Discrete and Continuous Models in Population Dynamics

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The big question

Do we do the right thing?

If population dynamics is based on individuals, why do people use differential equations?

The big question

The question you never asked your professor...

Where do differential equations come from?

Objectives

...and side effects

We will not answer the previous questions. ☹

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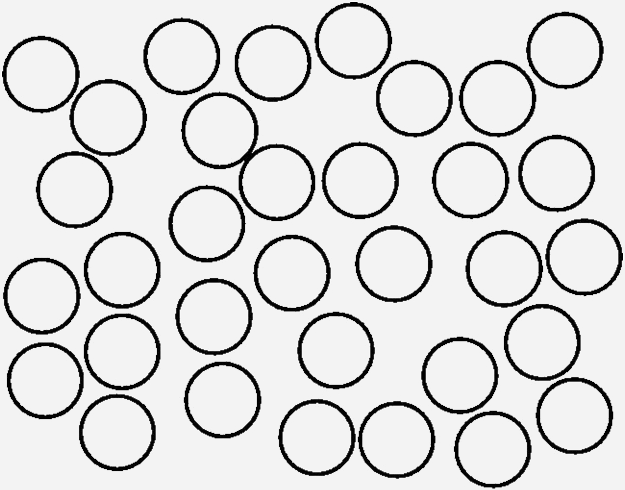
We start from a simple model in population dynamics and obtain, in the end, an ordinary differential equations.

As side-effects:

1. We establish the validity of the ODE model;
2. We find a better differential equation. This lead us naturally to singular partial differential equations.

How to model the evolution?



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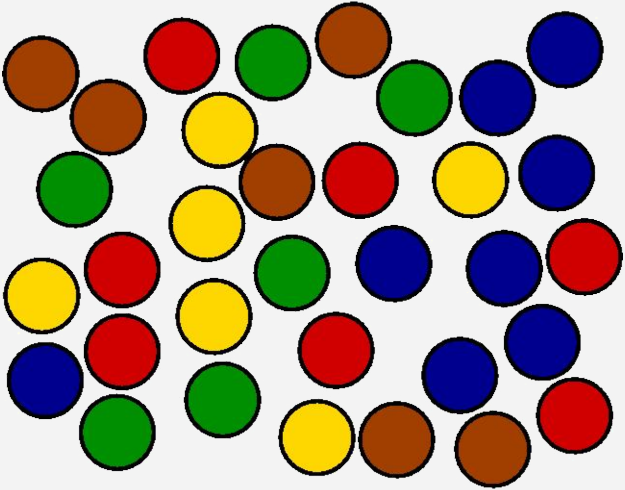

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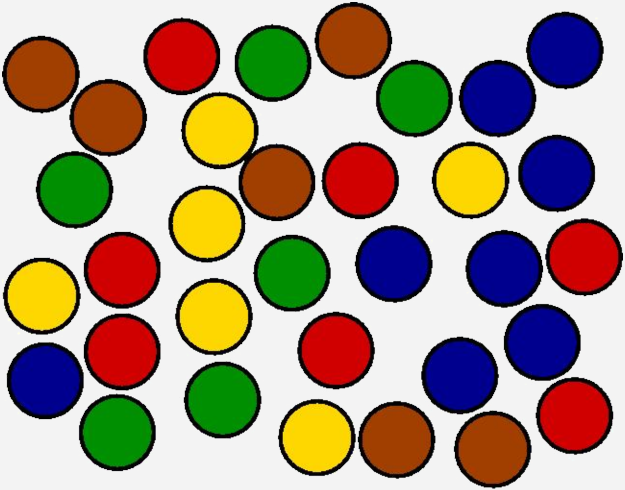

We consider a population of N individuals of n different types. We attribute to each type a number, called fitness.

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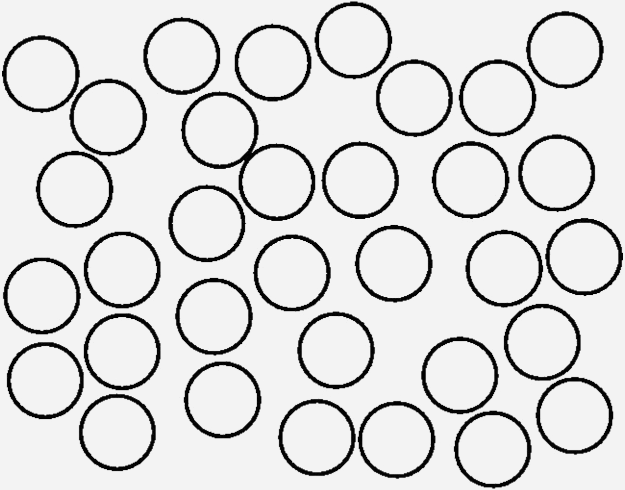

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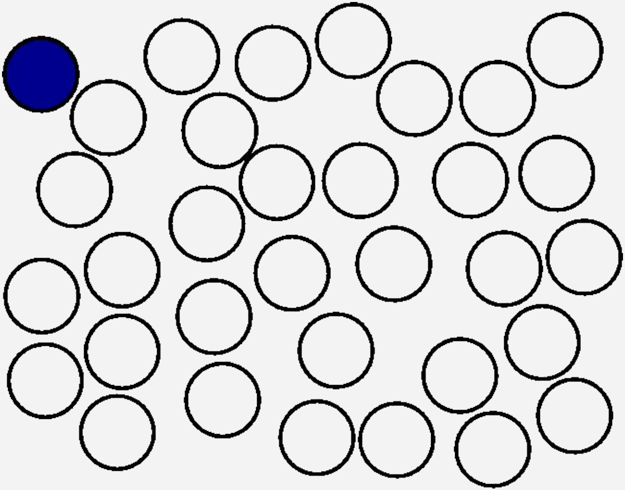

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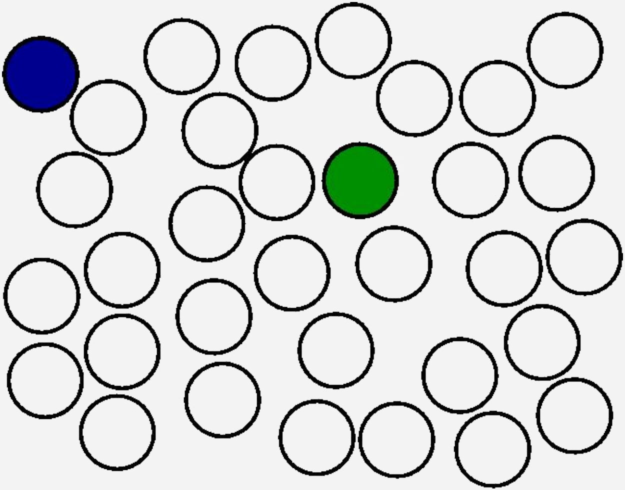

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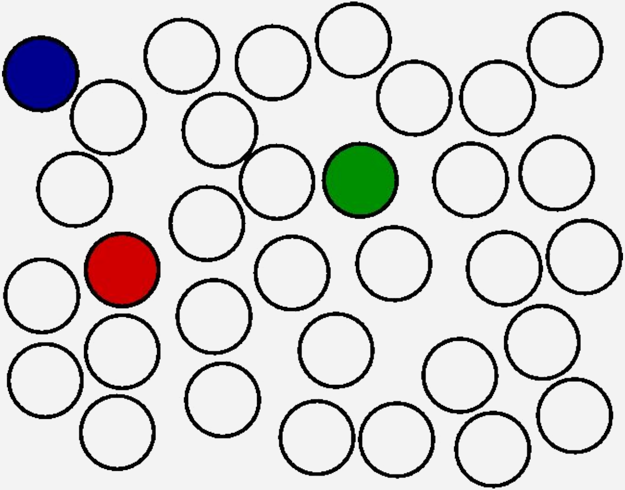

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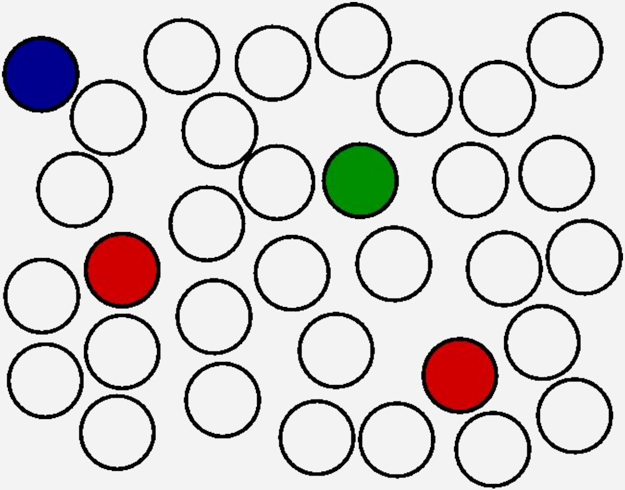

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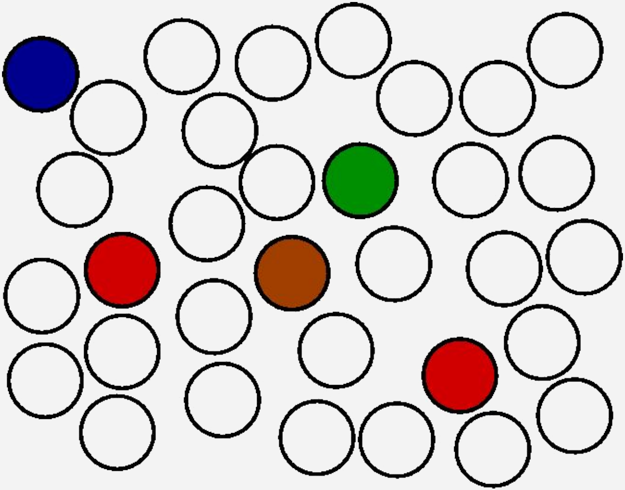

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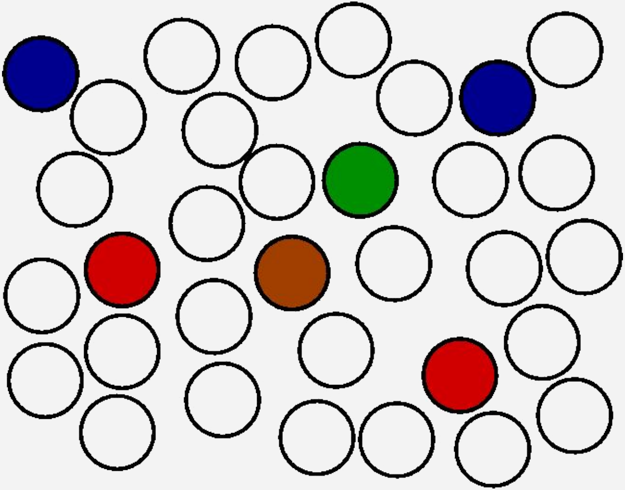

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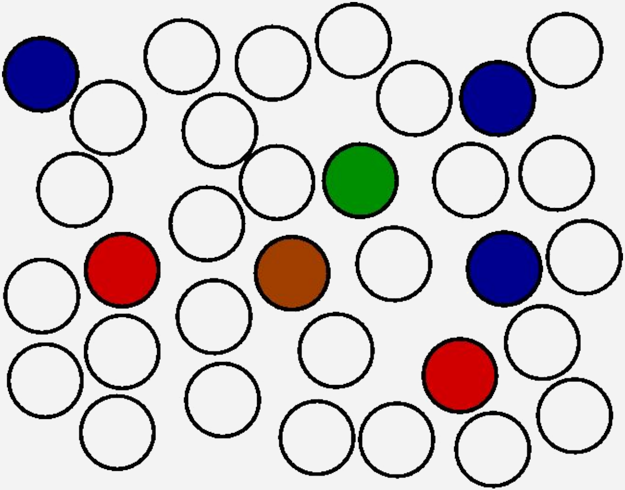

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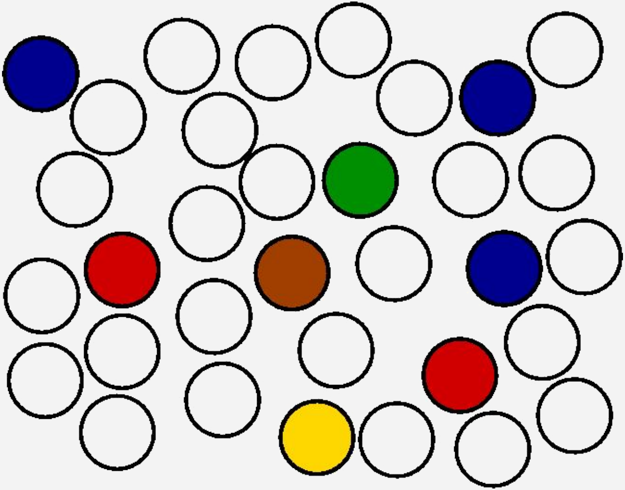

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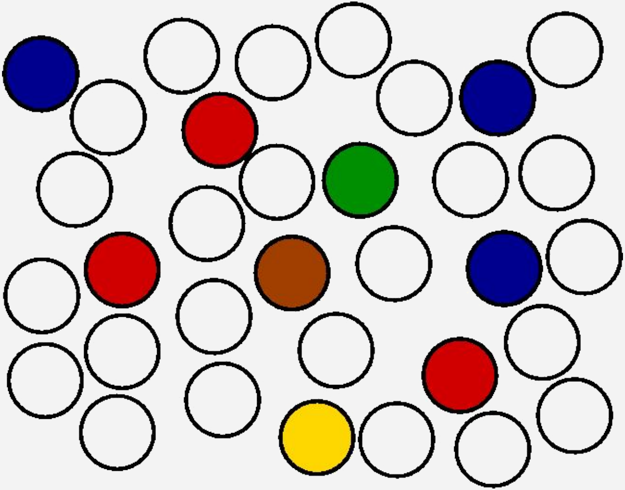

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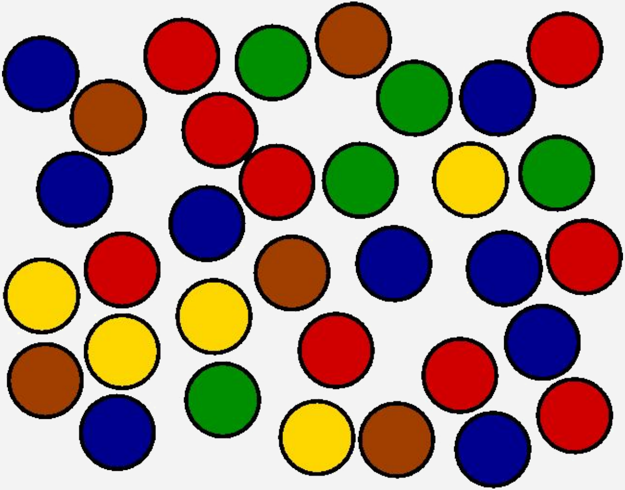

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The transition probability from a state $\mathbf{y}$ to a new state $\mathbf{x}$ is given by

$$\Theta_N(\mathbf{y} \to \mathbf{x}) = \frac{N!}{(Nx_1)!(Nx_2)! \cdots (Nx_n)!} \prod_{i=1}^{n} \left(\frac{y_i \Psi^{(i)}}{\bar{\Psi}} \right)^{Nx_i} \quad .$$

How to obtain the *fitness*?

A crash course on game theory

We consider two players, with two possible pure strategies, and associate a *pay-off matrix*:

$$\begin{array}{c|cc} & \text{I} & \text{II} \\ \hline \text{I} & A & B \\ \text{II} & C & D \end{array}\,, \qquad \text{with } A, B, C, D > 0.$$

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The Nash equilibrium is given by the strategy that is *the best reply against itself*: $p^* = \mathcal{R}(p^*)$.

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We say that E_p is an ESS if and only if:

$$\underbrace{\mathcal{W}(E_q, (1-\varepsilon)E_p + \varepsilon E_q)}_{\text{average invader's pay-off}} < \underbrace{\mathcal{W}(E_p, (1-\varepsilon)E_p + \varepsilon E_q)}_{\text{average resident's pay-off}}$$

for any strategy $E_q \neq E_p$ and ε small enough.

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We call n the number of type I individuals. *Fitnesses* are identified with mean pay-off:

$$\Psi^{(\mathrm{I})}(n,N) = \frac{n-1}{N-1}A + \frac{N-n}{N-1}B\ ,$$
$$\Psi^{(\mathrm{II})}(n,N) = \frac{n}{N-1}C + \frac{N-n-1}{N-1}D\ .$$

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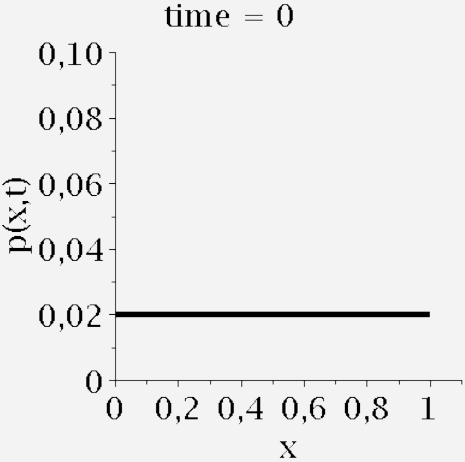
When $\alpha < 0$ and $\beta > 0$ (the *Hawk-and-Dove* game) this equation has three equilibria: $x = 0$, $x = 1$ and $x = x^* = \frac{\beta}{\beta-\alpha} \in (0,1)$.

2 types Wright-Fisher process



Simulation for $N = 50$, $\Psi^{(\mathbb{A})}(x) = 2$, $\Psi^{(\mathbb{B})}(x) = 1 + 3x$

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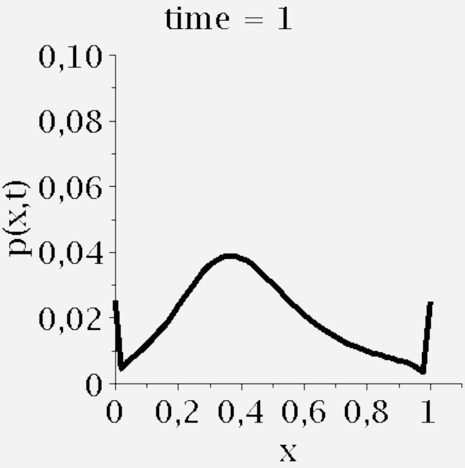

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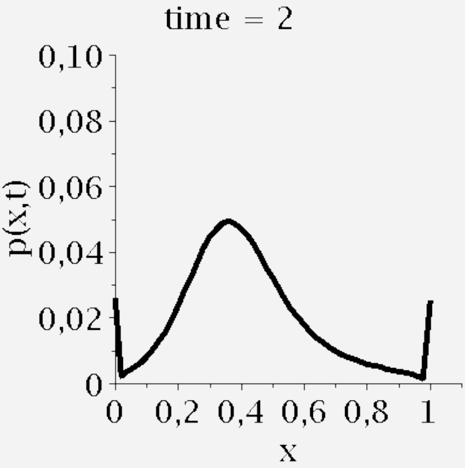

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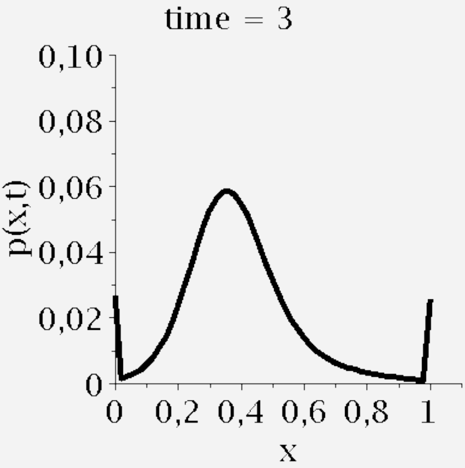

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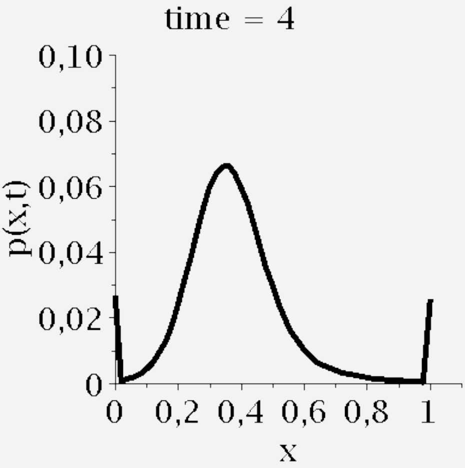

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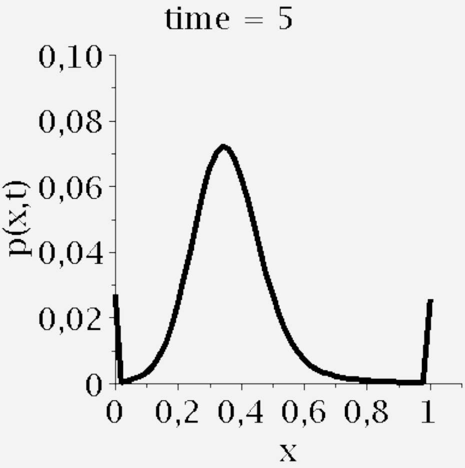

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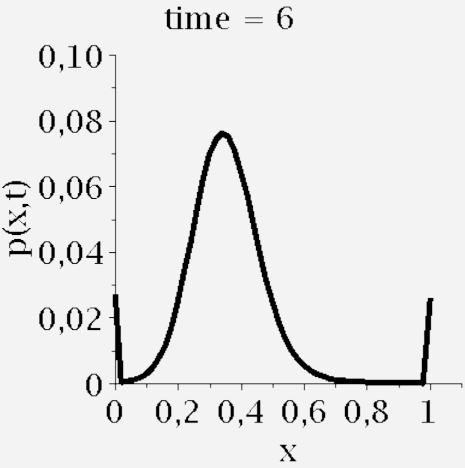

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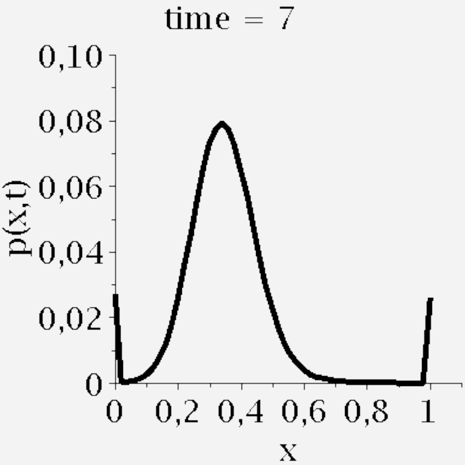

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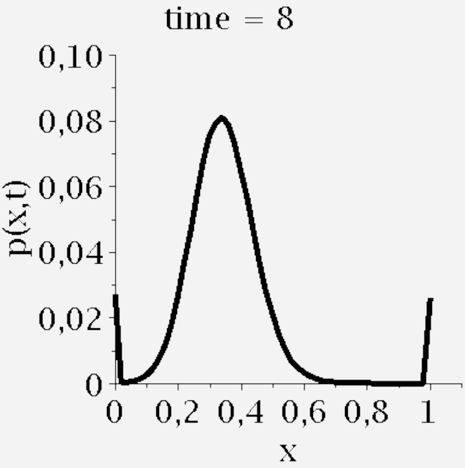

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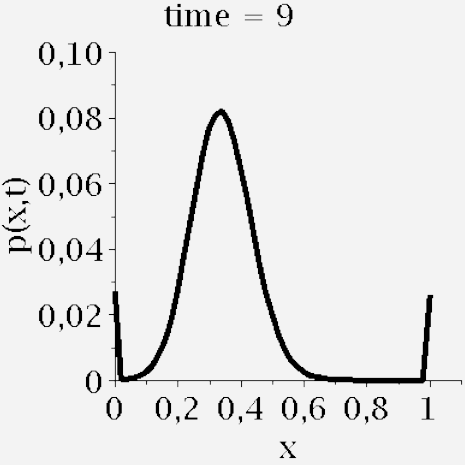

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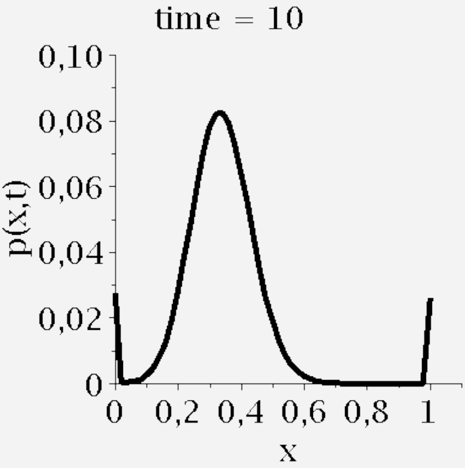

