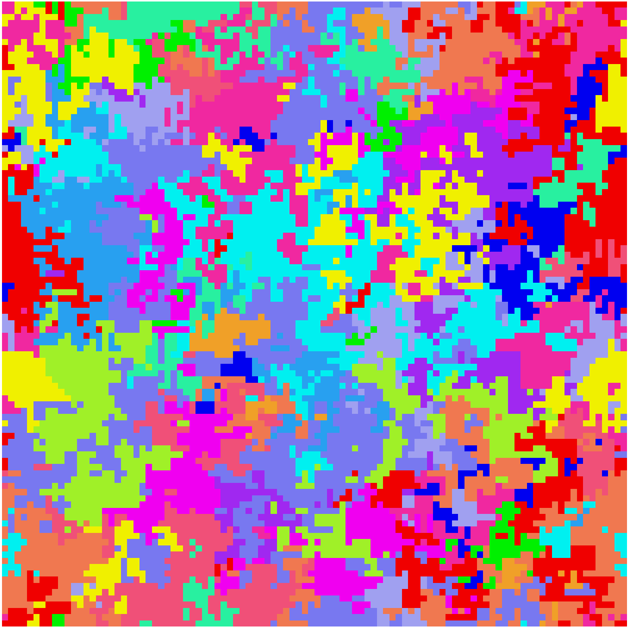
**Birth-Death dynamics:** Each individual gives birth at rate $\psi(x)$ and replaces the individual at $y$ with probability $p(y-x)$.

There are a number of other update schemes, but for simplicity we will stick to this one.

# Weak selection

We are going to consider games with $\bar{G}_{i,j} = \mathbf{1} + wG_{i,j}$ where $\mathbf{1}$ is a matrix of all 1's, and $w$ is small. Does not change the behavior of the replicator equation.

If $G_{i,j} \equiv 1$, Birth-Death dynamics give the **voter model**. Remove an individual and replace it with a copy of a neighbor chosen at random.



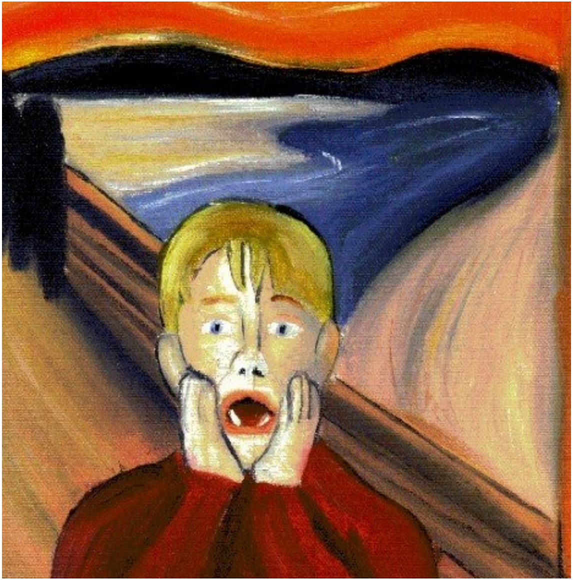


Figure: Warning: next two slides rated NC-17

# PDE limit for voter model perturbations

**Theorem.** Flip rates are those of the voter model $+\epsilon^2 h_{i,j}(0,\xi)$. If we rescale space to $\epsilon\mathbb{Z}^d$ and speed up time by $\epsilon^{-2}$ then in $d \geq 3$

$$u_i^\epsilon(t,x) = P(\xi^\epsilon_{t\epsilon^{-2}}(x) = i)$$

**converges to the solution of the system of PDE:**

$$\frac{\partial u_i}{\partial t} = \frac{\sigma^2}{2}\Delta u_i + \phi_i(u)$$

If the second term is not there this is the heat equation of mathematical physics. Intuitively the PDE describe the density of particles that diffuse and react.