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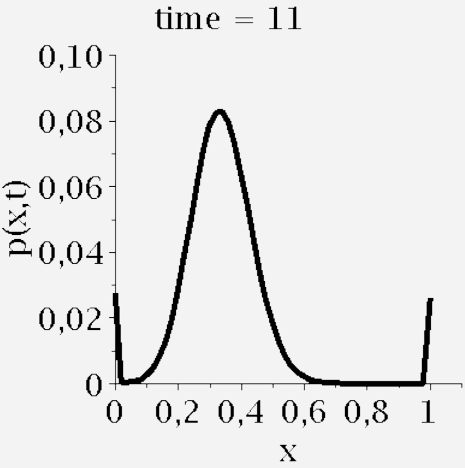

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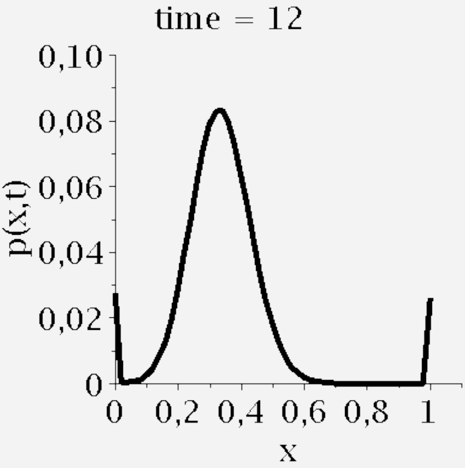

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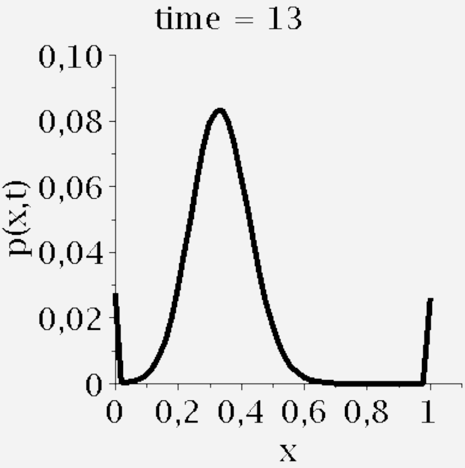

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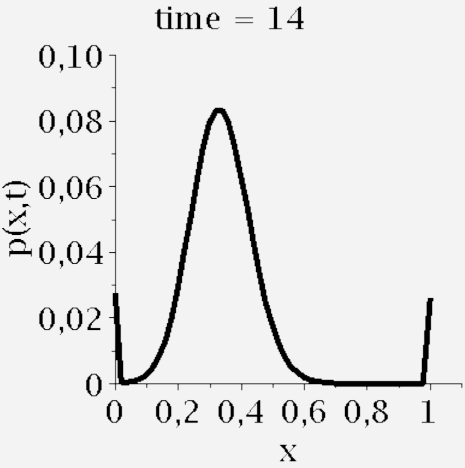

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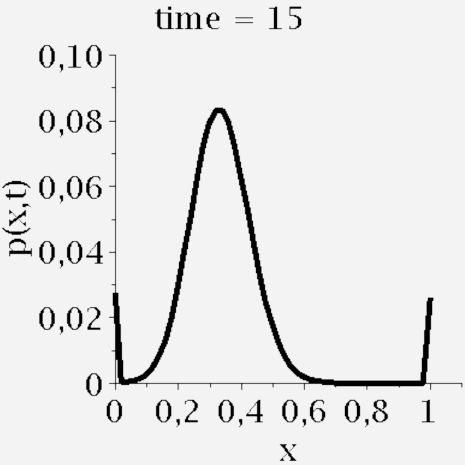

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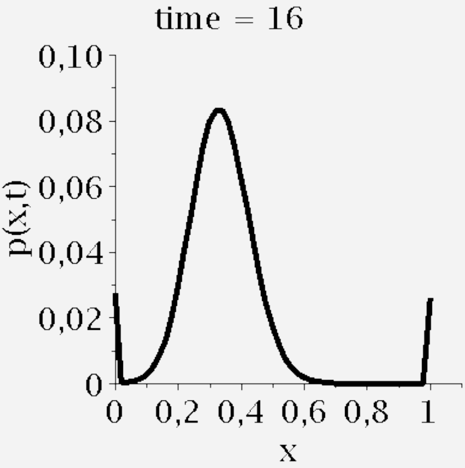

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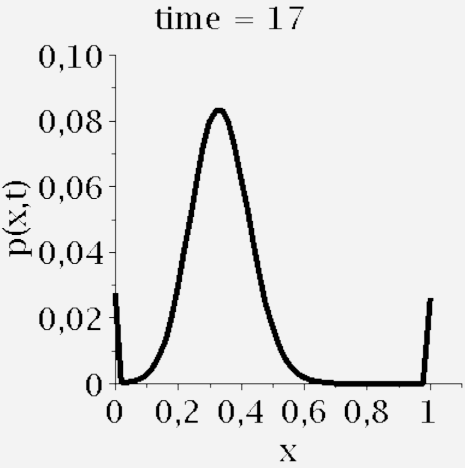

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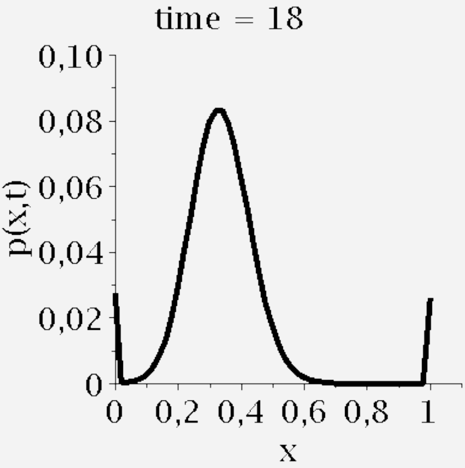

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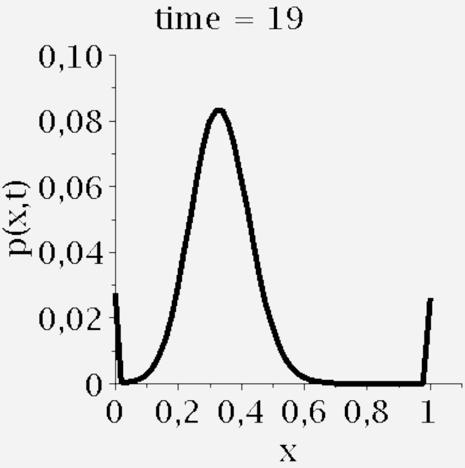

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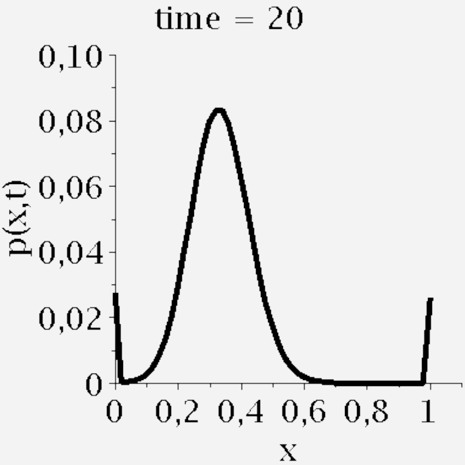

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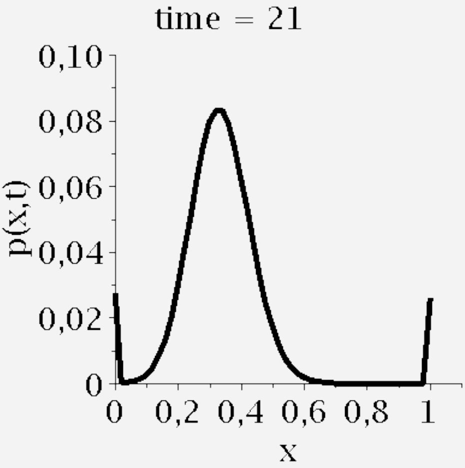

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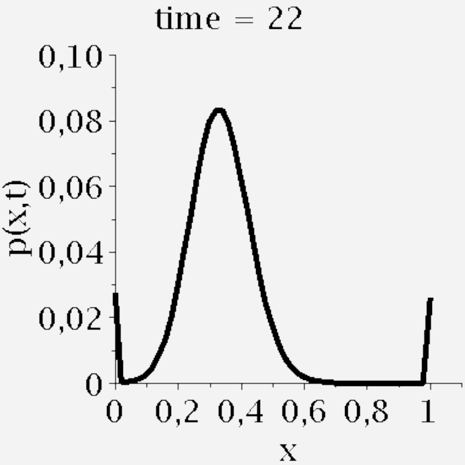

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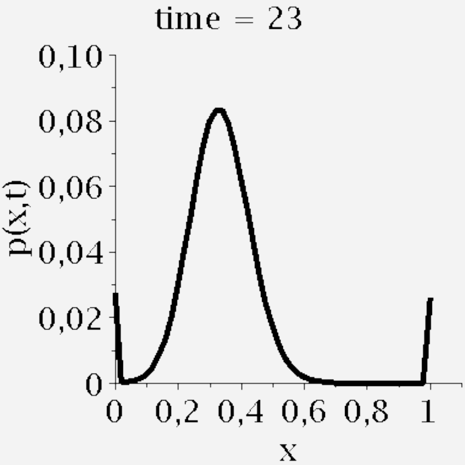

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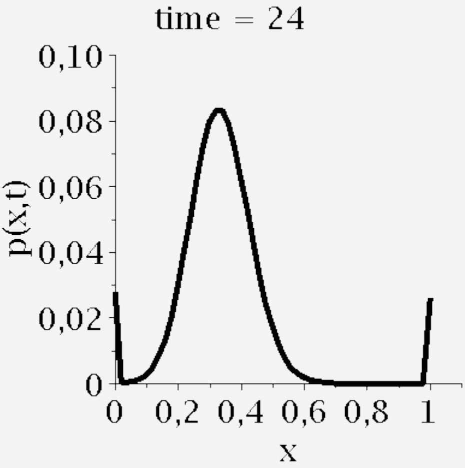

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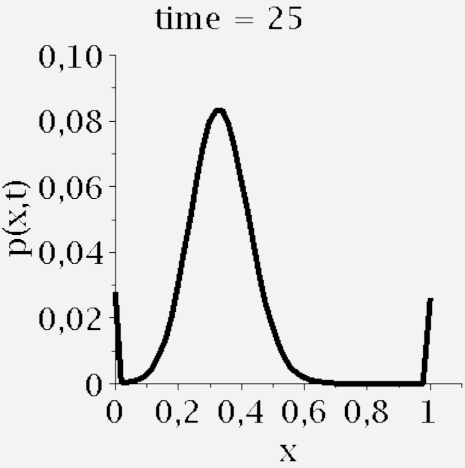

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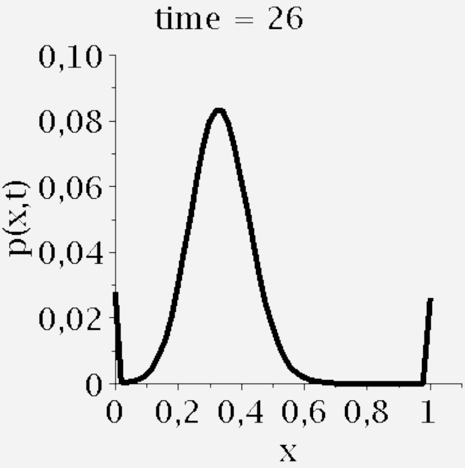

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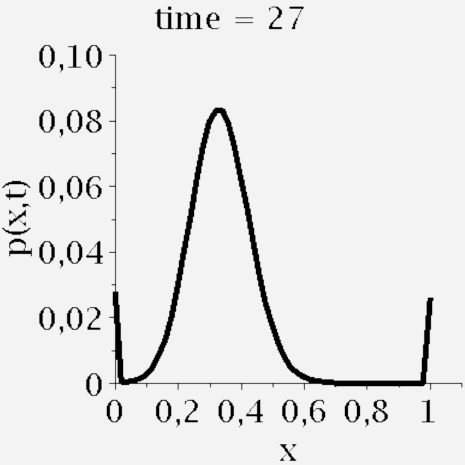

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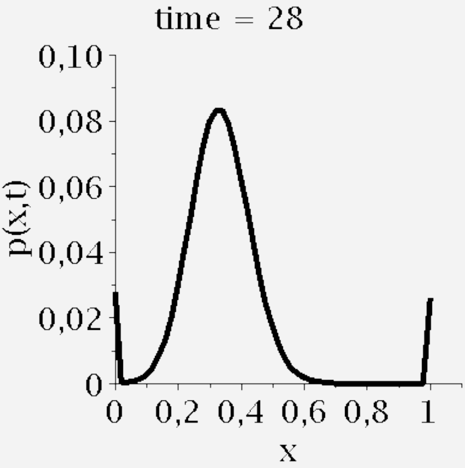

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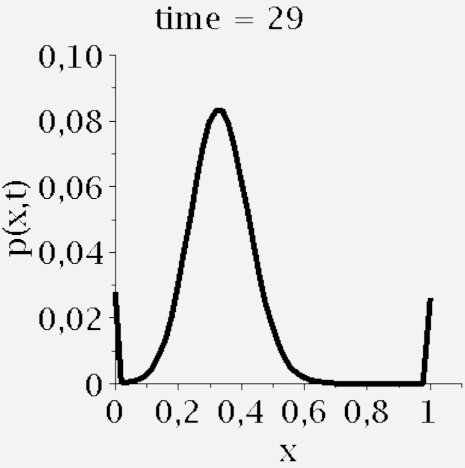

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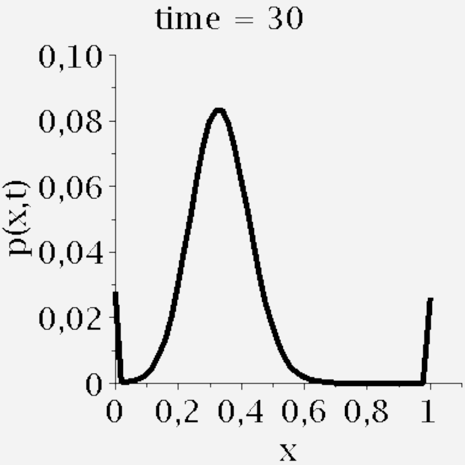

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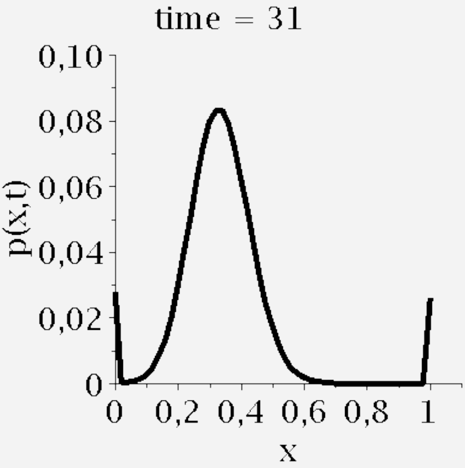

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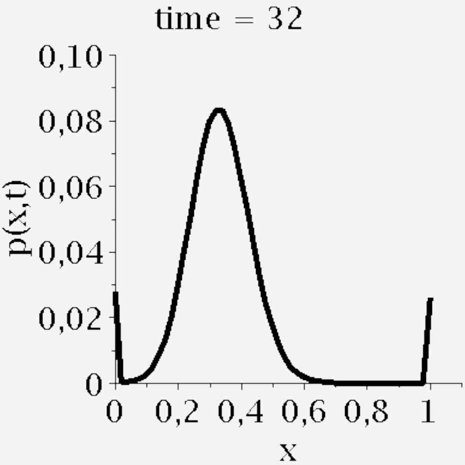

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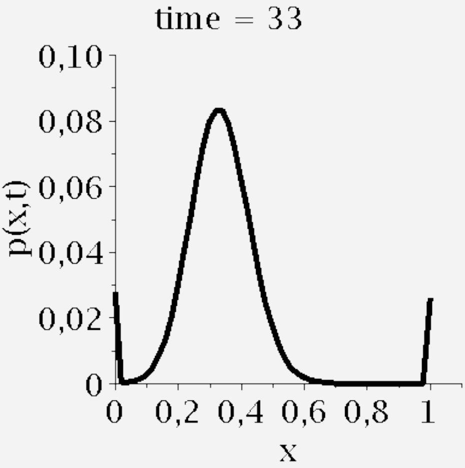

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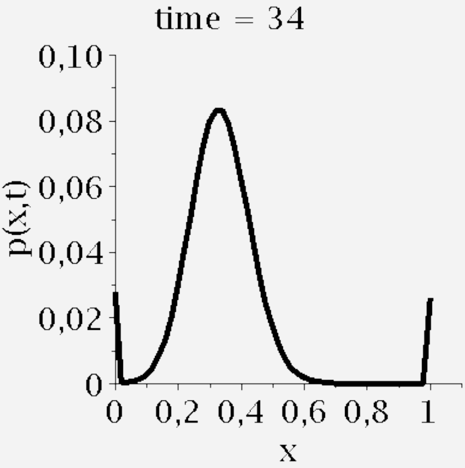

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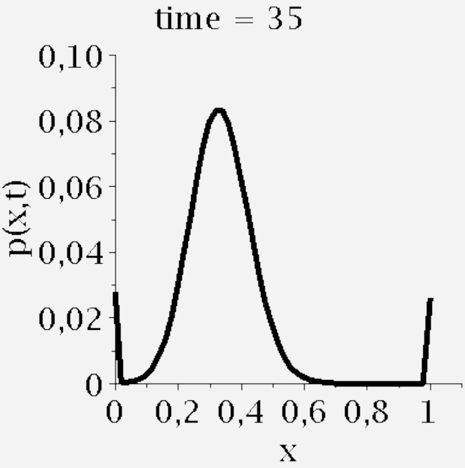

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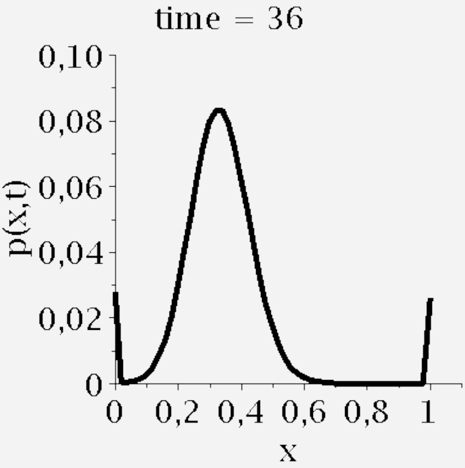

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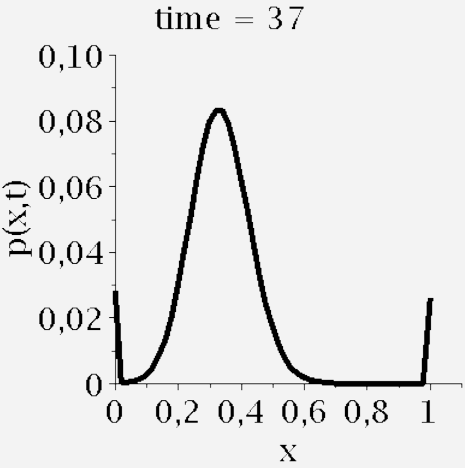

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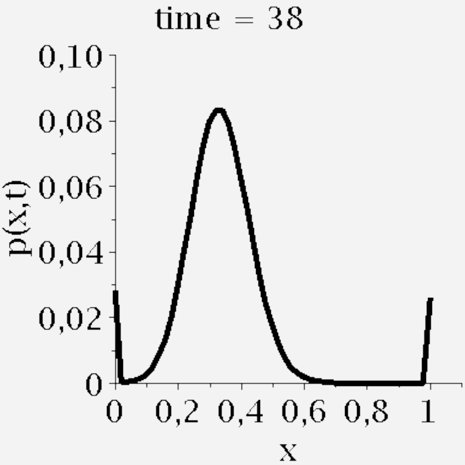

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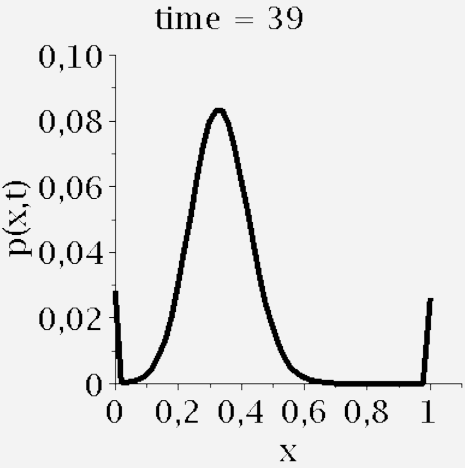

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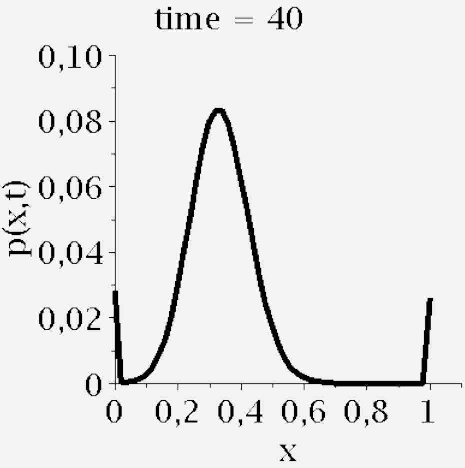

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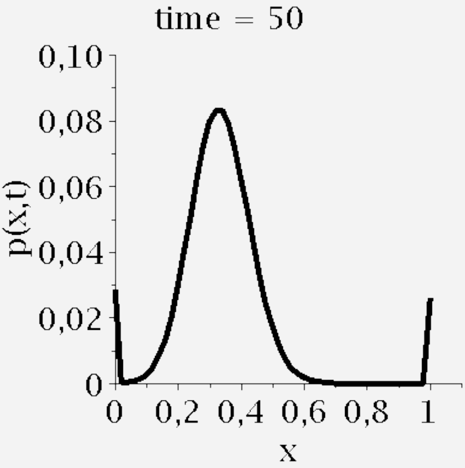

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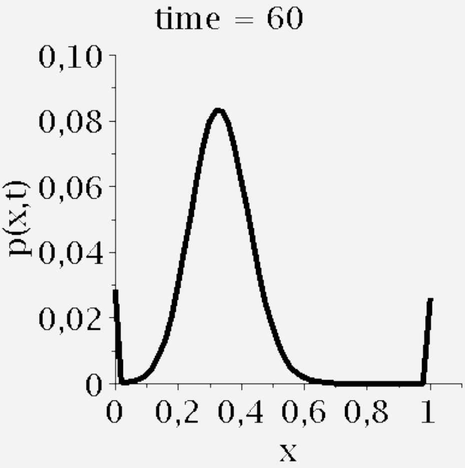

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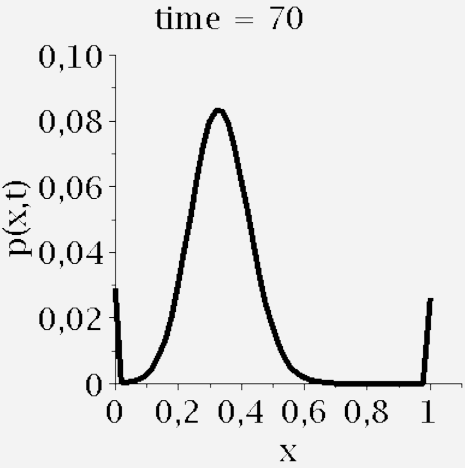

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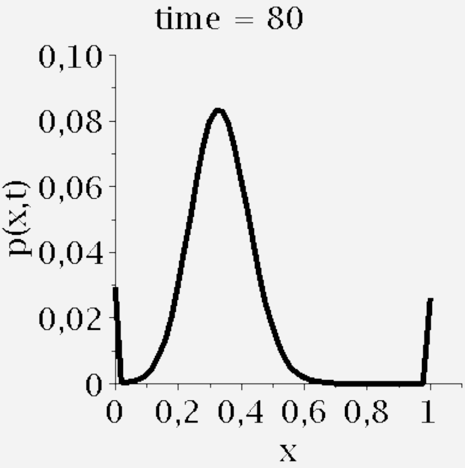