# Reaction term

There are two probabilities $p_1$ and $p_2$ associated with random walk on the spatial structure so that the reaction term $\phi_i(u)$ is $p_1$ times the replicator equation for $H = G + A$ where

$$A_{i,j} = \frac{p_2}{p_1}(G_{i,i} + G_{i,j} - G_{j,i} - G_{j,j}).$$

In the $d = 3$ nearest neighbor case $\theta = p_2/p_1 \approx 0.5$. If the diagonal entries are 0 then $H = G + A$ is

$$H_{i,j} = (1+\theta)G_{i,j} - \theta G_{j,i}.$$

# Why is this exciting?

1. The influence of spatial structure is encapsulated in two numbers that are the same for all games. (obserevation of Tarnita ... Nowak)

2. The effect of space is simply to change some of the entries in the game matrix (Ohtsuki and Nowak for pair approximation)

3. and replace the replicator equation by a PDE.

# Back to our example

$H_{i,j} = (3/2)G_{i,j} - (1/2)G_{j,i}$. which simplifies to

$$\begin{array}{ccc} & \mathbf{1} & \mathbf{2} \\ \mathbf{1} & 0 & \bar{b} = (3/2)\lambda - 2 \\ \mathbf{2} & \bar{c} = 2 - \lambda/2 & 0 \end{array}$$

If $\lambda < 4/3$ we have $\bar{b} < 0$ so $2 \gg 1$ and 2's win.
If $4/3 < \lambda < 4$ then coexistence occurs, equilibrium frequencies

$$\approx (\bar{b}/(\bar{b}+\bar{c}), \bar{c}/(\bar{b}+\bar{c})$$

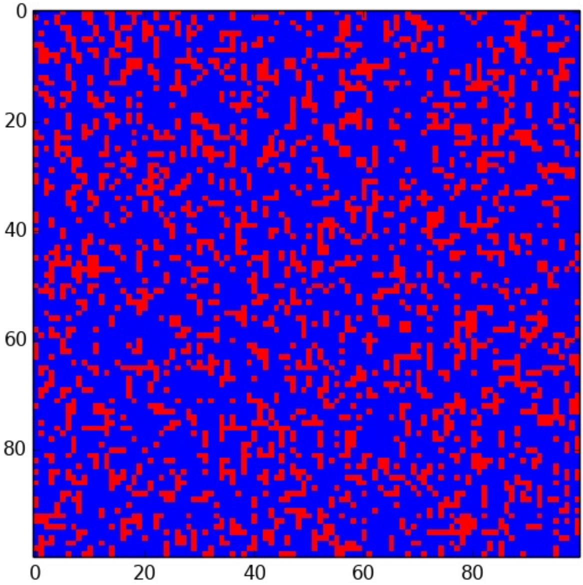
If $\lambda > 4$ we have $\bar{c} < 0$ so $1 \gg 2$ and 1's win.

Homogeneously mixing case: coexistence for all $\lambda > 1$.

# Simulation data

| $\lambda$ | $4/3$ | $3/2$ | 3 | 3.5 | 4 |
|---|---|---|---|---|---|
| **Original game** | 0.11 | 0.25 | 0.75 | 0.83 | 0.89 |
| $w$ = **1/2** | 0.01 | 0.19 | 0.79 | 0.88 | 0.96 |
| $w$ = **1/10** | 0.00 | 0.16 | 0.82 | 0.92 | 0.98 |
| **w to 0 limit** | 0 | 0.17 | 0.83 | 0.93 | 1 |

# 3D Simulation $\lambda = 3$, w $= 1/2$, blue $= 1$



# Rock Paper Scissors

If the $\alpha_i > 0$, $\beta_i < 0$ then $1 \gg 2 \gg 3 \gg 1$

|  | **1** | **2** | **3** |
|---|---|---|---|
| **1** | $0$ | $\alpha_3$ | $\beta_2$ |
| **2** | $\beta_3$ | $0$ | $\alpha_1$ |
| **3** | $\alpha_2$ | $\beta_1$ | $0$ |

If the game $G$ has an interior fixed point it must be:

$$\rho_1 = (\beta_1\beta_2 + \alpha_1\alpha_3 - \alpha_1\beta_1)/D$$
$$\rho_2 = (\beta_2\beta_3 + \alpha_2\alpha_1 - \alpha_2\beta_2)/D$$
$$\rho_3 = (\beta_3\beta_1 + \alpha_3\alpha_2 - \alpha_3\beta_3)/D$$

In RPS the three numerators are positive, so fixed point exists.

# Rock-Paper-Scissors: Replicator Equation

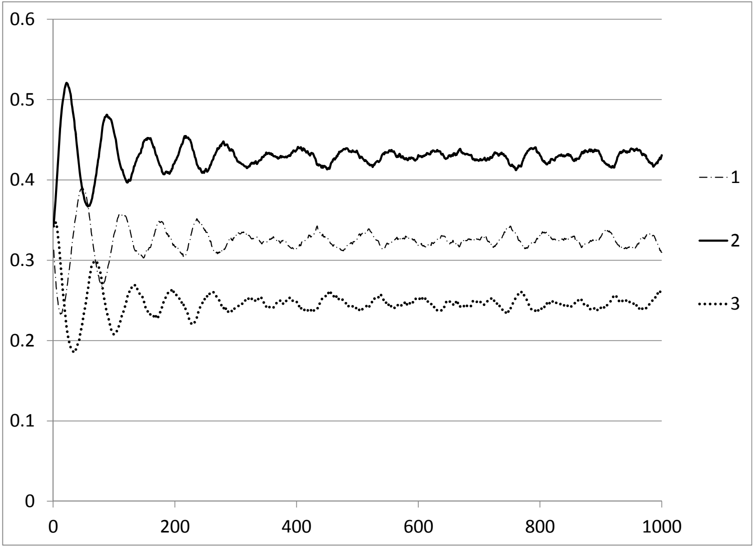
**Theorem.** Hofbauer and Sigmund. *Let* $\Delta = \beta_1\beta_2\beta_3 + \alpha_1\alpha_2\alpha_3$. *If* $\Delta > 0$ *solutions converge to the fixed point. If* $\Delta < 0$ *their distance from the boundary tends to 0. If* $\Delta = 0$ *there is a one-parameter family of periodic orbits.*

| $G_1$ | **0** | **1** | **2** |
|---|---|---|---|
| **0** | 0 | 4 | $-3$ |
| **1** | $-1$ | 0 | 5 |
| **2** | 6 | $-2$ | 0 |

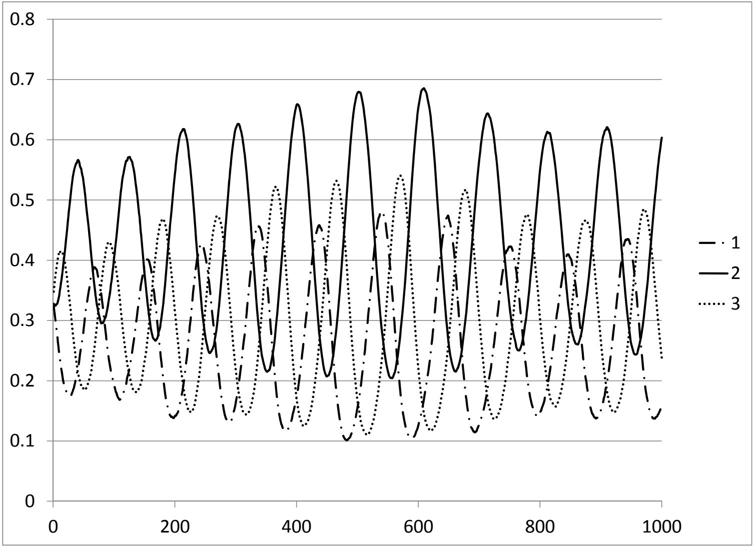
| $G_2$ | **0** | **1** | **2** |
|---|---|---|---|
| **0** | 0 | 1 | $-2$ |
| **1** | $-3$ | 0 | 2 |
| **2** | 3 | $-2$ | 0 |

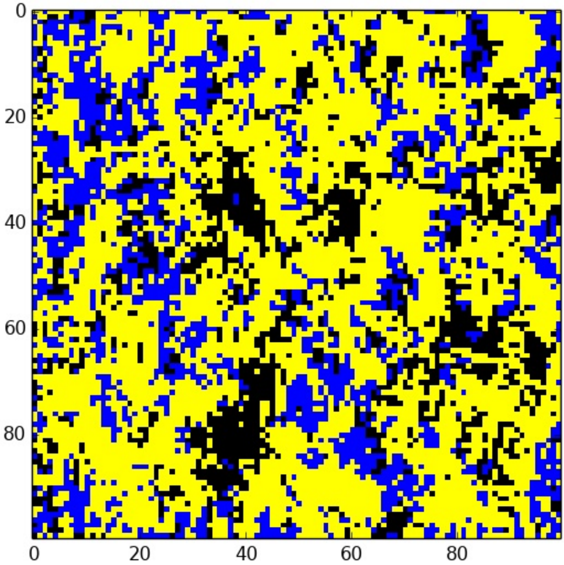
$G_1$ is constant sum and has $\Delta > 0$. $G_2$ has $\Delta < 0$.