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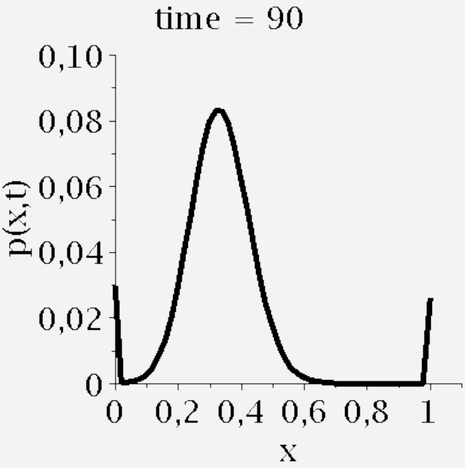

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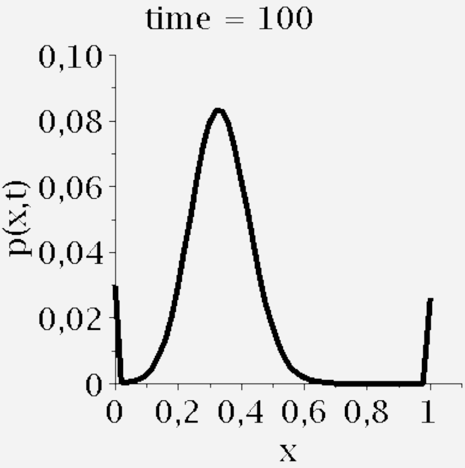

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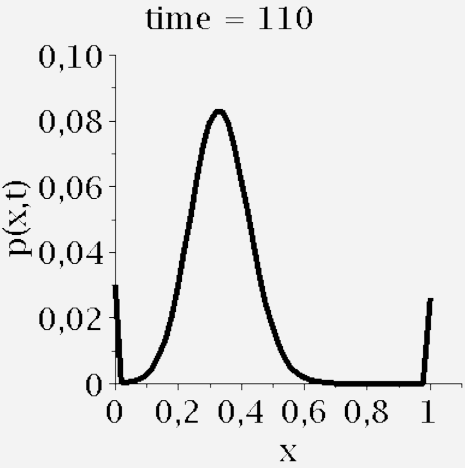

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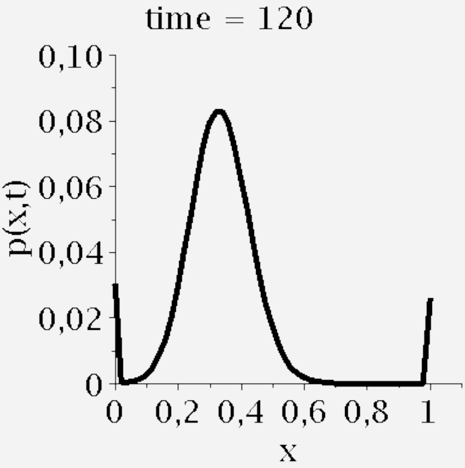

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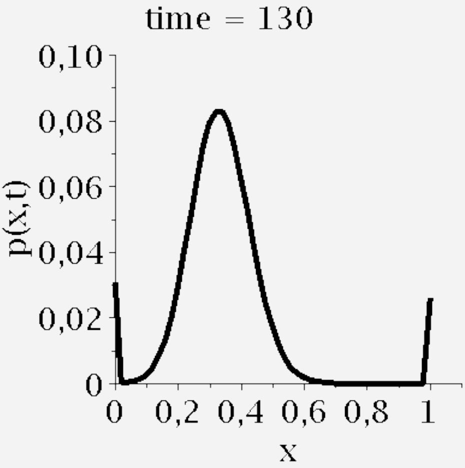

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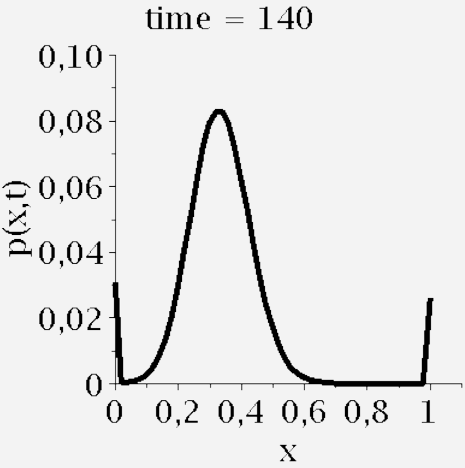

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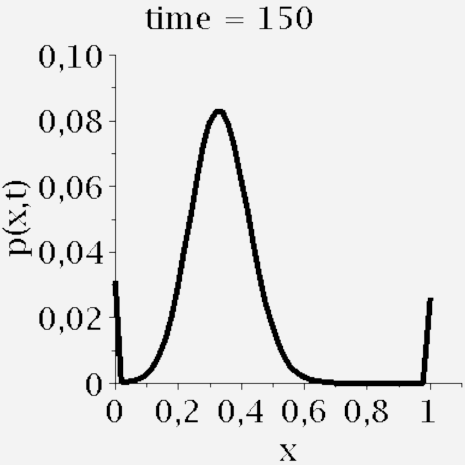

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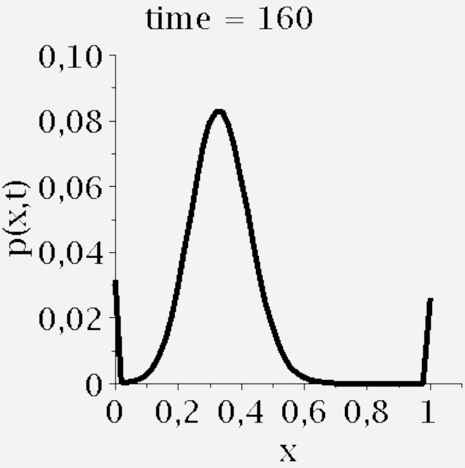

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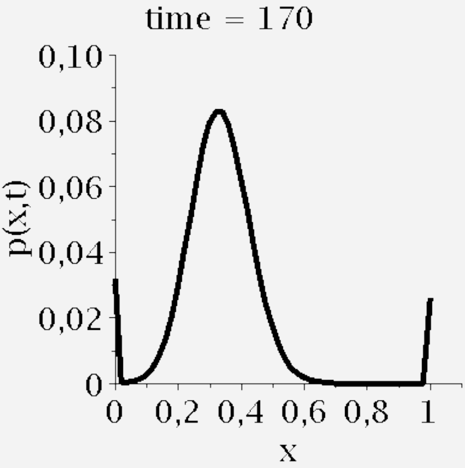

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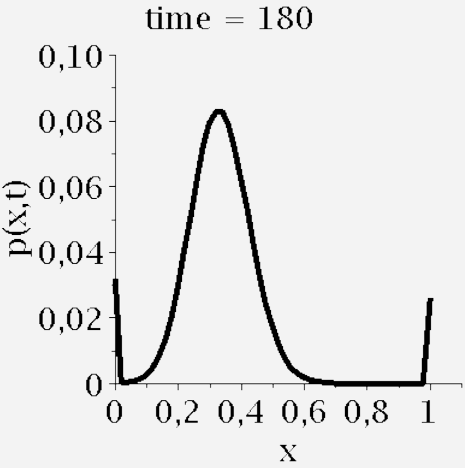

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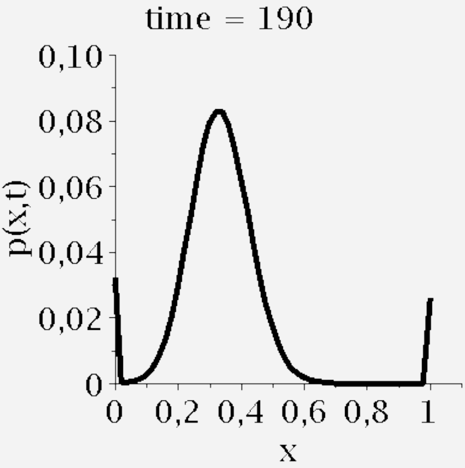

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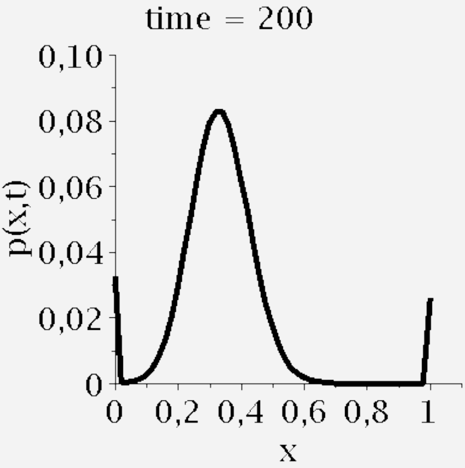

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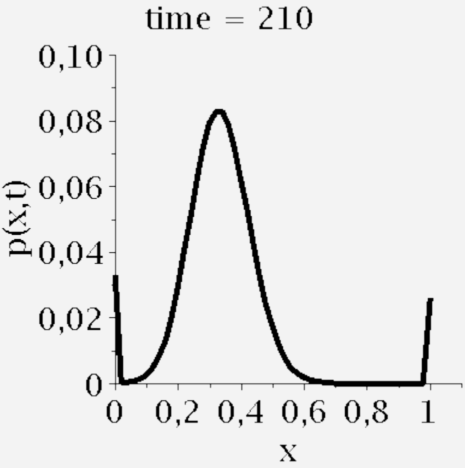

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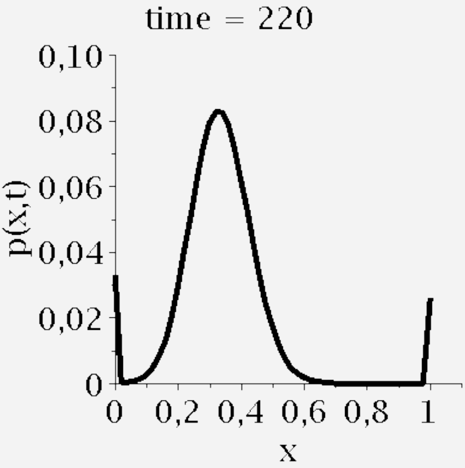

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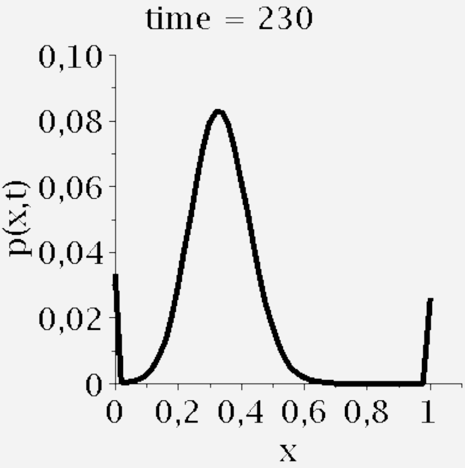

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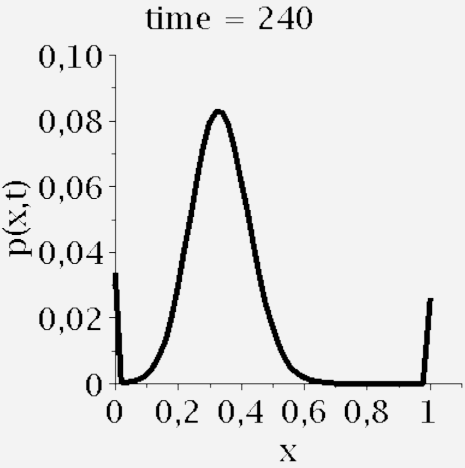

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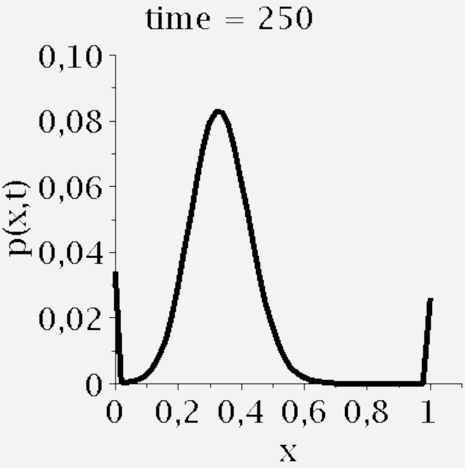

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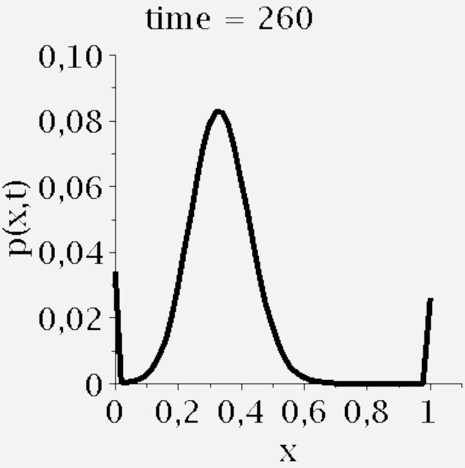

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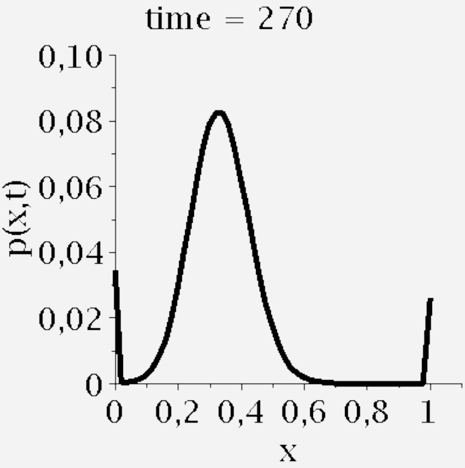

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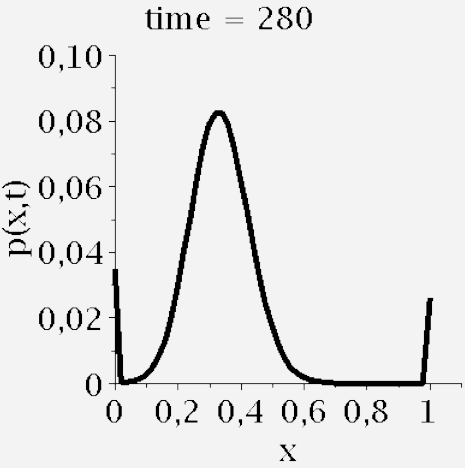

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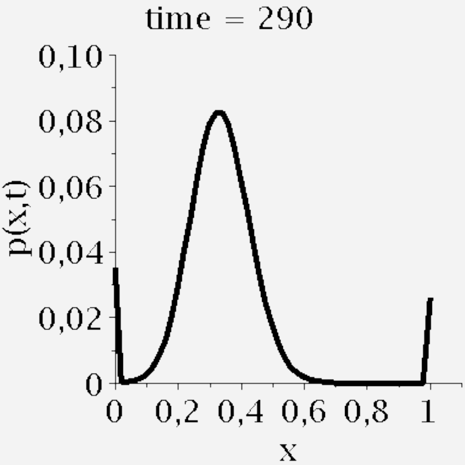

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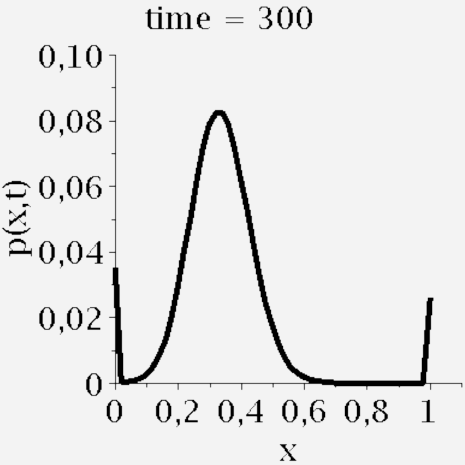

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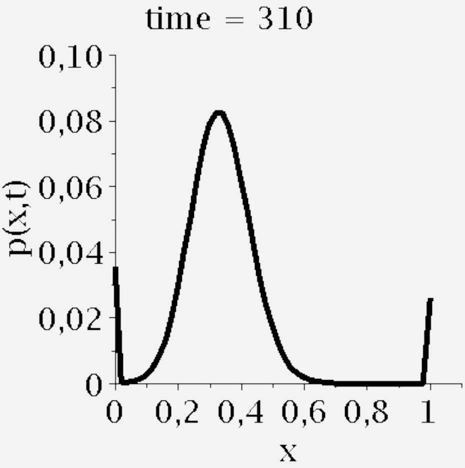

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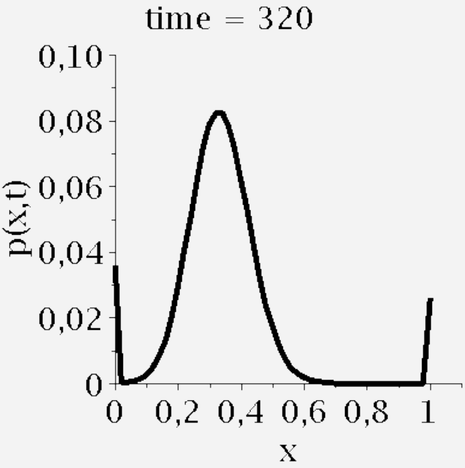

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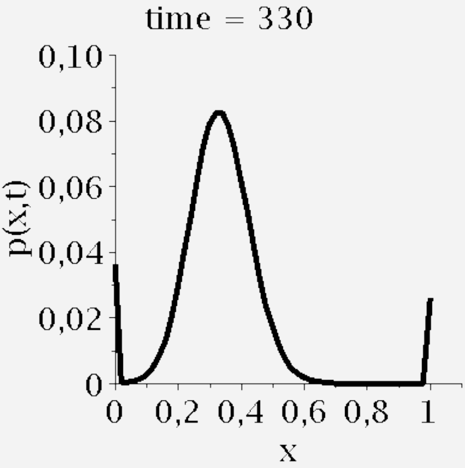

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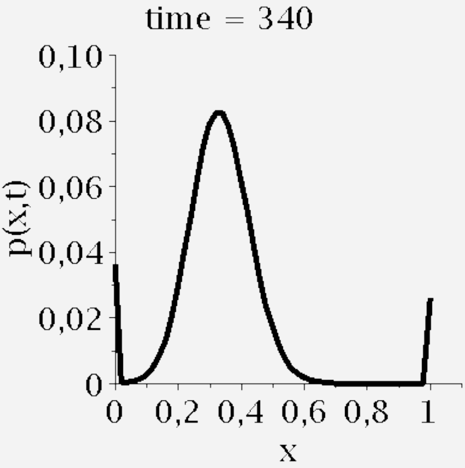

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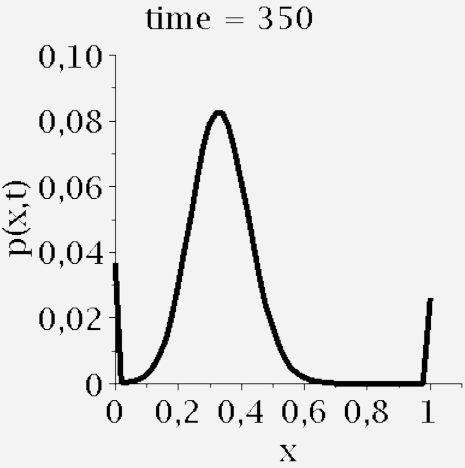

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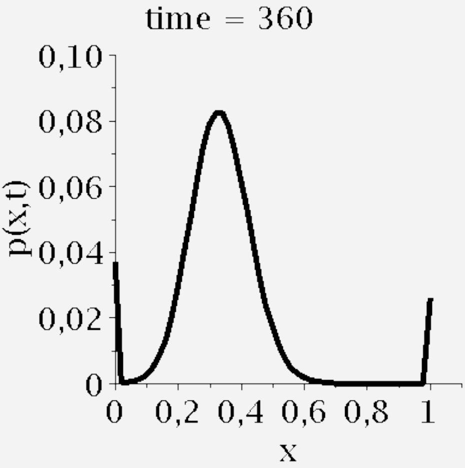

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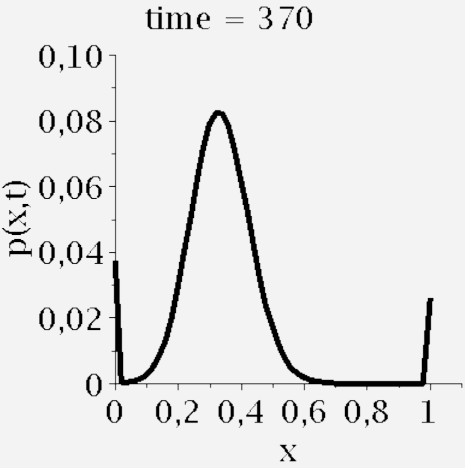

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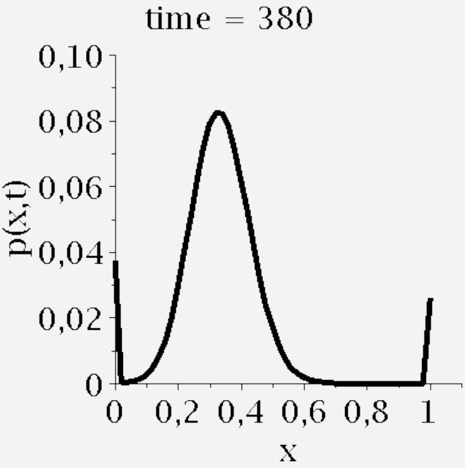

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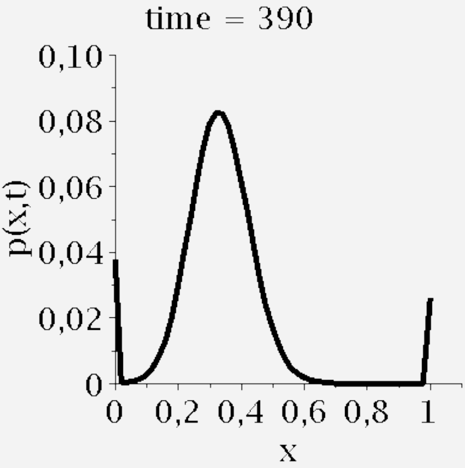

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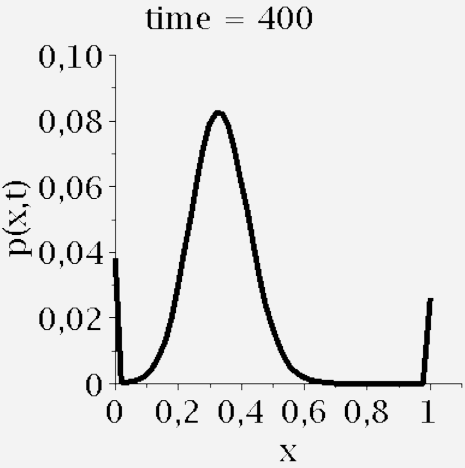

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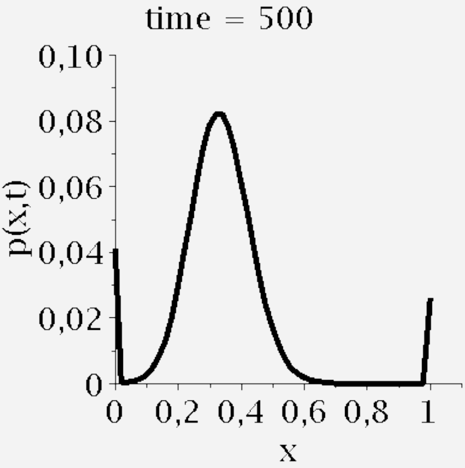

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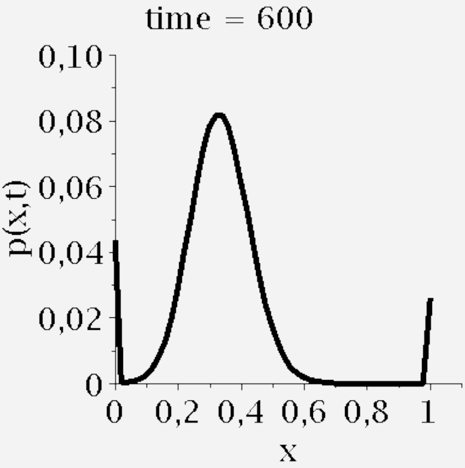