# Game $G_1$, Replicator eq converges to fixed point

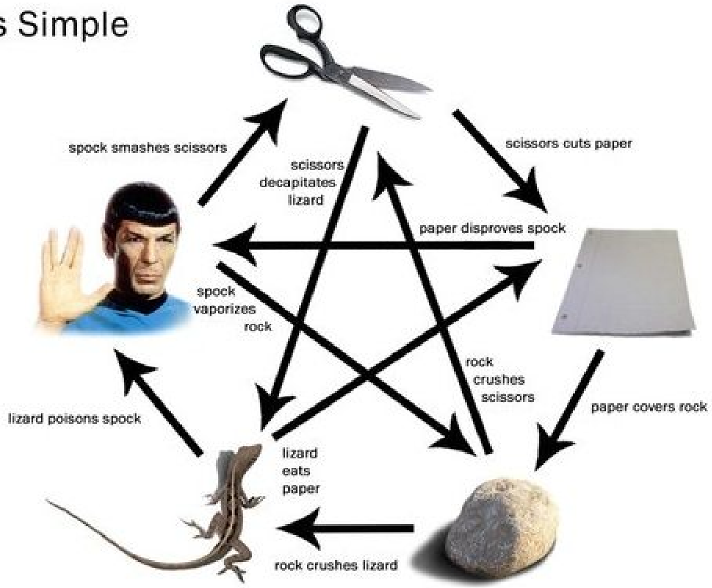


# Game $G_2$, Replicator eq spirals out to boundary




0
20
40
60
80
0
20
40
60
80

# Its Simple



spock smashes scissors
scissors cuts paper
scissors decapitates lizard
paper disproves spock
spock vaporizes rock
rock crushes scissors
paper covers rock
lizard poisons spock
lizard eats paper
rock crushes lizard

# Stag Hunt

Modify so that 0's on diagonal

| $G$ | $Stag$ | $Hare$ |
|---|---|---|
| $Stag$ | $0$ | $-1$ |
| $Hare$ | $-2$ | $0$ |

(1/3, 2/3) unstable equilibrium. Replicator equation is

$$\frac{du}{dt} = \phi(u) = u(1-u)[3u-1]$$

If $u(0) < 1/3$ converges to 0. if $u(0) > 1/3$ converges to 1.
**Bistable.** The limit depends on starting frequency.

# Stag Hunt: Spatial Game

$$H_{ij} = (3/2)G_{i,j} - (1/2)G_{j,i}$$

| $H$ | $Stag$ | $Hare$ |
|---|---|---|
| $Stag$ | 0 | $-1/2$ |
| $Hare$ | $-5/2$ | 0 |

$(\bar{u}, 1-\bar{u}) = (1/6, 5/6)$ unstable equilibrium.

**In this spatial game strategy 2 always takes over.**

Why?. PDE $\frac{du}{dt} = \sigma^2 u''/2 + u(1-u)[3u - 1/2]$ has traveling wave solution

$$u(t,x) = w(x - ct), \quad u(-\infty) = 1, \quad u(\infty) = 0.$$

Strategy 1 take over if and only if $c > 0$ which holds if and only if $\bar{u} < 1/2$. **No bistability in spatial games. Durrett and Levin (1994)**

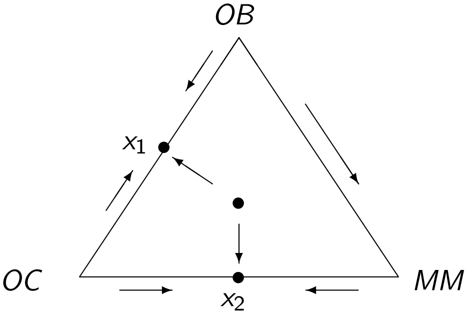
# Dingli et al (2009) British J. Cancer

Normal bone remodeling is a consequence of a dynamic balance between osteoclast ($OC$) mediated bone resorption and bone formation due to osteoblast ($OB$) activity. Cancer disrupts this due to action of multiple mlyeloma ($MM$) cells.