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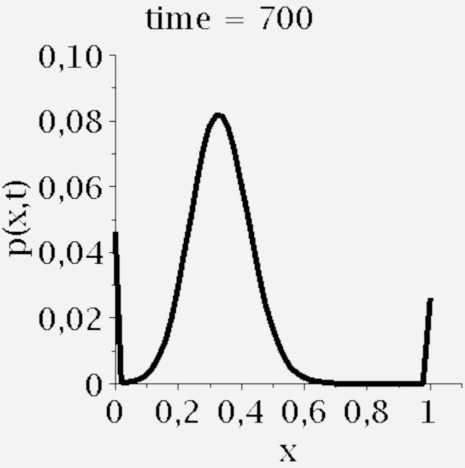

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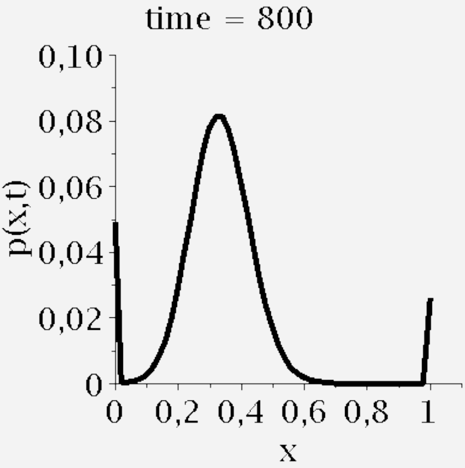

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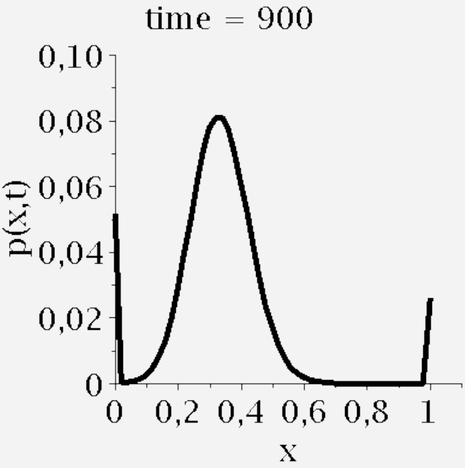

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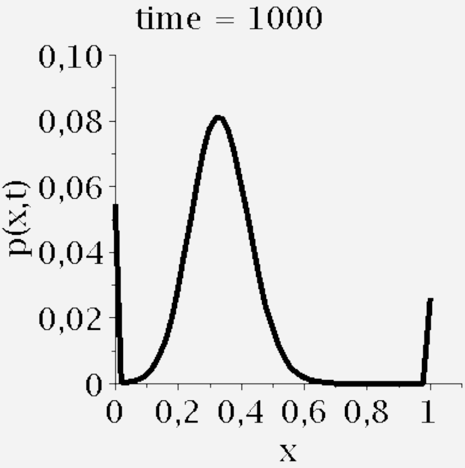

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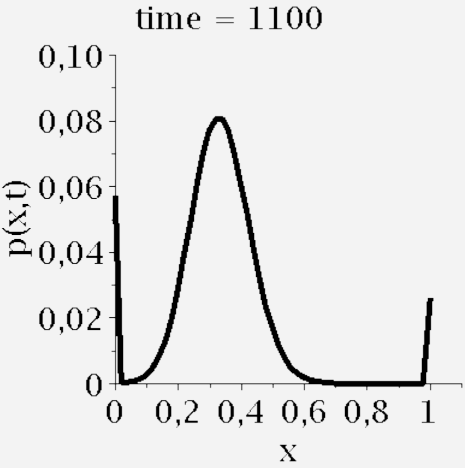

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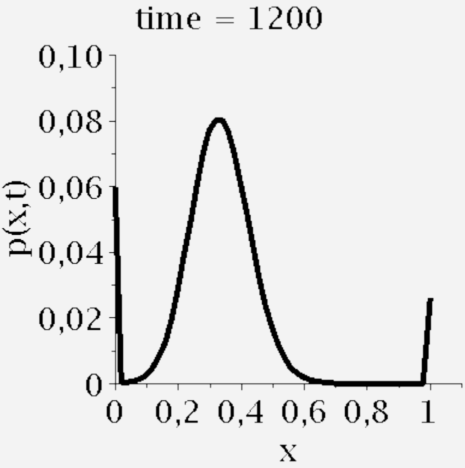

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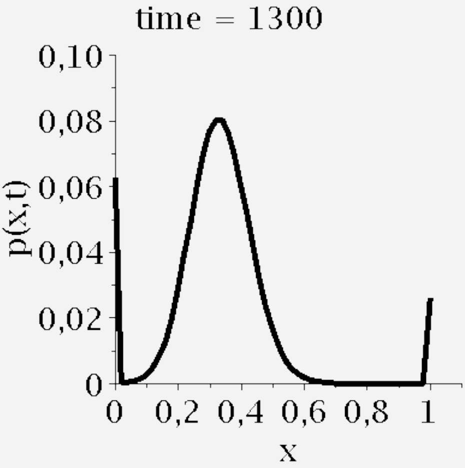

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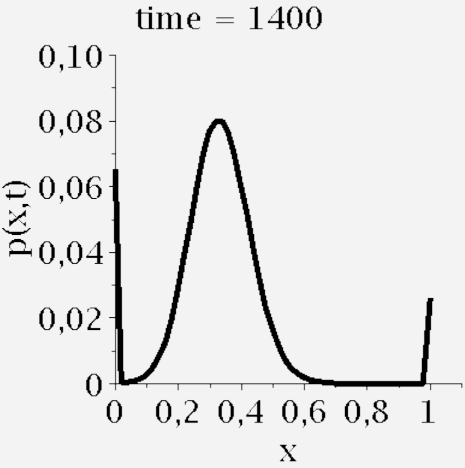

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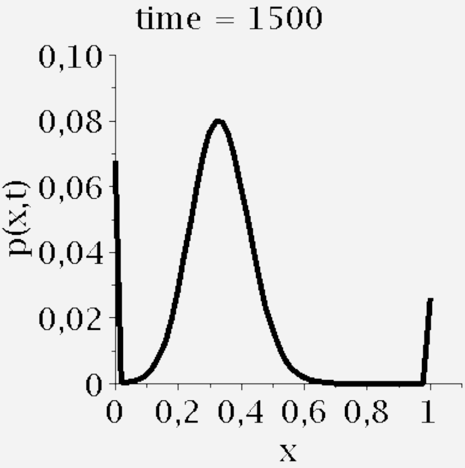

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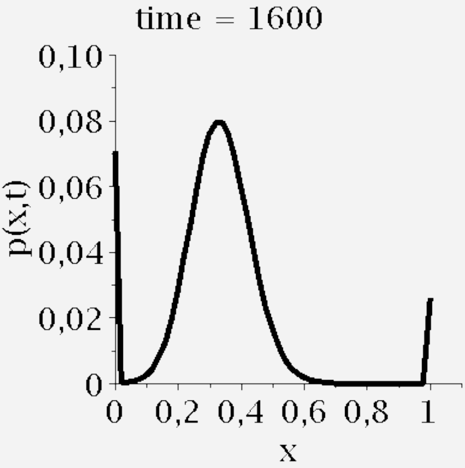

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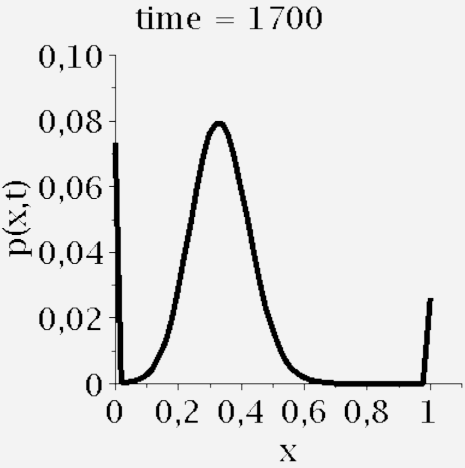

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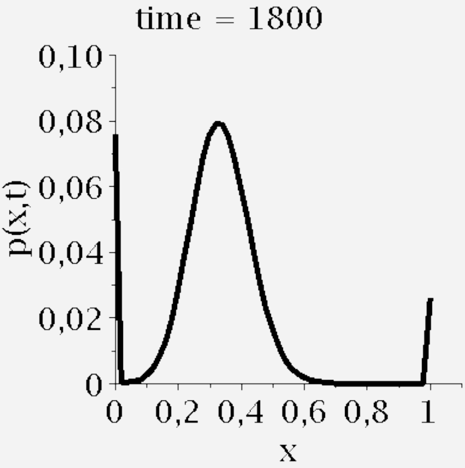

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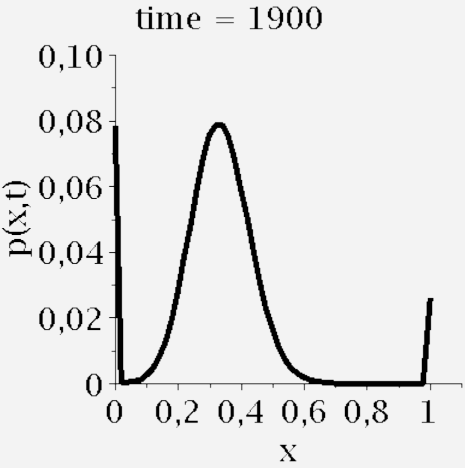

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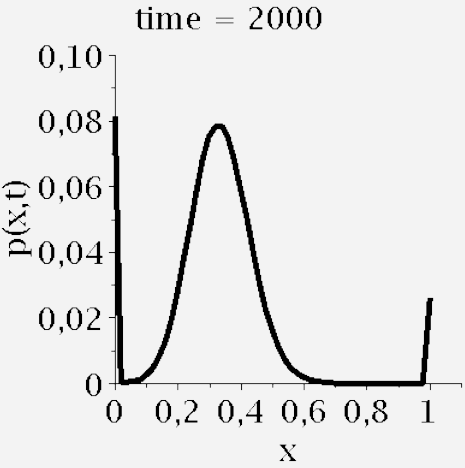

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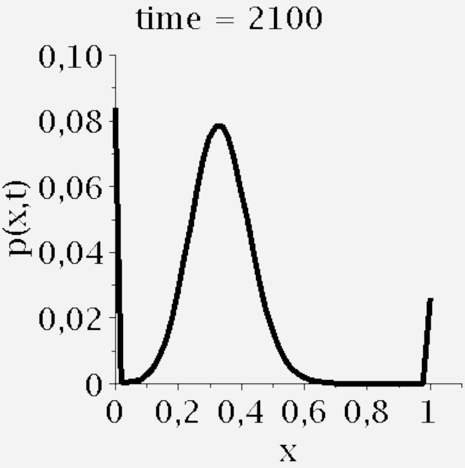

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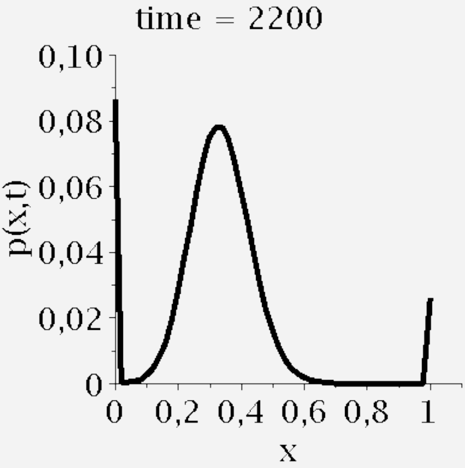

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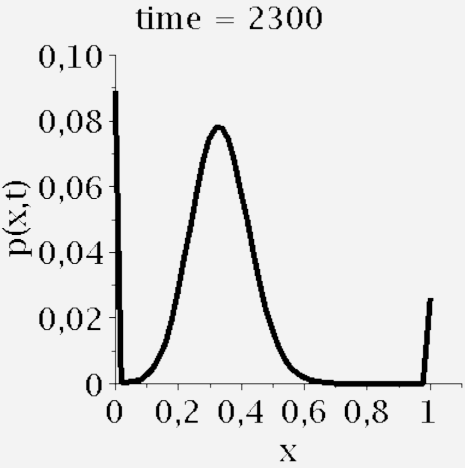

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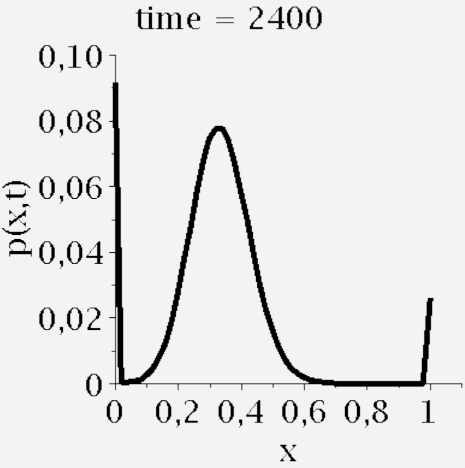

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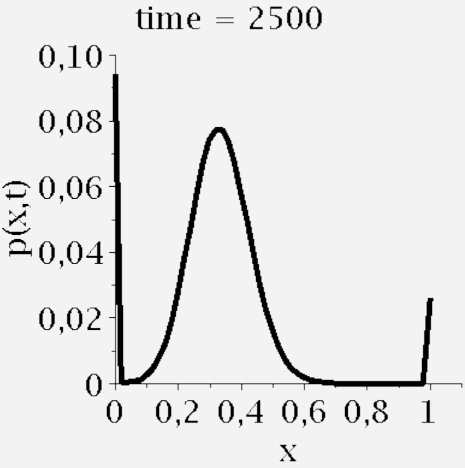

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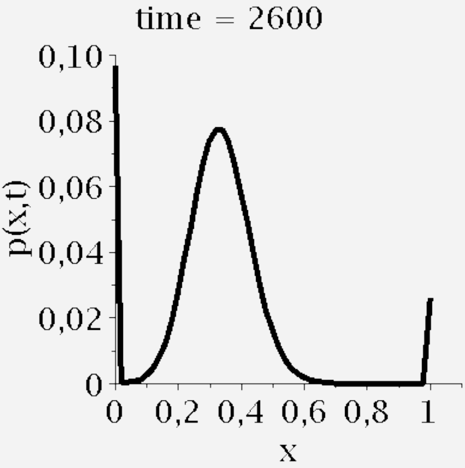

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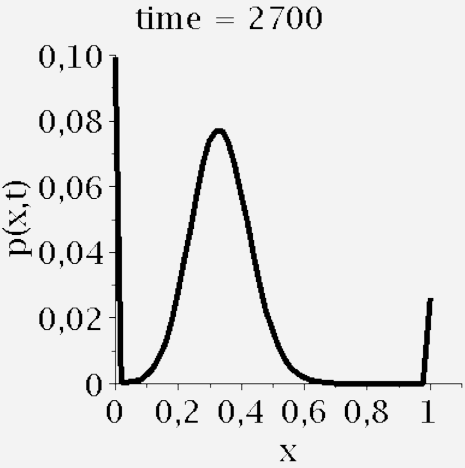

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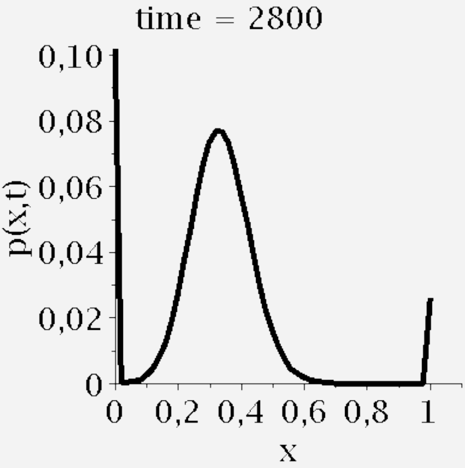

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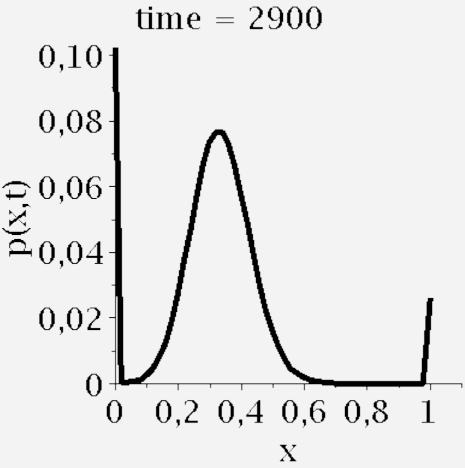

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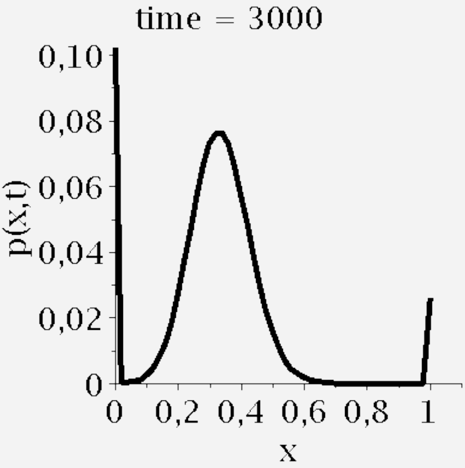

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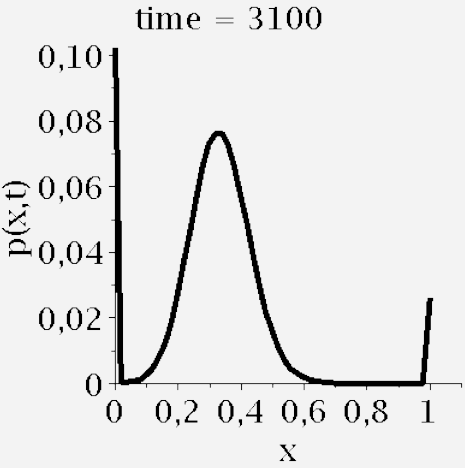

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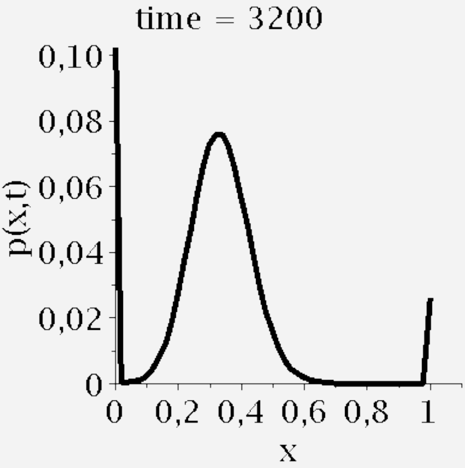

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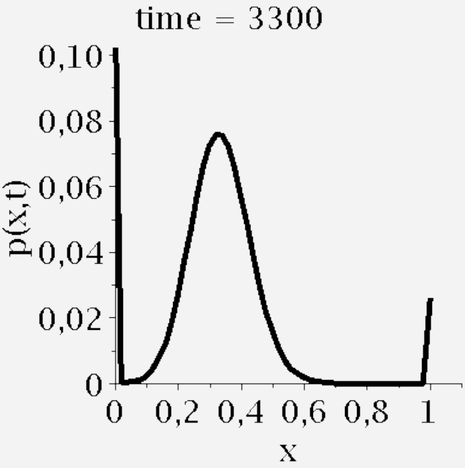

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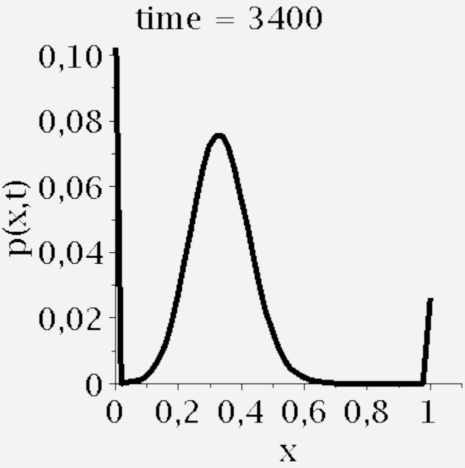

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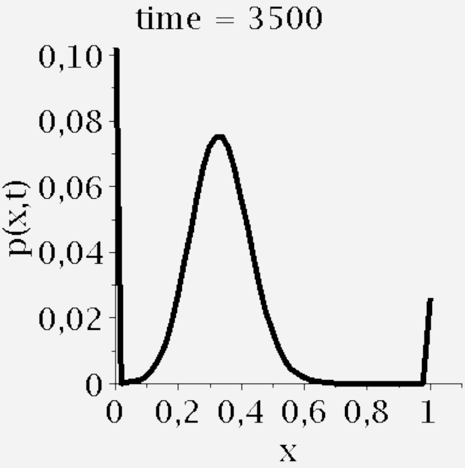

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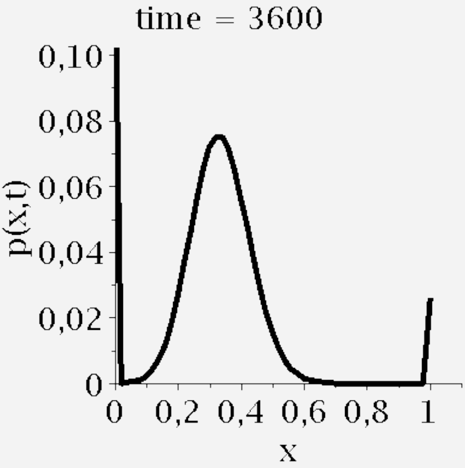

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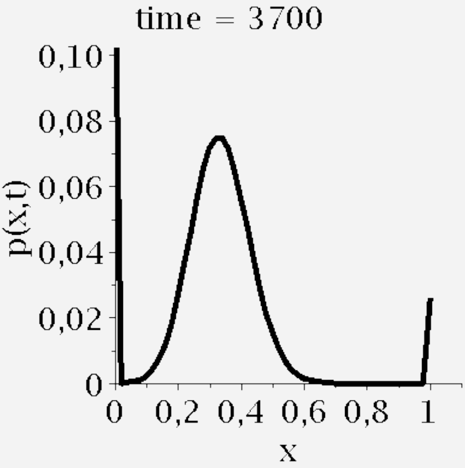

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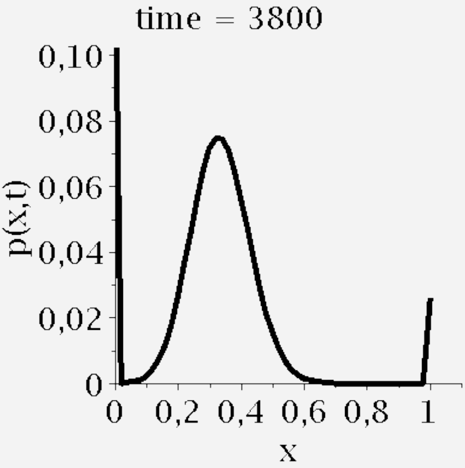

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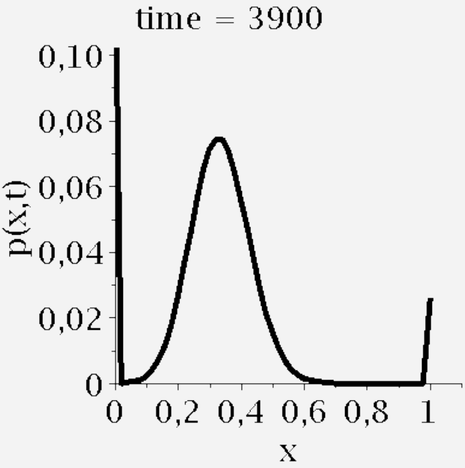

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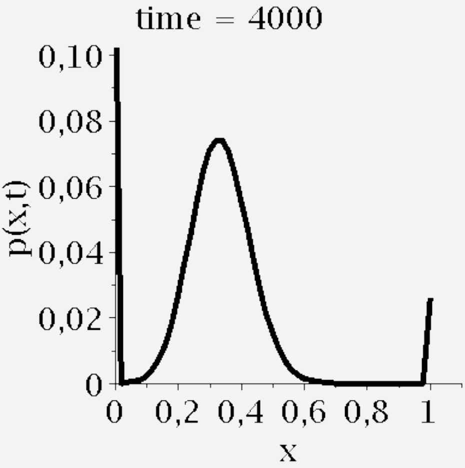