| $G$ | $OC$ | $OB$ | $MM$ |
|---|---|---|---|
| $OC$ | 0 | 2 | $c$ |
| $OB$ | 2 | 0 | $-1$ |
| $MM$ | $c$ | 0 | 0 |

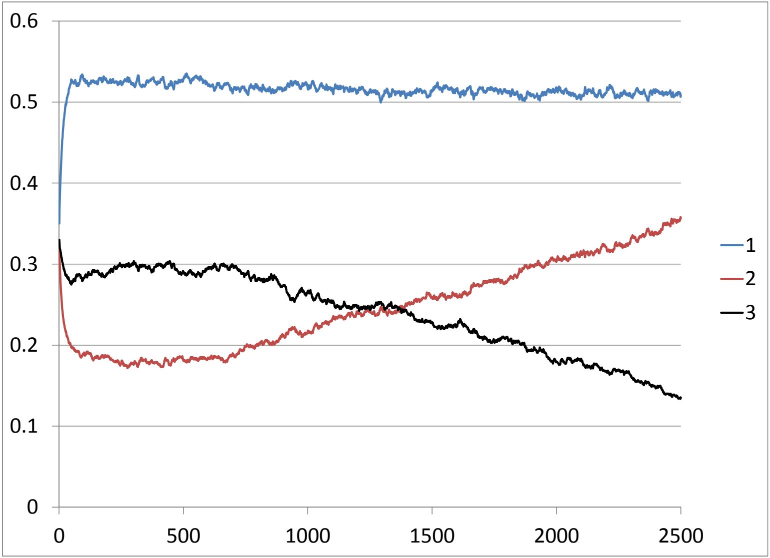
| $H$ | 1 | 2 | 3 |
|---|---|---|---|
| 1 | 0 | 2 | $c$ |
| 2 | 2 | 0 | $-3/2$ |
| 3 | $c$ | $1/2$ | 0 |

Bistable for $c \in [0.5, 1.5]$.

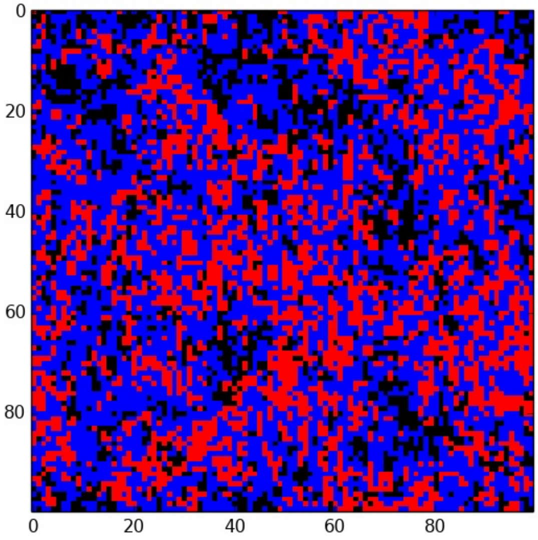


OB
x1
OC
x2
MM

$x_1$ wins $c = 1.5$, $x_2$ eq wins $c = 1$. Simulation is for $c = 1.25$.



# c = 1.25 at time 500. 1=blue, 2=red, 3=black



# Summary

Our main contribution is to describe a procedure for determining the behavior of spatial three strategy games with weak selection.

Rewrite $G$ so the diagonal is 0. One then forms the modified game $H_{ij} = (1+\theta)G_{ij} - \theta G_{j,i}$, where $\theta$ is a constant that depends on the spatial structure but not on the entries in the game matrix. $\theta \approx 1/2$ in the three dimensional nearest neighbor case.

The behavior of the spatial game with matrix $G$ can then be predicted from that of the replicator equation for $H$. We say predicted because in some cases (e.g. bistable games or unstable RPS) the behavior is not the same (stronger strategy always wins or there is coexistence). The last two conclusions have not been proved mathematically.

# References

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