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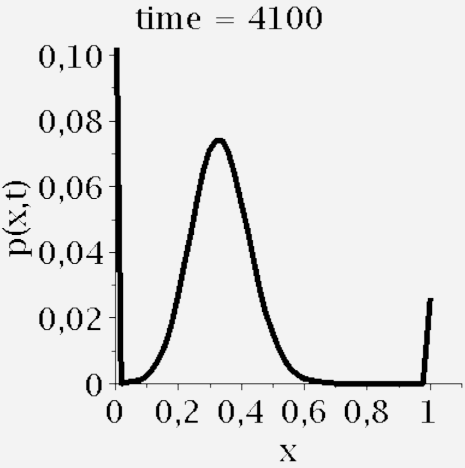

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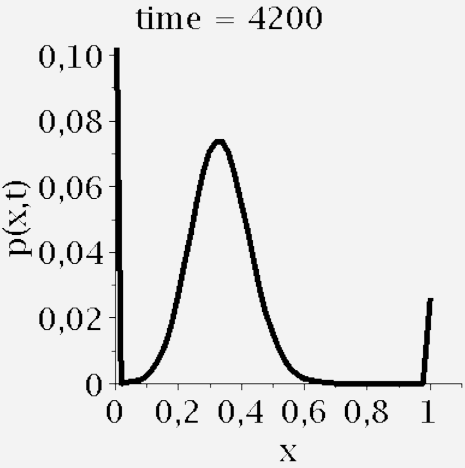

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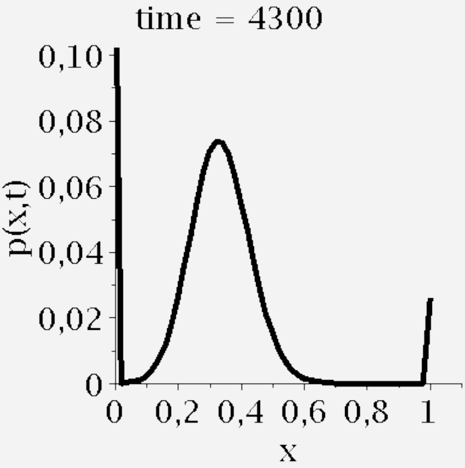

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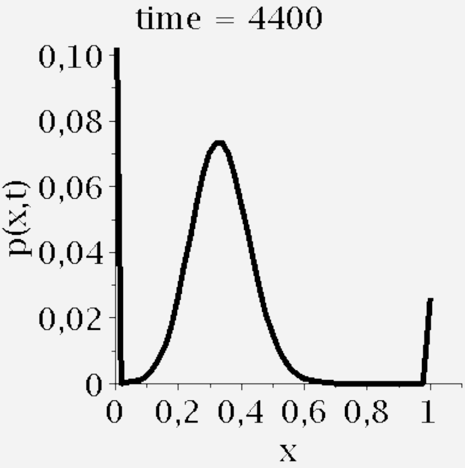

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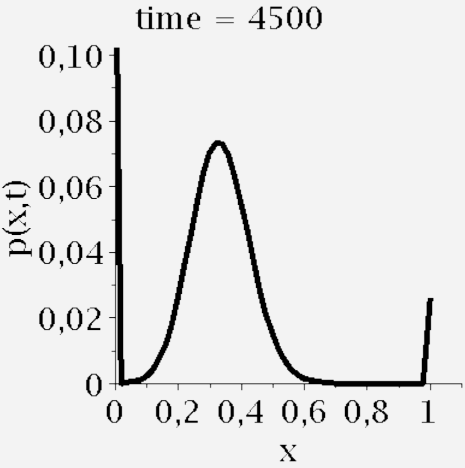

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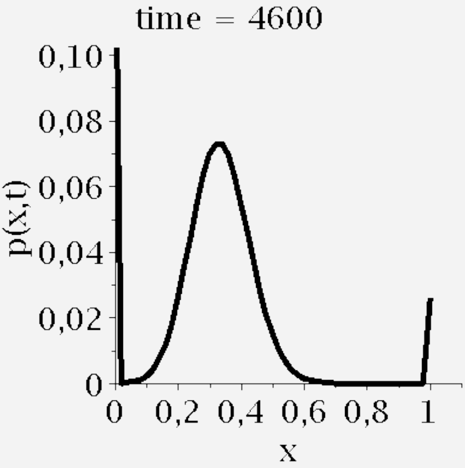

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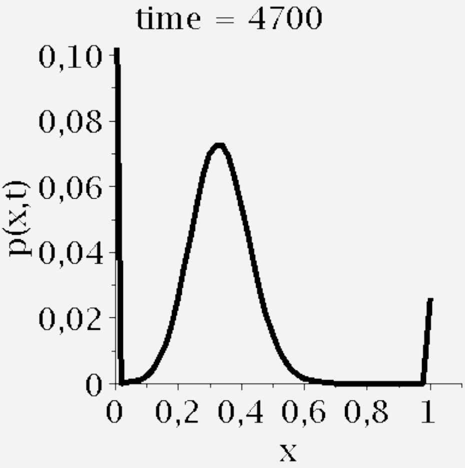

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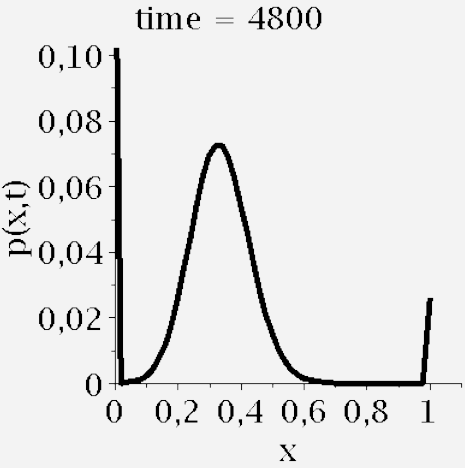

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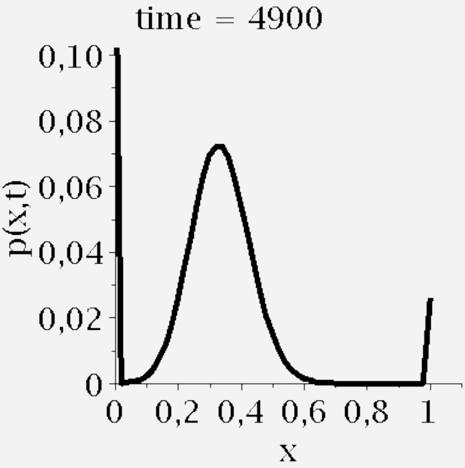

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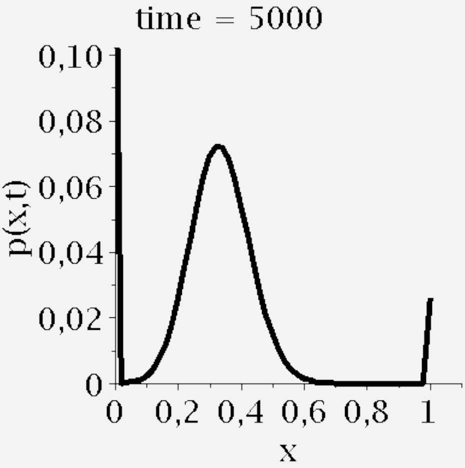

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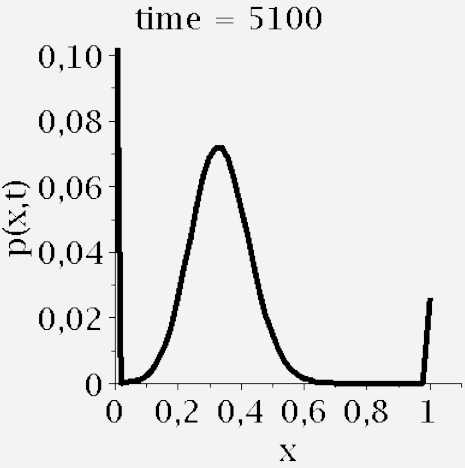

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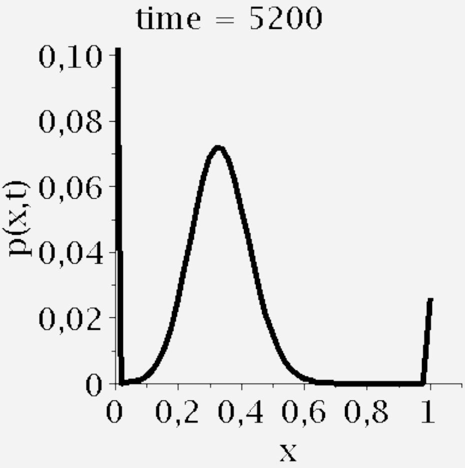

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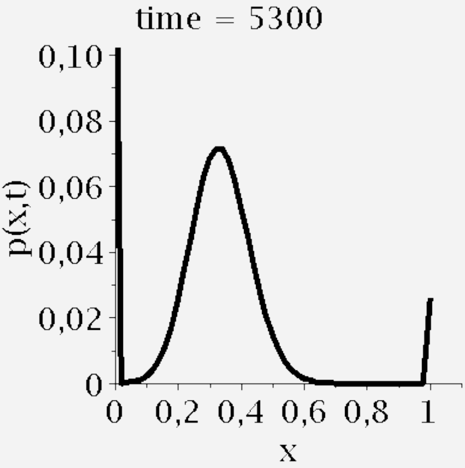

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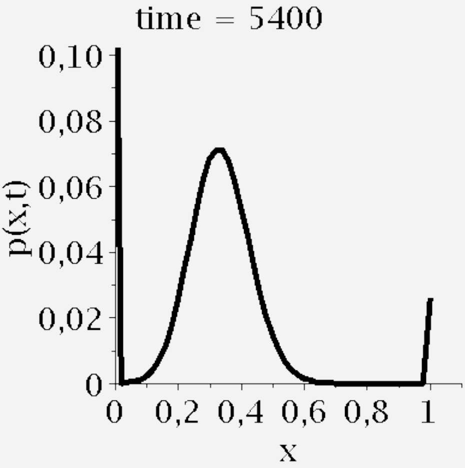

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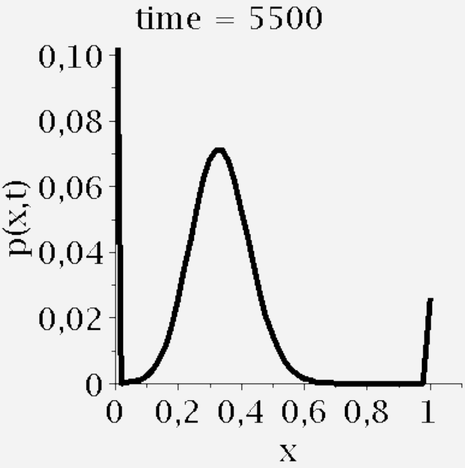

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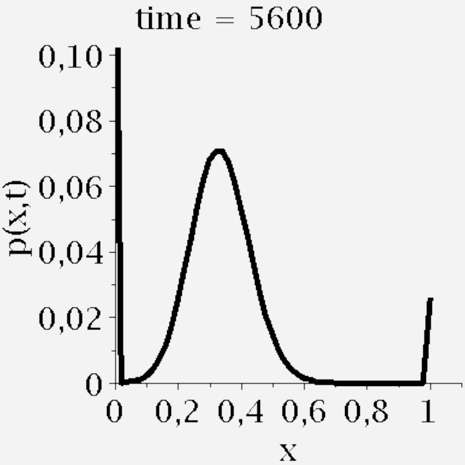

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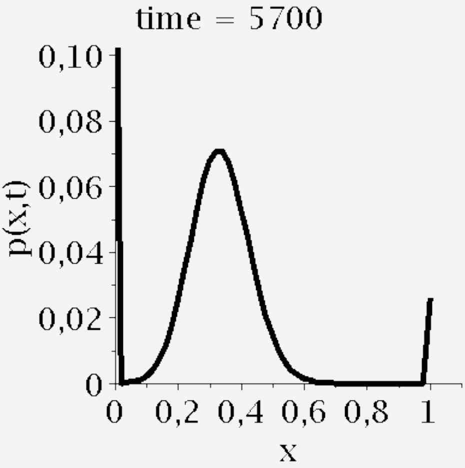

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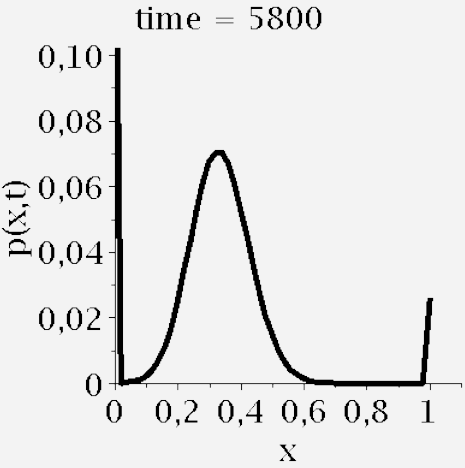

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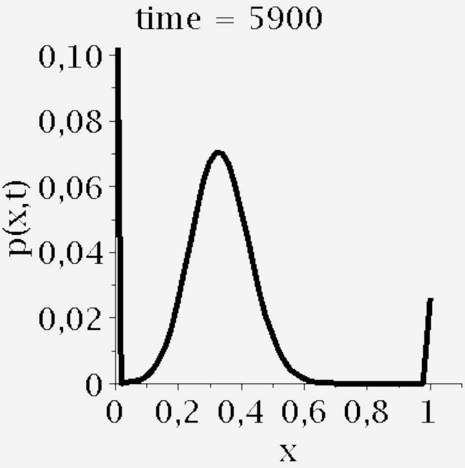

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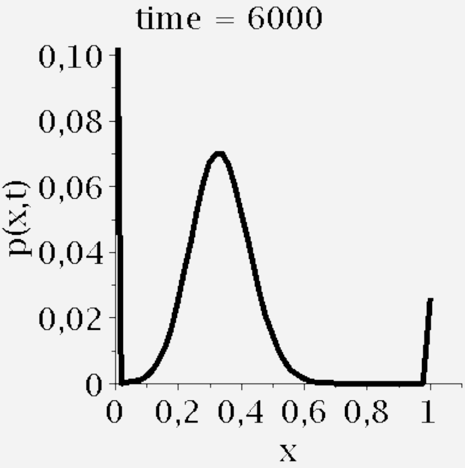

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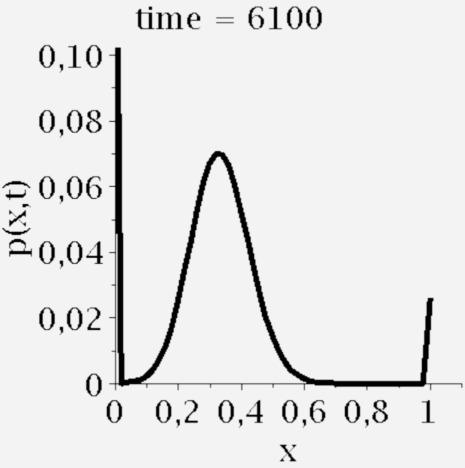

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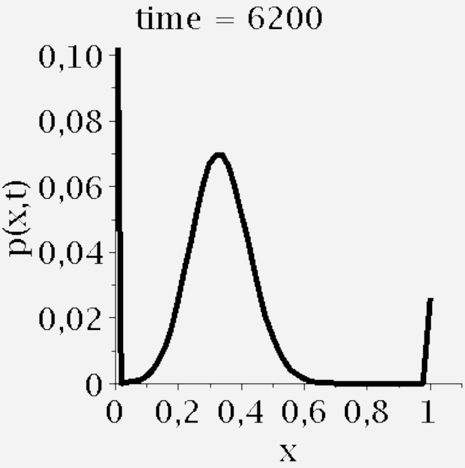

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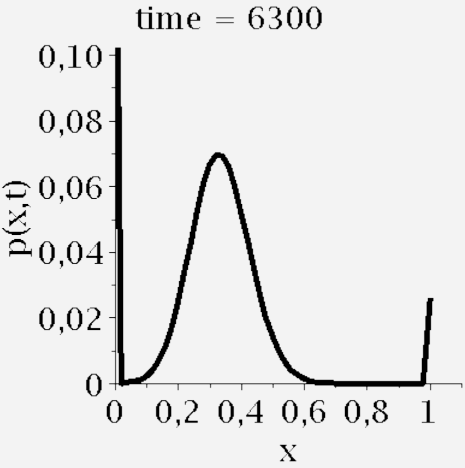

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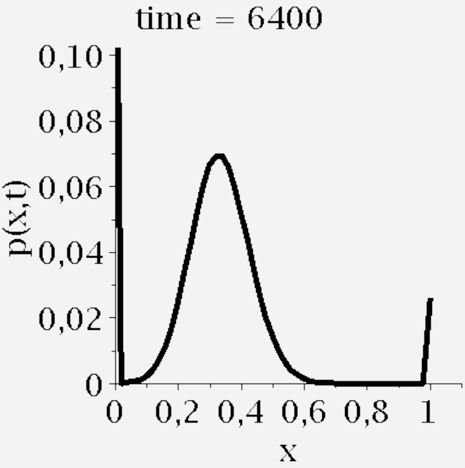

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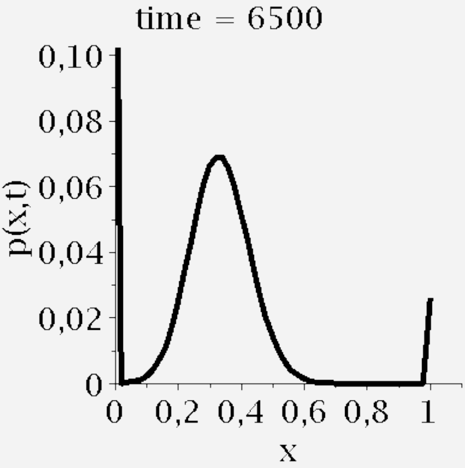

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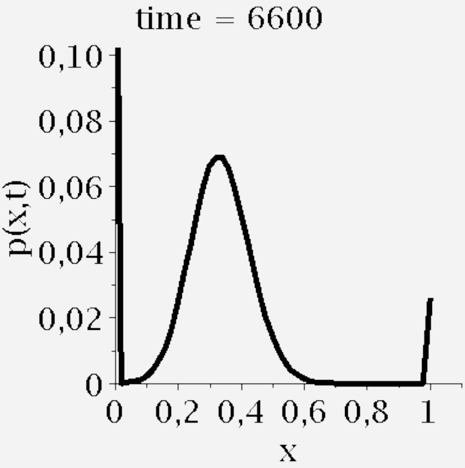

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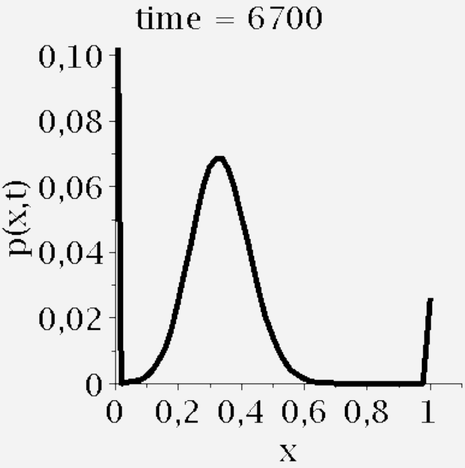

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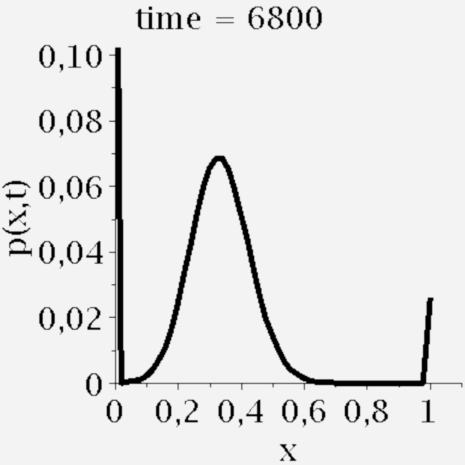

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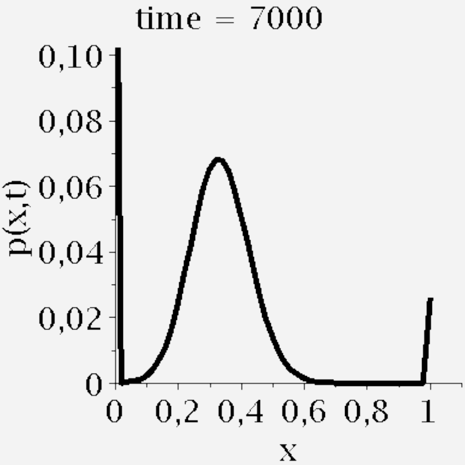

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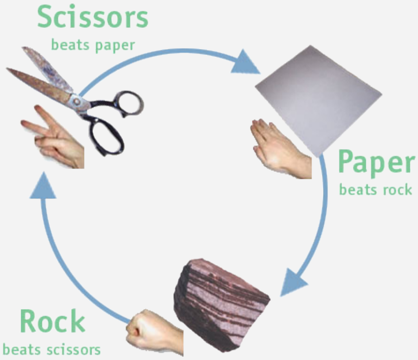
3 thypes Wright-Fisher process

Now, we consider $n = 3$ types and define the *Rock-Scissor-Paper* game:



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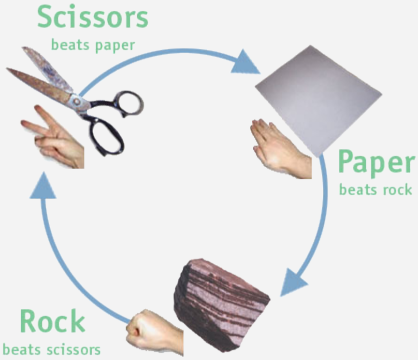

Fitnesses are calculated from the matrix:

	Rock	Scissor	Paper
Rock	30	81	29
Scissor	6	30	104
Paper	106	4	30

$$\Psi^{(\mathbb{A})}(x) = 30x + 81y + 29z\ ,$$

$$\Psi^{(\mathbb{B})}(x) = 6x + 30y + 104z\ ,$$

$$\Psi^{(\mathbb{C})}(x) = 106x + 4y + 30z\ .$$

3 types Wright-Fisher process

The replicator dynamics is given by:

$$\dot{x} = x(-74x + 4y - 1 + 75x^2 + 96xy + 48y^2) \ ,$$
$$\dot{y} = y(-173x - 122y + 74 + 75x^2 + 96xy + 48y^2) \ ,$$

where $x \geq 0$ is the frequency of type 1, $y \geq 0$ of type 2 and $z = 1 - x - y \geq 0$ (i.e., $x + y \leq 1$) of type 3.

3 types Wright-Fisher process

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The only stationary solutions are:

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1. $(x, y) = (0, 0)$, everybody is of type 3;

3 types Wright-Fisher process

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3 types Wright-Fisher process

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3 types Wright-Fisher process

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The only stationary solutions are:

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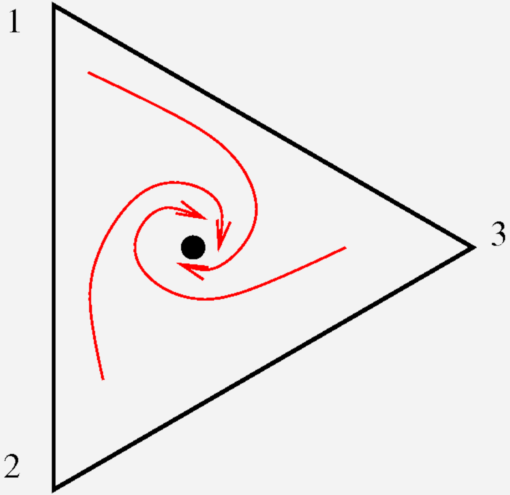
2. $(x, y) = (0, 1)$, everybody is of type 2;
3. $(x, y) = (1, 0)$, everybody is of type 1;
4. $(x, y) = \left(\frac{1}{3}, \frac{1}{3}\right)$, a mixed population.

3 types Wright-Fisher process

The flow of the replicator dynamics is given by:



3 types Wright-Fisher process

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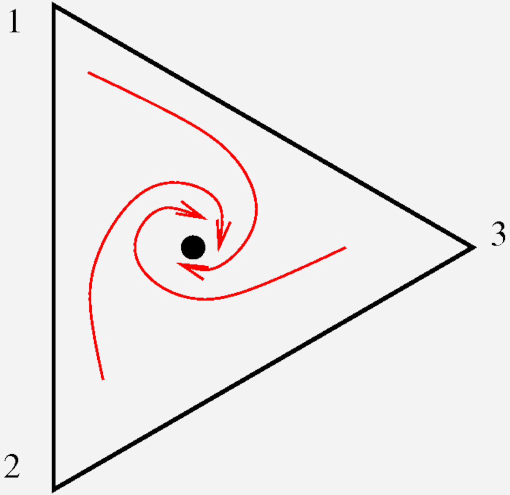
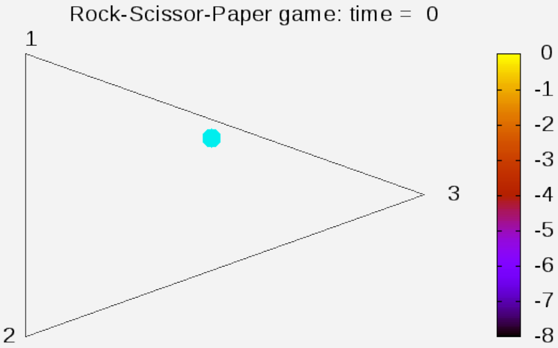


The vertexes of the simplex are unstable stationary points, while the center of the simplex is the only stable stationary point of the replicator dynamics.

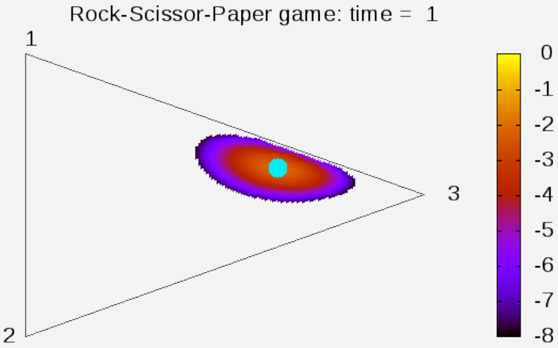
3 types Wright-Fisher process



Simulation for $N = 150$ and the pay-off matrix given by $\begin{pmatrix} 30 & 81 & 29 \\ 6 & 30 & 104 \\ 106 & 4 & 30 \end{pmatrix}$.

The green spot denotes the average and the cyan spot the interior peak.

3 types Wright-Fisher process



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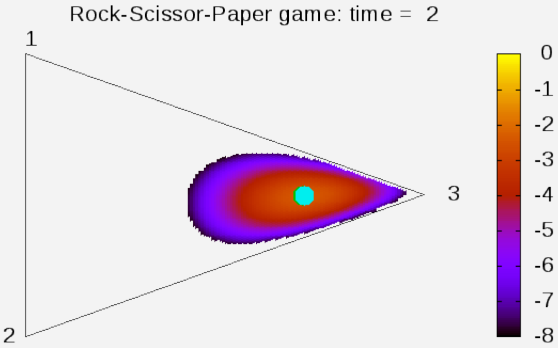

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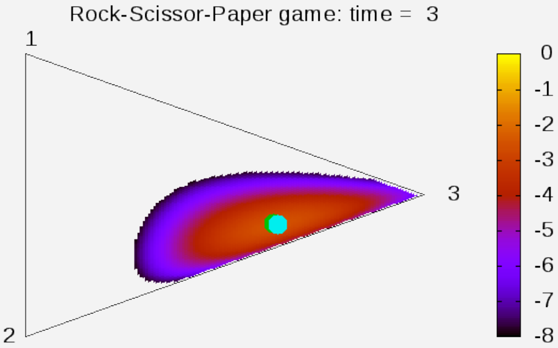

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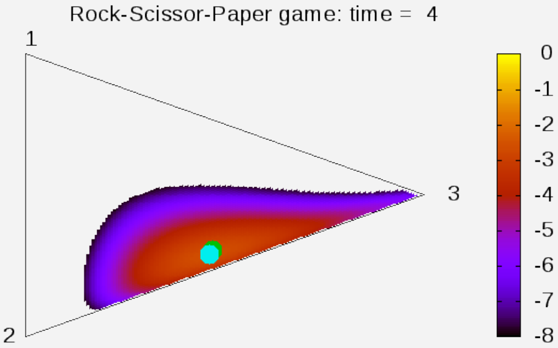

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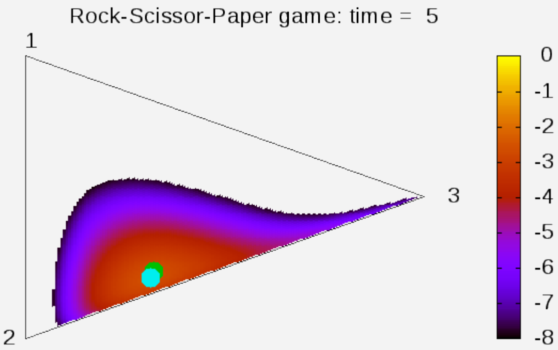

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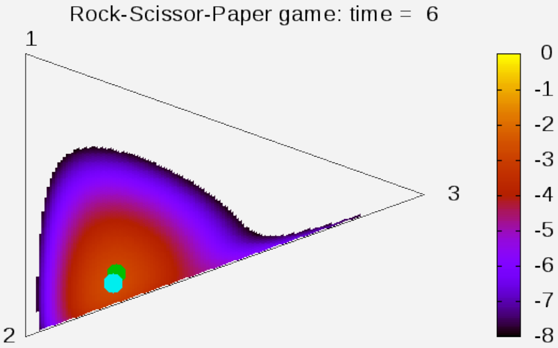

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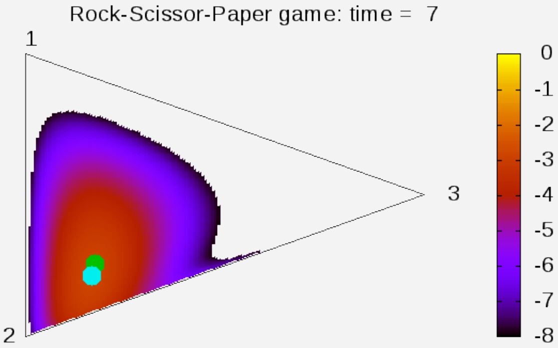

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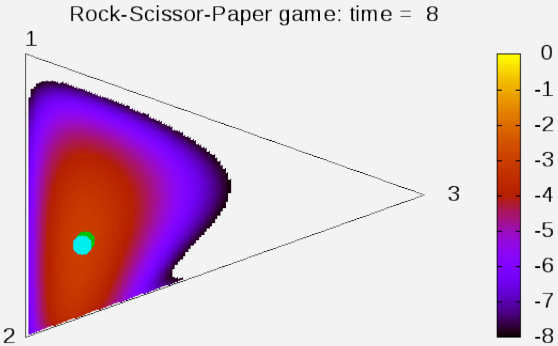

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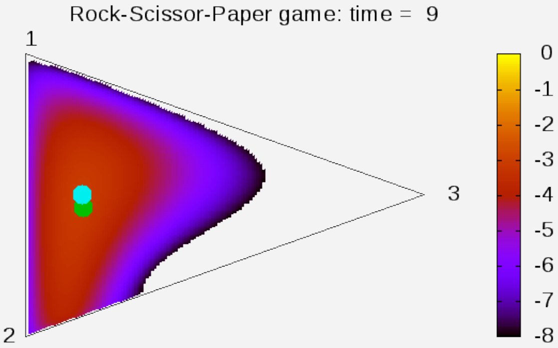

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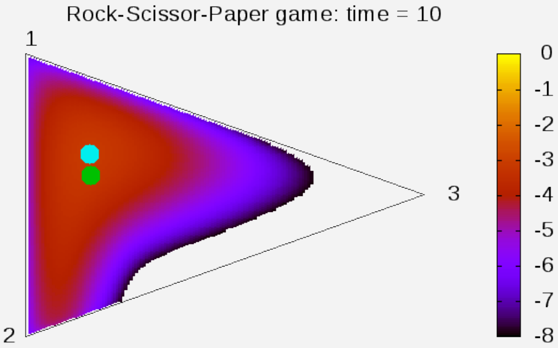

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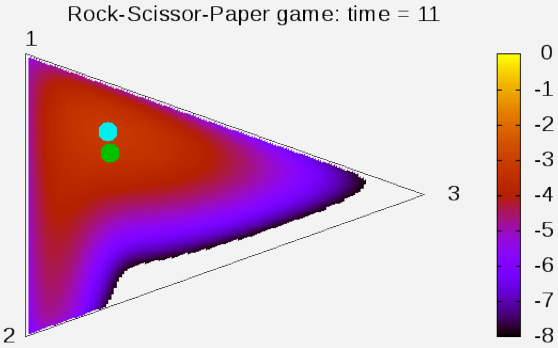

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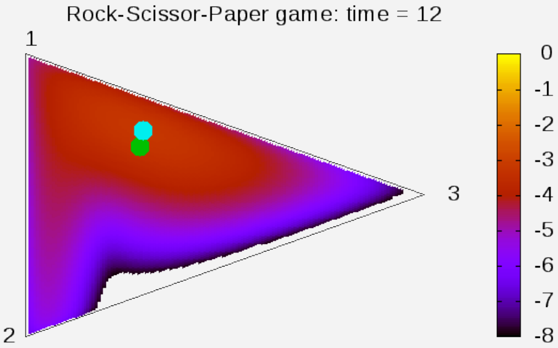

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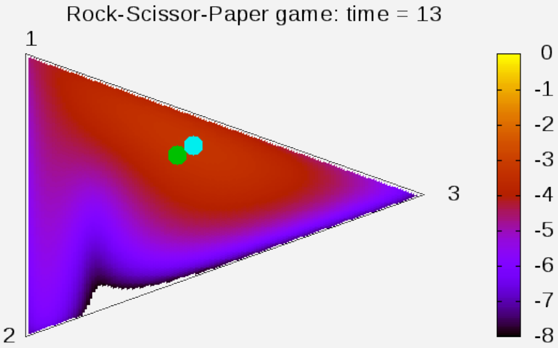

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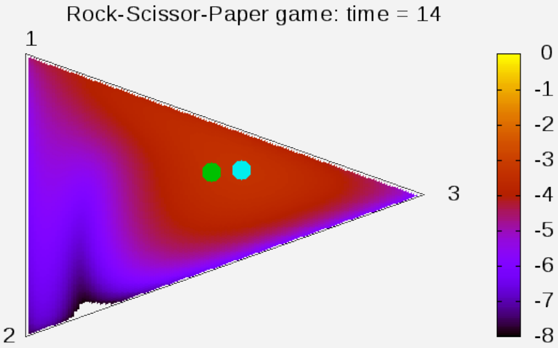

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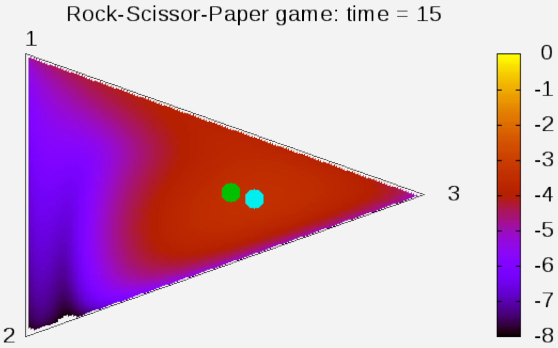

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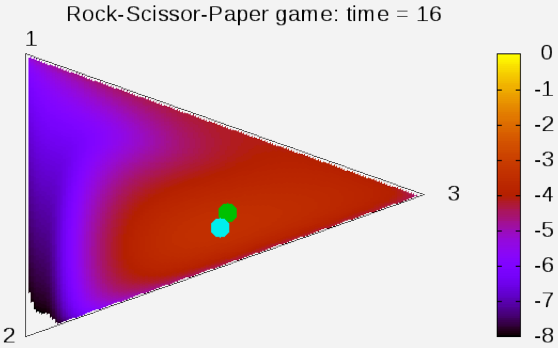

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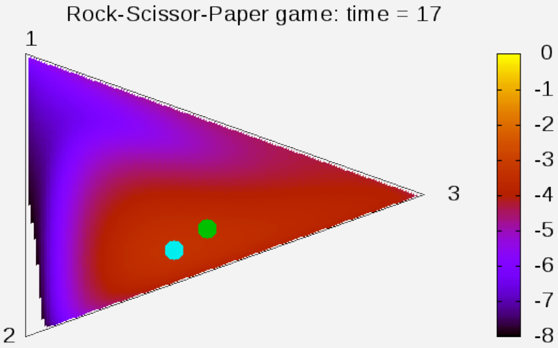

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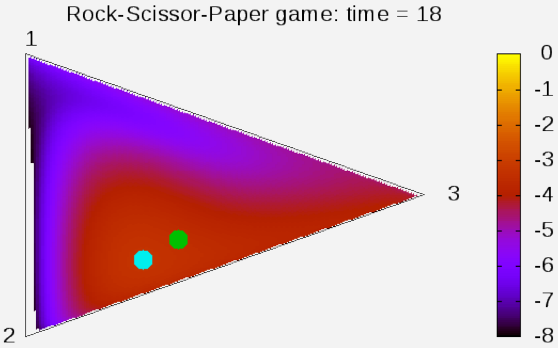

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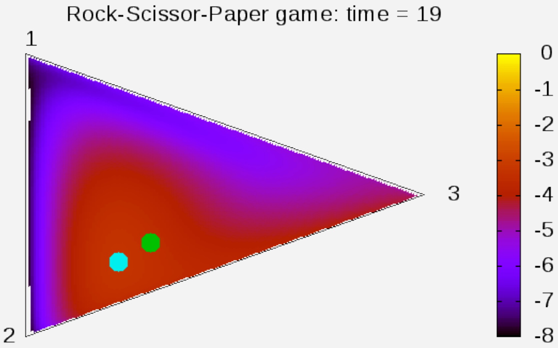

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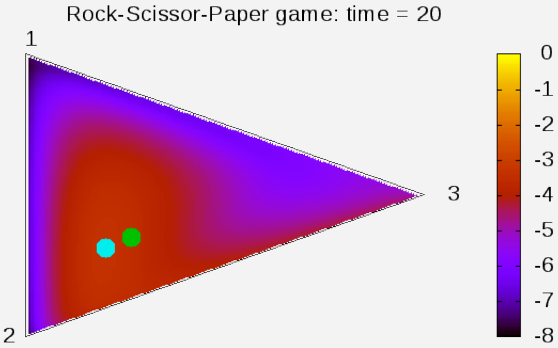

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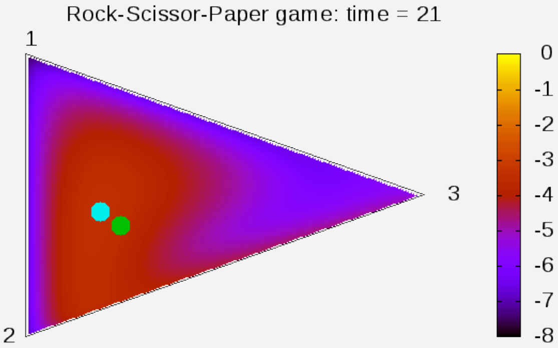

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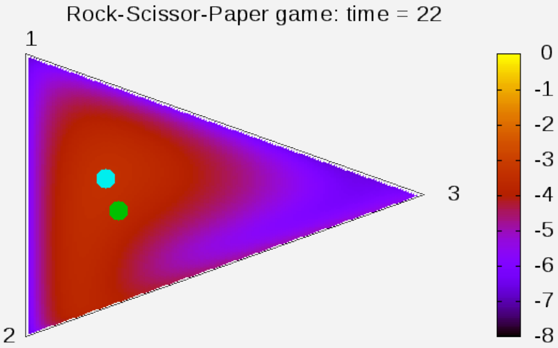

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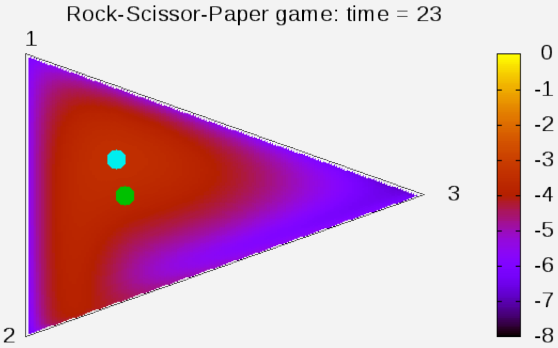

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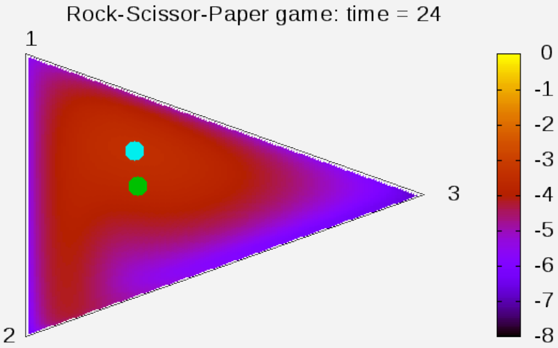

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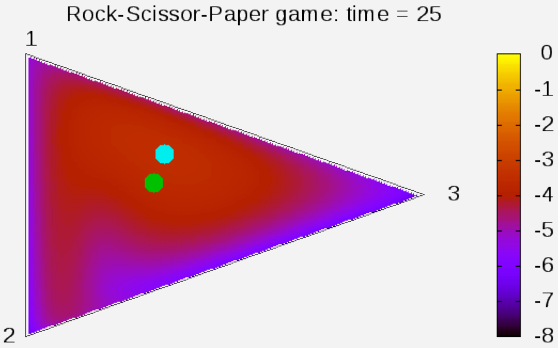

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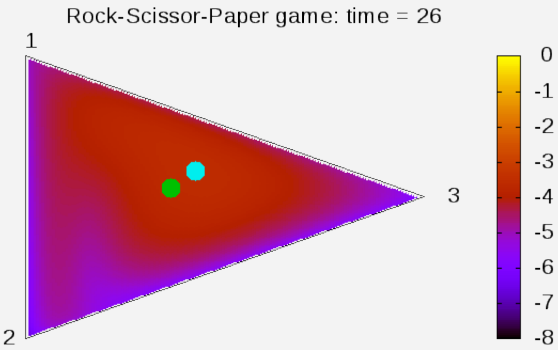

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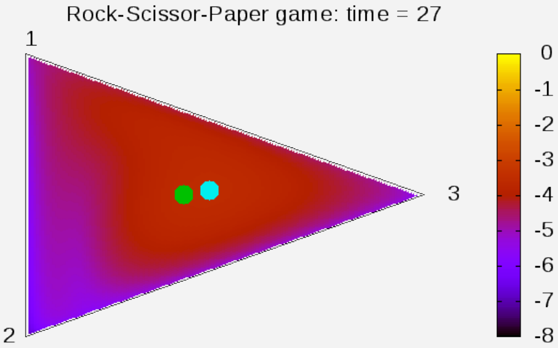

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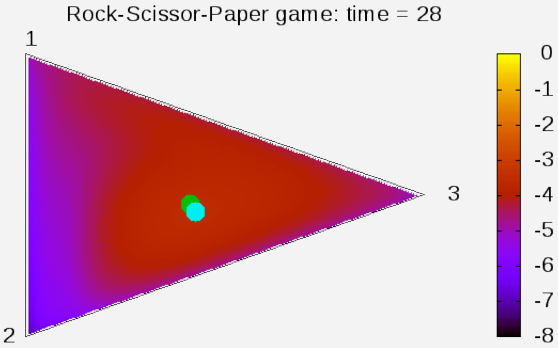

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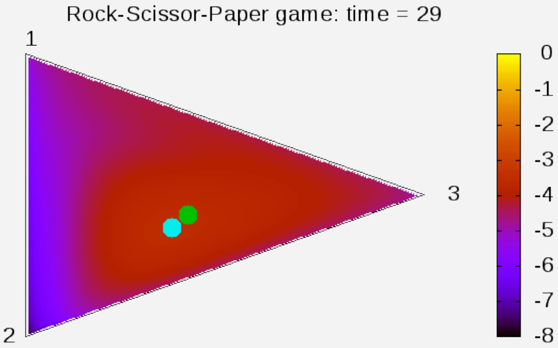

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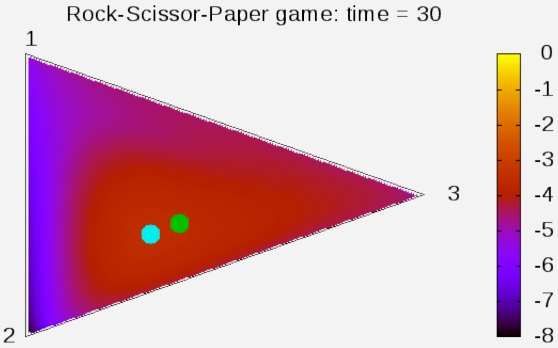

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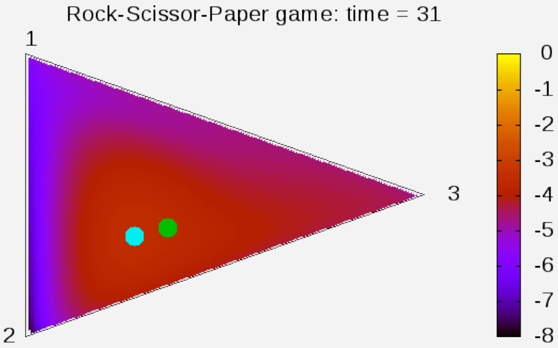

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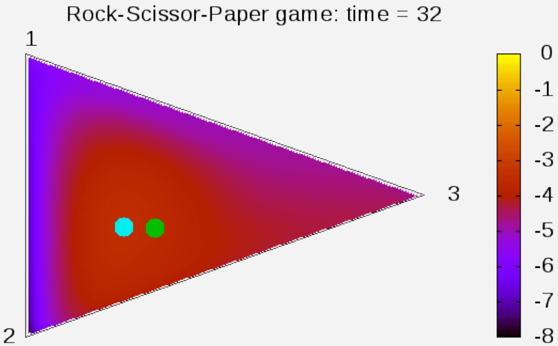

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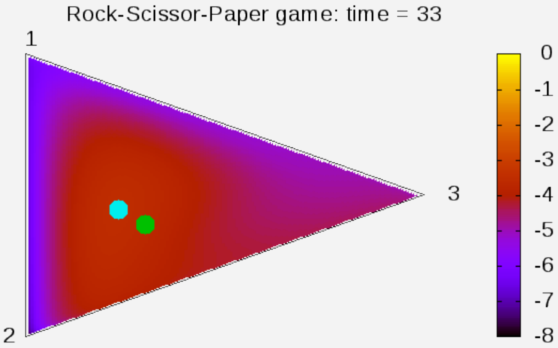

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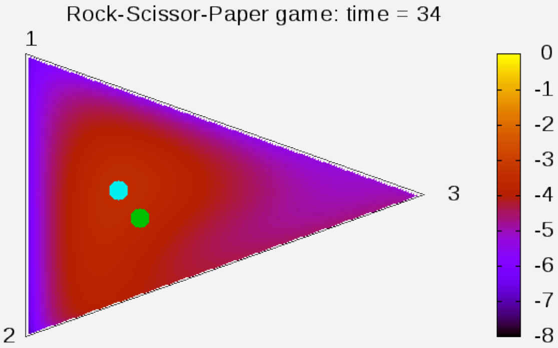

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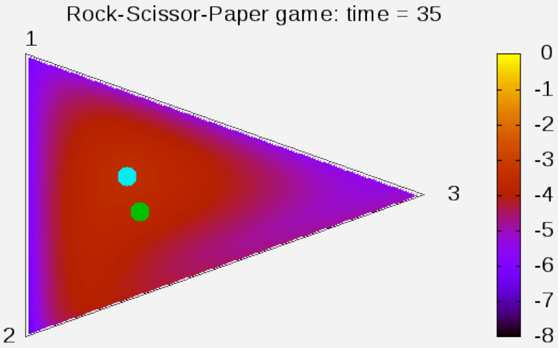

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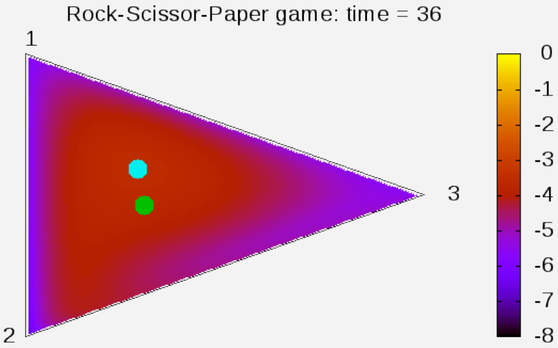

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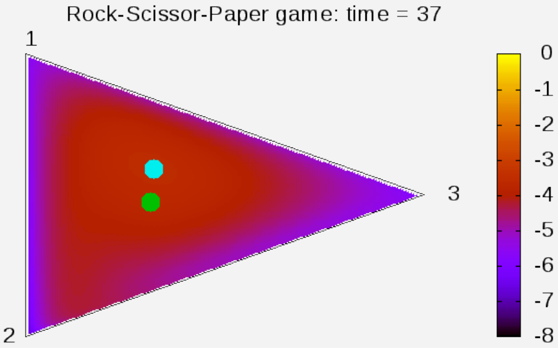

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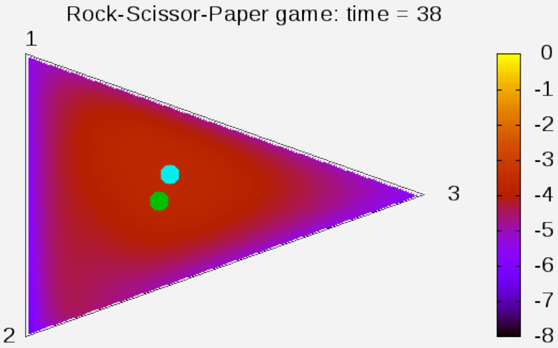

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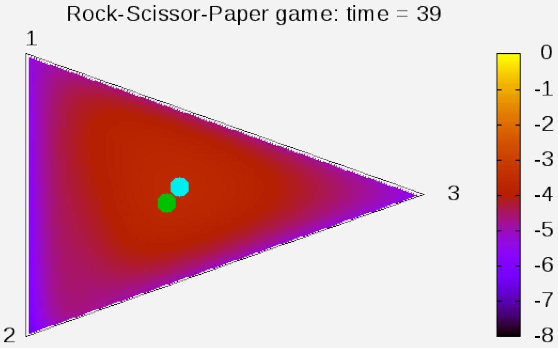

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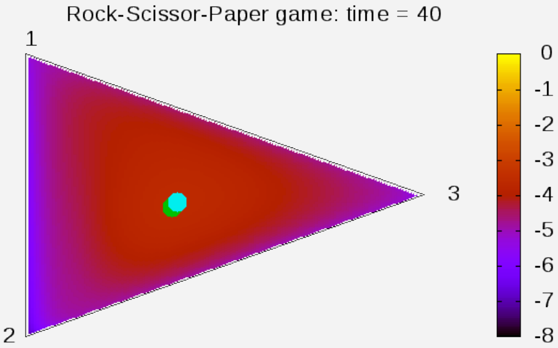

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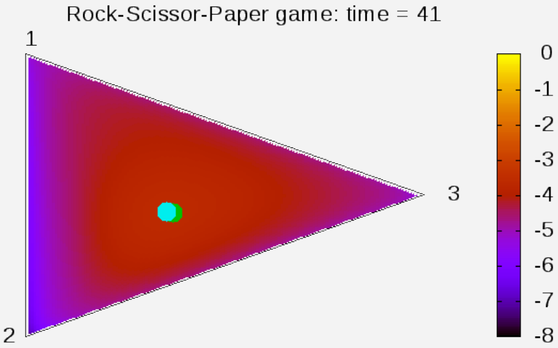

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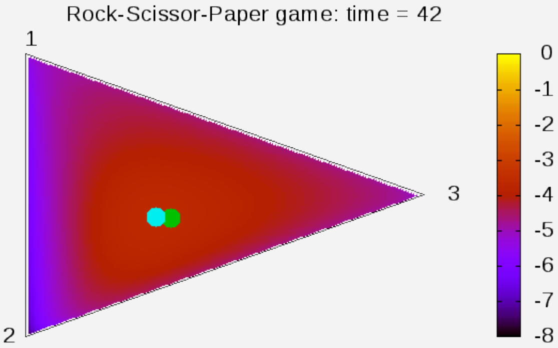

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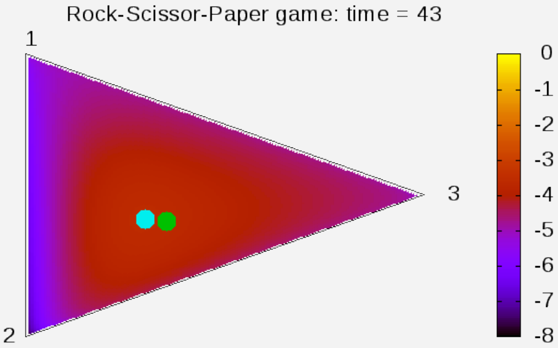

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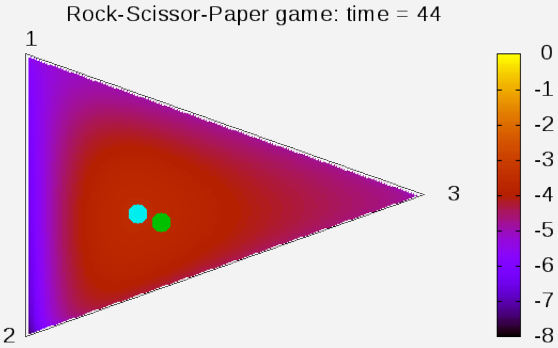

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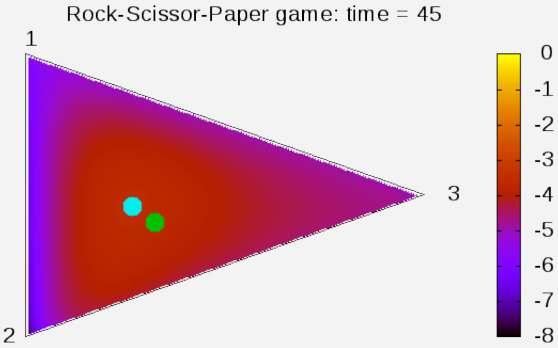

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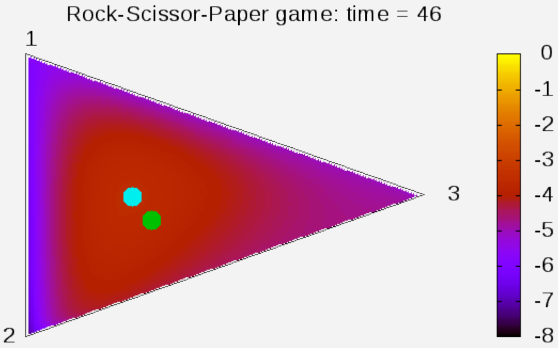

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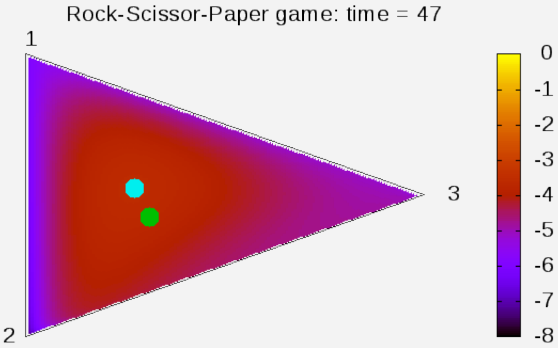

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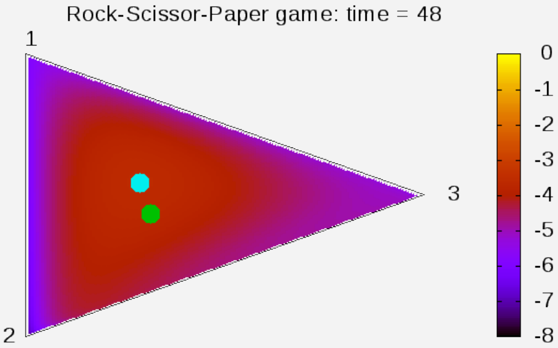

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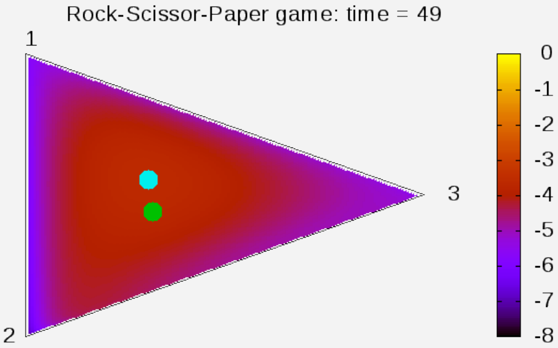

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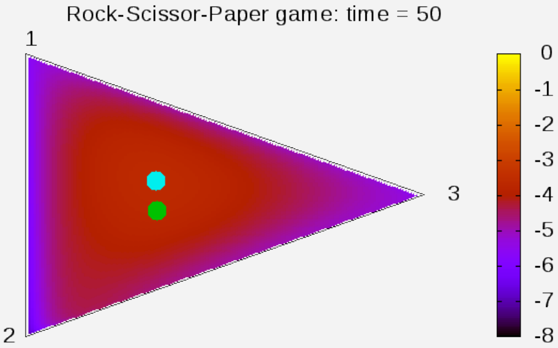

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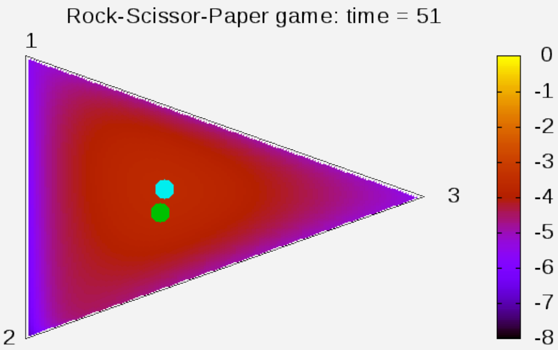

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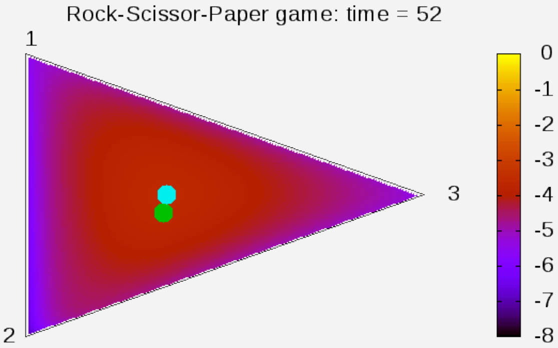

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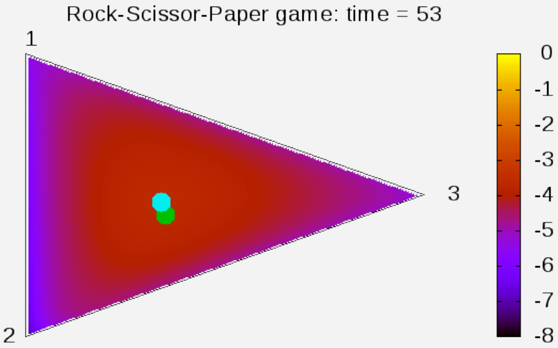

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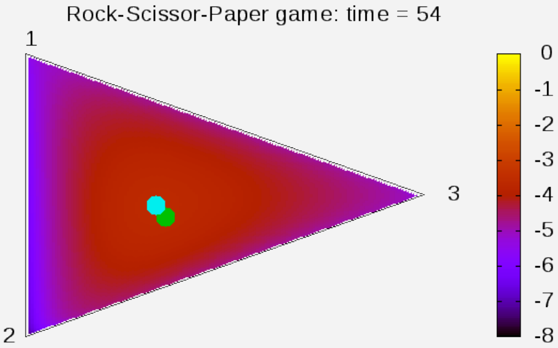

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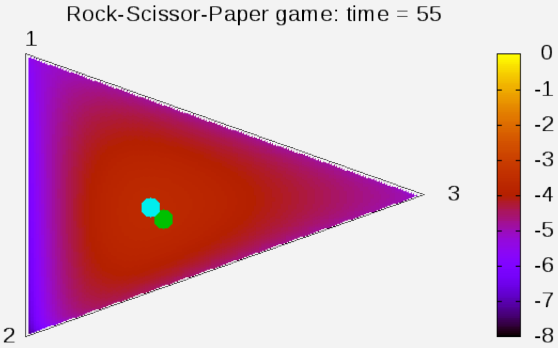

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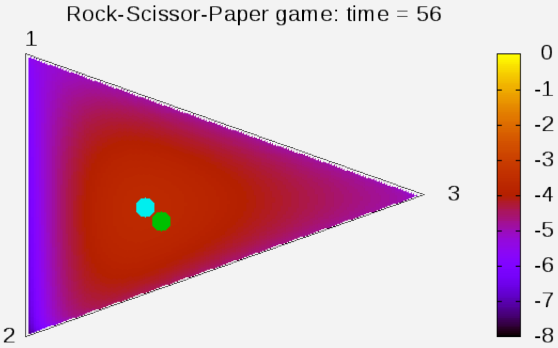

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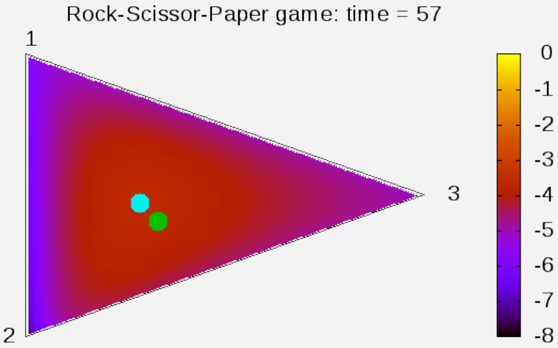

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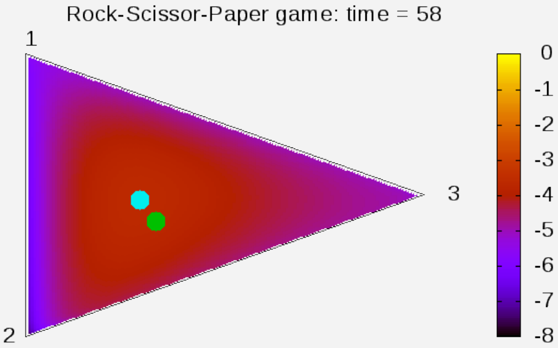

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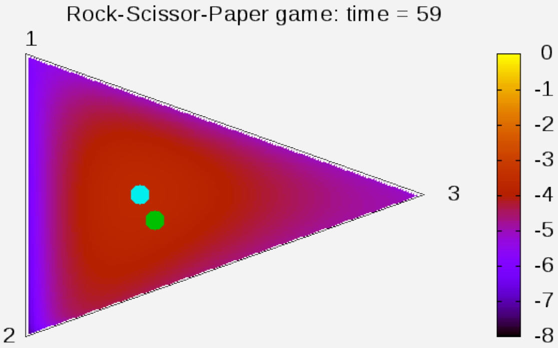

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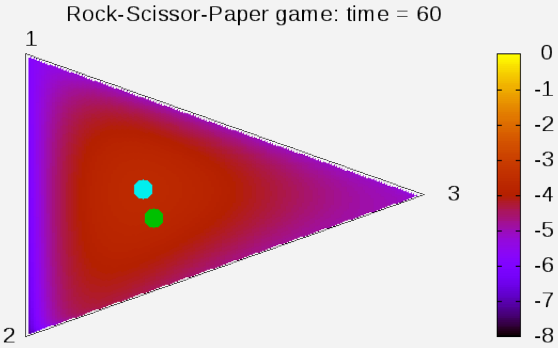

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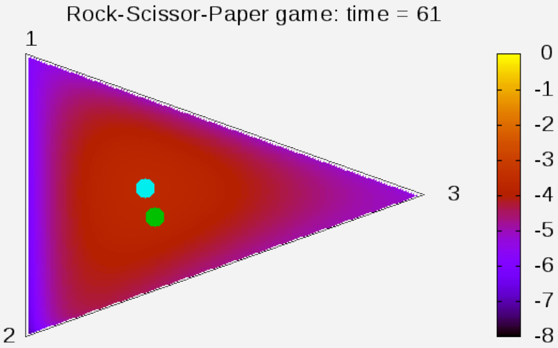

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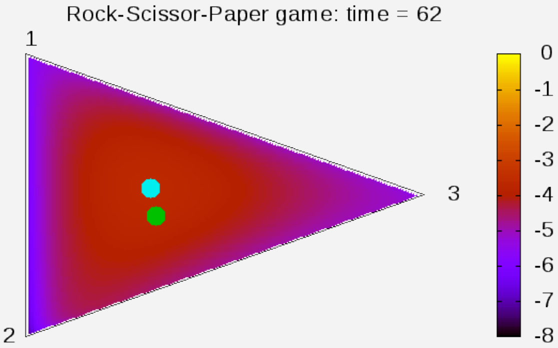

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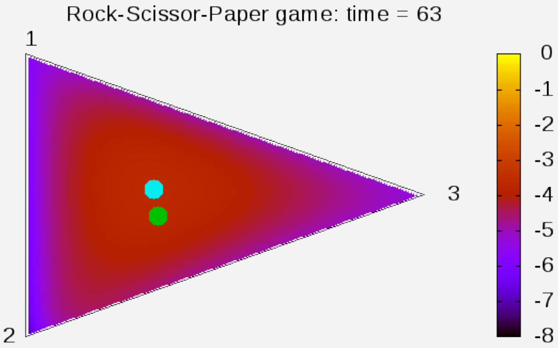

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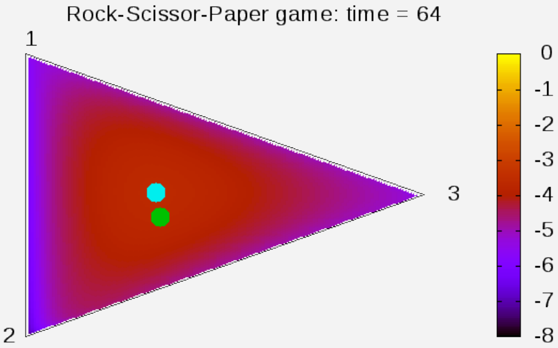

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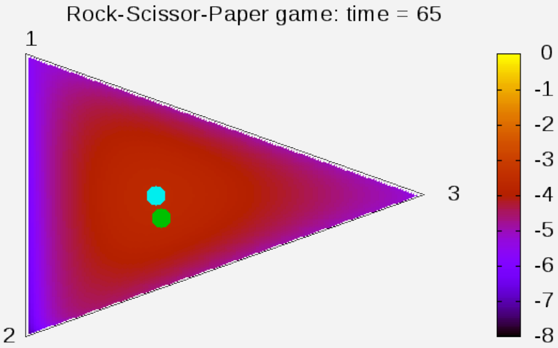

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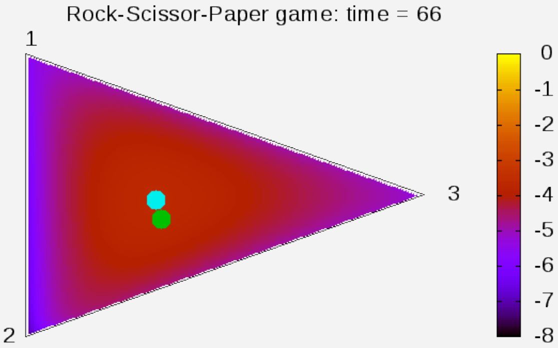

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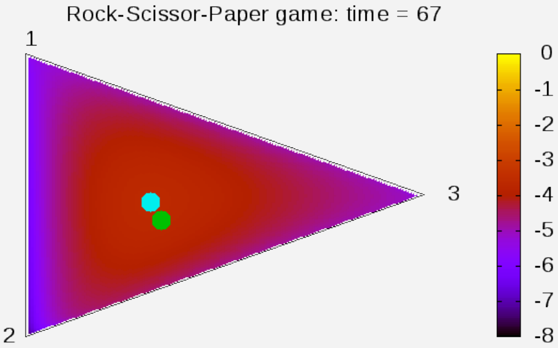

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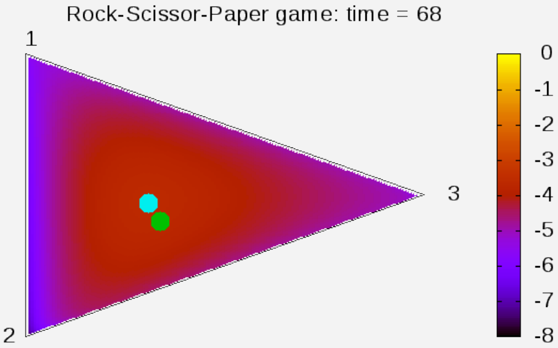

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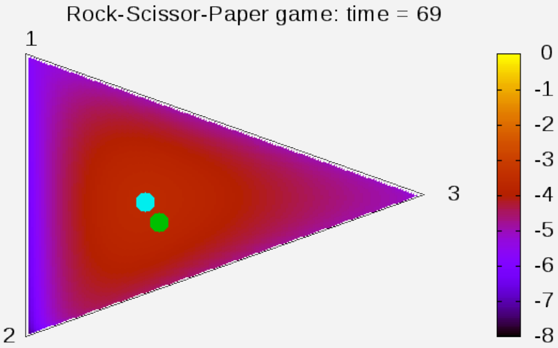

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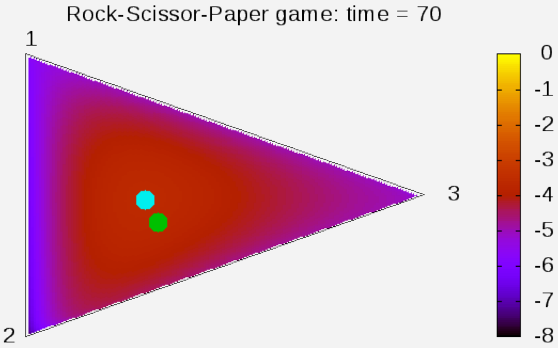

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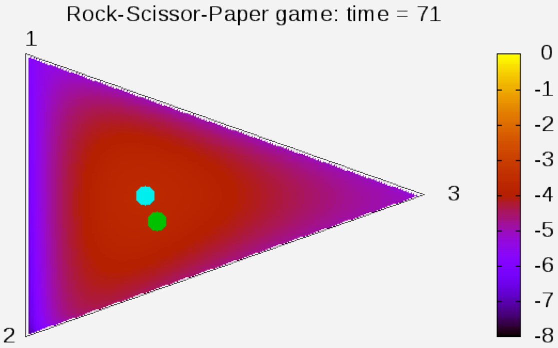

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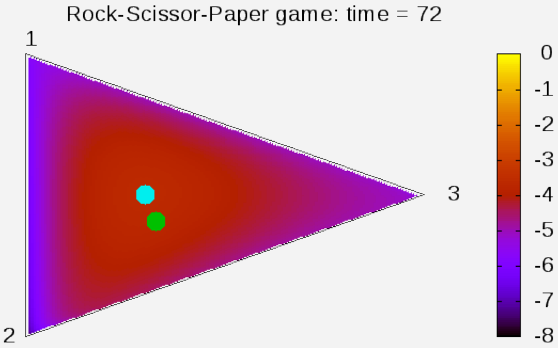

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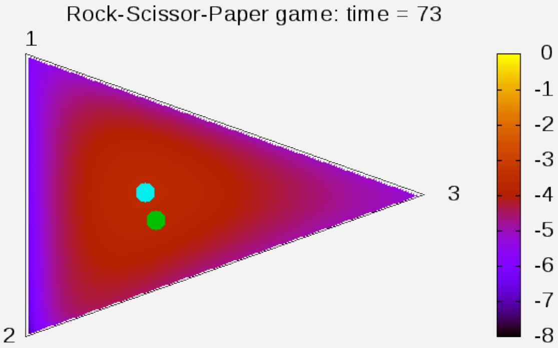

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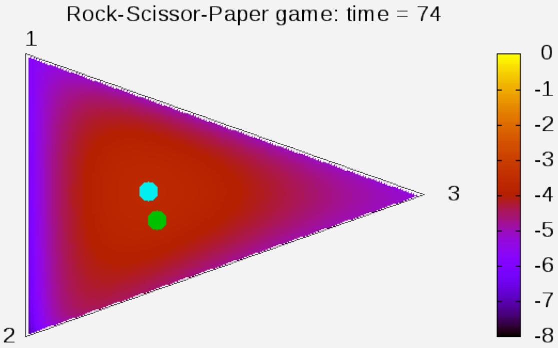

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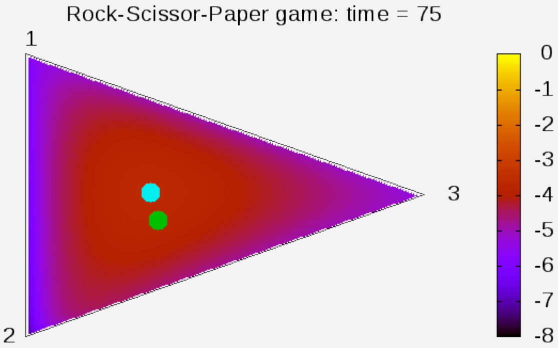

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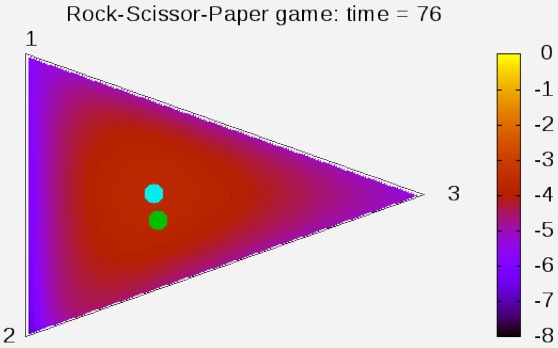

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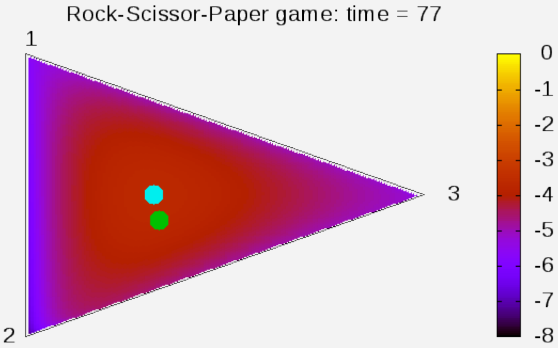

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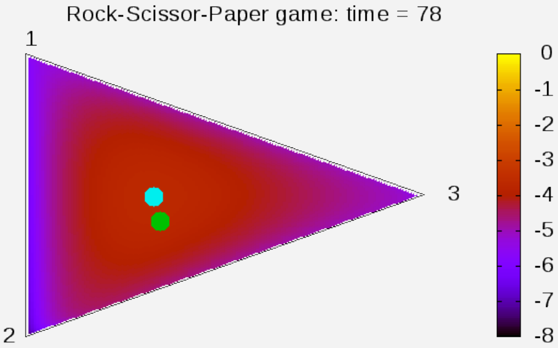

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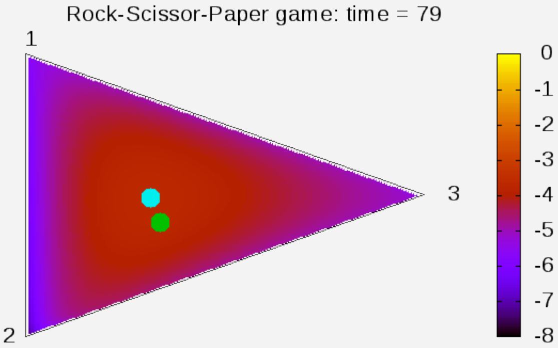

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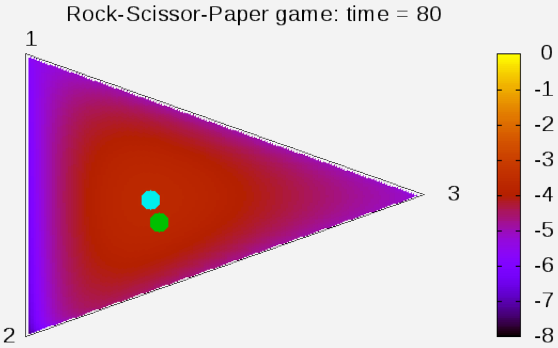

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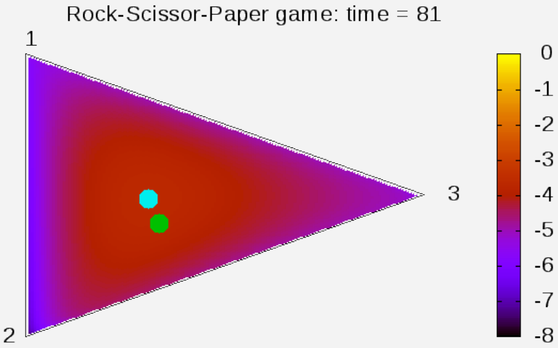

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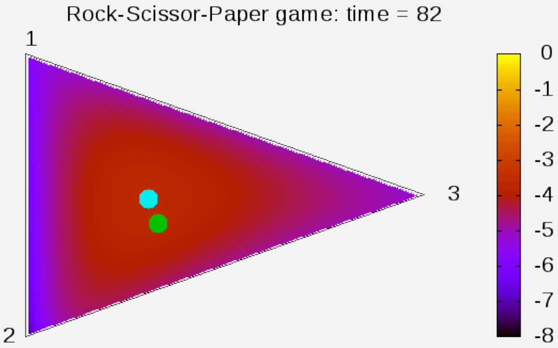

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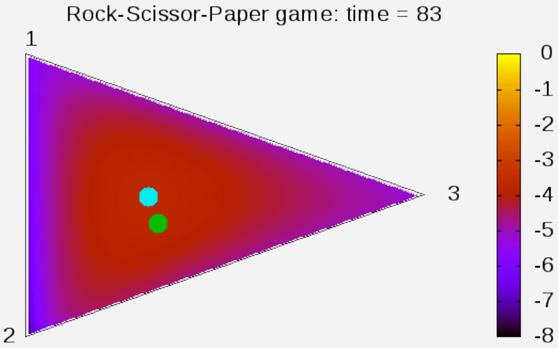

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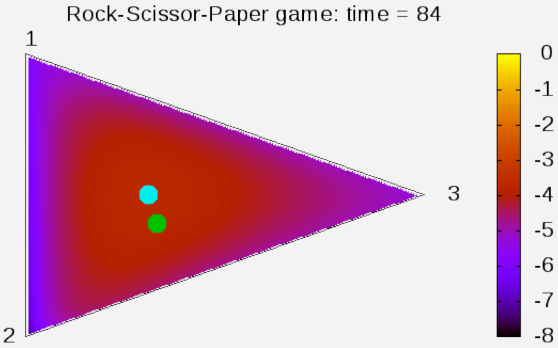

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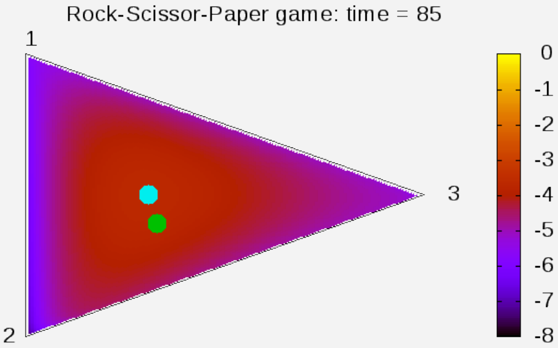

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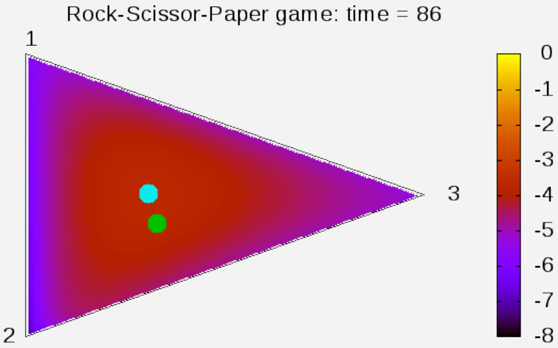

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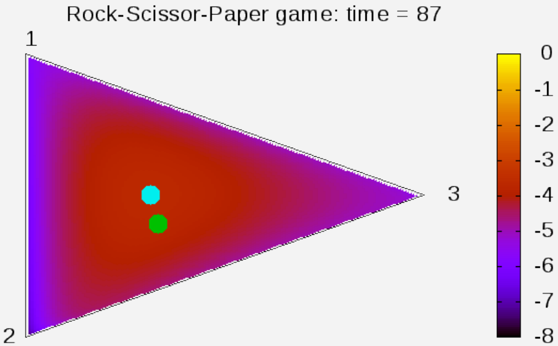

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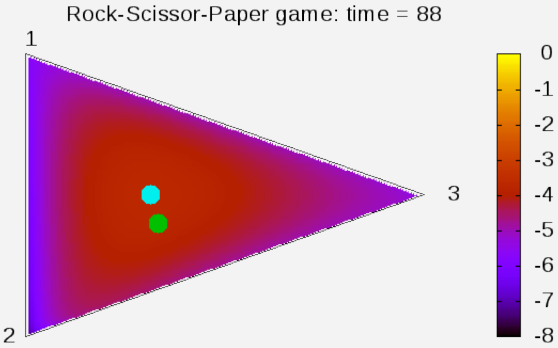

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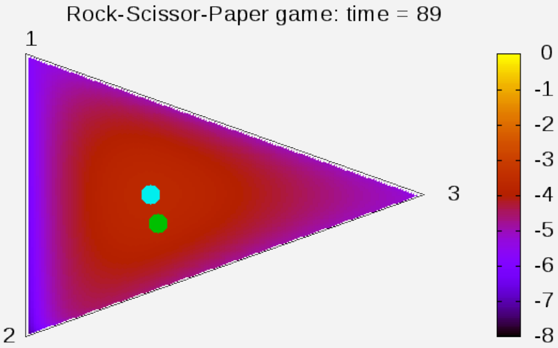

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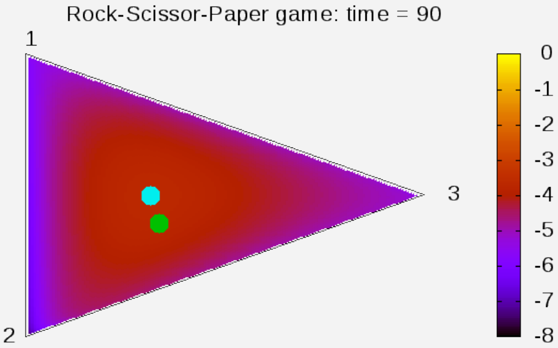

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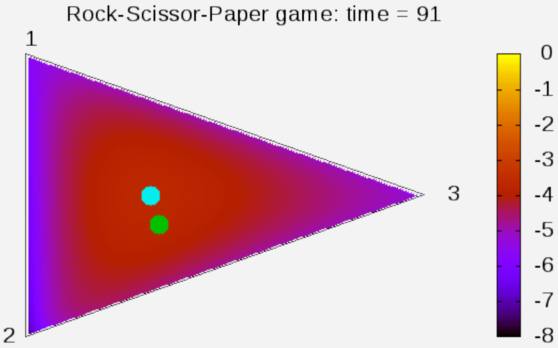

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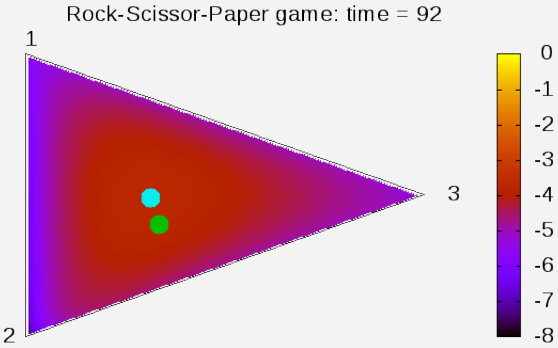

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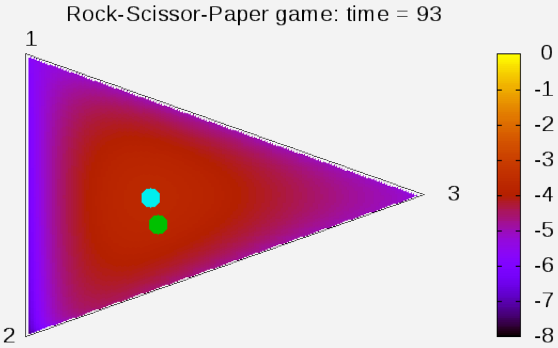

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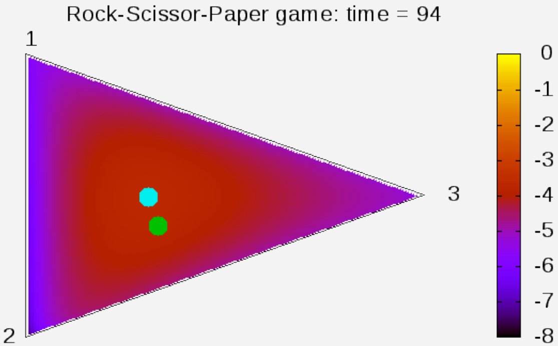

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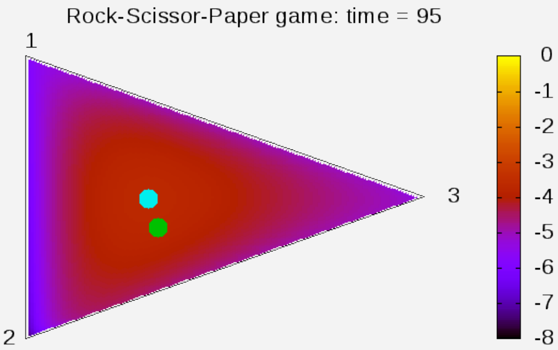

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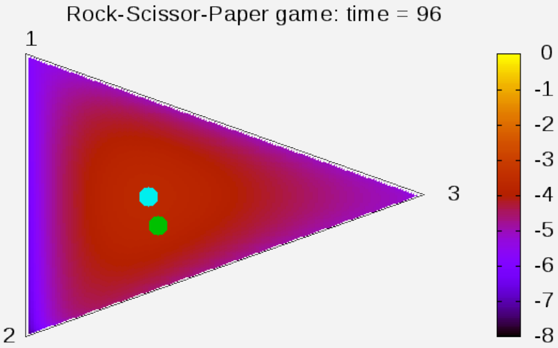

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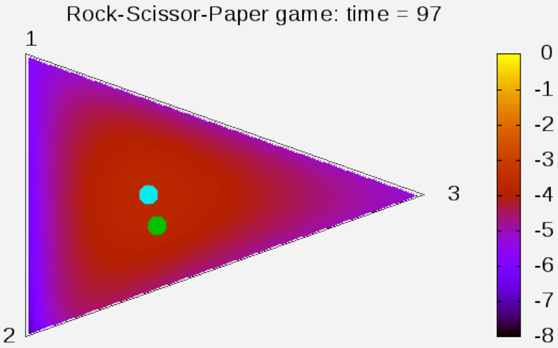

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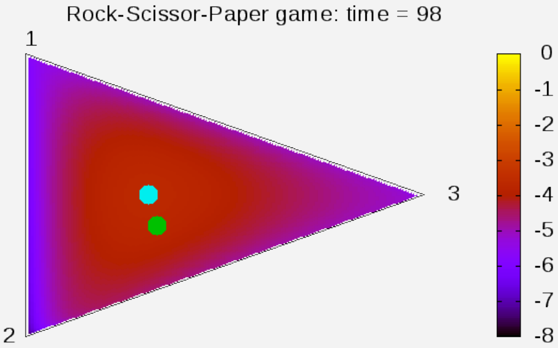

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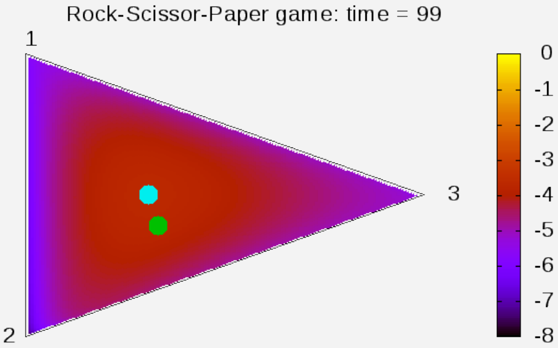

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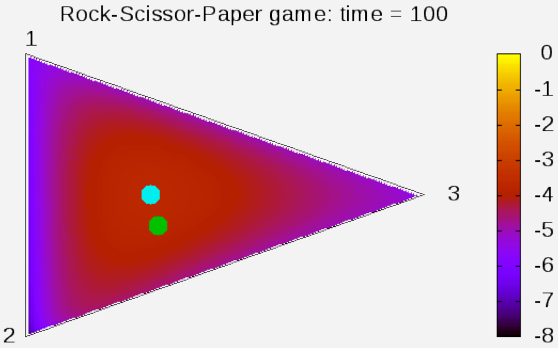

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The Wright-Fisher process

Transition matrix for two types

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The Wright-Fisher process

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$$P(x,t,N,\Delta t) = \sum_{y=0,\frac{1}{N},\ldots,1} \Theta_N(y \to x) P(y,t,N,\Delta t)$$

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$$\mathbf{P}(t+\Delta t) = \mathbf{M}\mathbf{P}(t)$$

where

$$\mathbf{P}(t) := (P(0,t,N,\Delta t), P(1/N,t,N,\Delta t), \cdots, P(1,t,N,\Delta t))$$

and $\mathbf{M}$ is a stochastic matrix.

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This implies that $\mathcal{P}(\kappa\Delta t) = \mathbf{M}^\kappa \mathcal{P}(0)$.

Theorem

$$\lim_{\kappa\to\infty}\mathbf{M}^{\kappa}=\begin{pmatrix}1 & 1-F_1 & \cdots & 1-F_N\\ 0 & 0 & \cdots & 0\\ & & \vdots & \\ 0 & F_1 & \cdots & F_N\end{pmatrix}.$$

where the F_n satisfy $F_n=\sum_{m=0}^{N}\Theta_N\left(\frac{n}{N}\to\frac{m}{N}\right)F_m$, with $F_0=0$ and $F_N=1$.
In particular, any stationary state will be concentrated at the endpoints.
If $\mathbf{1}$ denotes the vector $(1,1,\ldots,1)^\dagger$, $\mathbf{F}=(F_0,F_1,\ldots,F_N)^\dagger$ and if $\langle\cdot,\cdot,\rangle$ denotes the usual inner product, then we have that $\langle\mathbf{P}(t),\mathbf{1}\rangle=\langle\mathbf{P}(0),\mathbf{1}\rangle$ and $\langle\mathbf{P}(\mathbf{t}),\mathbf{F}\rangle=\langle\mathbf{P}(\mathbf{0}),\mathbf{F}\rangle$.

Continuous models

General idea: 2 types

We look for a differential equation that approximates the discrete evolution of P when $N \to \infty$ and $\Delta t \to 0$.

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   More precisely, we assume that $\Psi^{(i)}(x) = 1 + (\Delta t)^{\nu}\psi^{(i)}(x)$.

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More precisely, we assume that $\Psi^{(i)}(x) = 1 + (\Delta t)^{\nu}\psi^{(i)}(x)$.

2. The limit function $p = \lim_{N\to\infty,\Delta t\to 0} \frac{P}{1/N}$ is such that

$$p\left(x \pm \frac{1}{N}, t\right) = p(x,t) \pm \frac{1}{N}\partial_x p(x,t) + \frac{1}{2N^2}\partial_x^2 p(x,t) + \mathcal{O}(N^{-3}) \ ,$$

$$p\left(x, t+\Delta t\right) = p(x,t) + (\Delta t)\,\partial_t p(x,t) + \mathcal{O}\left((\Delta t)^2\right) \ .$$

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3. The time-step is such that $\varepsilon(\Delta t) = N^{-\mu}$

Continuous models

Formal asymptotic: Wright-Fisher process for two types

Using all these assumptions, we find the asymptotic expansion:

$$\partial_t p = -\frac{1}{(\Delta t)^{1-\nu}}\partial_x \left(x(1-x)\left(\psi^{(\mathbb{A})}(x) - \psi^{(\mathbb{B})}(x)\right) p\right) + \frac{1}{2N\Delta t}\partial_x^2 \left(x(1-x)p\right) \ .$$

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or the *replicator-diffusion equation*

$$\partial_t p = \frac{\varepsilon}{2} \partial_x^2 \left(x(1-x)p \right) - \partial_x \left(x(1-x) \left(\psi^{(\mathbb{A})}(x) - \psi^{(\mathbb{B})}(x) \right) p \right) \ .$$

Continuous models

Formal asymptotic: Wright-Fisher process for two types

The invariants become the following conservation laws:

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 p(x,t)\,\mathrm{d}x = 0, \qquad \frac{\mathrm{d}}{\mathrm{d}t}\int_0^1 \phi(x)p(x,t)\,\mathrm{d}x = 0,$$

where ϕ satisfies

$$\frac{\varepsilon}{2}\phi'' + \left(\psi^{(\mathbb{A})}(x) - \psi^{(\mathbb{B})}(x)\right)\phi' = 0, \quad \phi(0) = 0, \quad \phi(1) = 1\ .$$

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This implies:

$$\phi(x) = \frac{\int_0^x \exp\left[-\frac{2}{\varepsilon}\int_0^{x'}\left(\psi^{(\mathbb{A})}(x'') - \psi^{(\mathbb{B})}(x'')\right)\mathrm{d}x''\right]\mathrm{d}x'}{\int_0^1 \exp\left[-\frac{2}{\varepsilon}\int_0^{x'}\left(\psi^{(\mathbb{A})}(x'') - \psi^{(\mathbb{B})}(x'')\right)\mathrm{d}x''\right]\mathrm{d}x'} \ .$$

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If we start from the initial condition $p^{\mathrm{I}} = \delta_{x_0}$, then the fixation probability is $\phi(x_0)$.

Comparisons

The Kimura equation

The equation

$$\partial_t f = \frac{\varepsilon}{2} x(1-x)\partial_x^2 f + \gamma x(1-x)\partial_x f \ ,$$

with boundary condition given by $f(0,t) = 0$ and $f(1,t) = 1$ is known as the Kimura equation.

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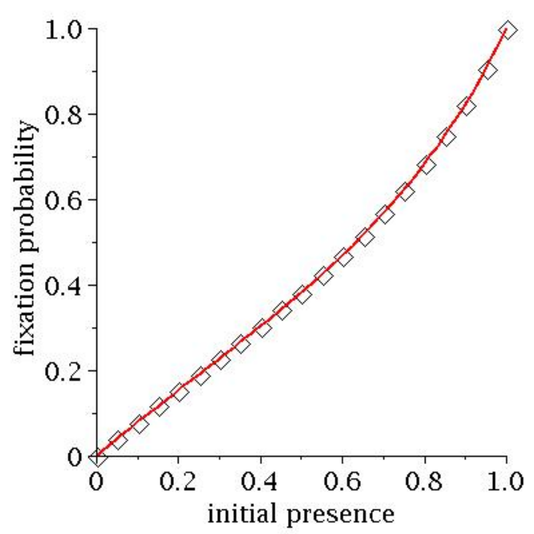
The adjoint of the replicator-diffusion equation generalizes the Kimura equation for more general fitnesses.

The final state is the final fixation probability: $\lim_{t\to\infty} f(x,t) = \phi(x)$.

Comparisons

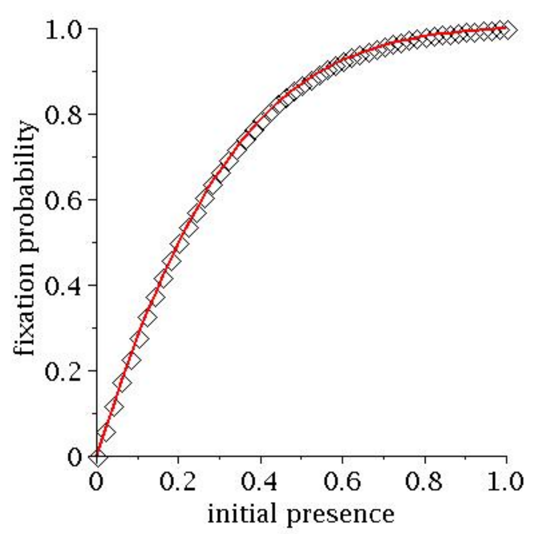
Fixation probability for homogeneous populations



Fixation probability for $N = 20$ and pay-off matrix $\begin{pmatrix} 1 & 3 \\ 4 & 2 \end{pmatrix}$. The red line indicates the function $\phi(x)$ for $\varepsilon = 0.1125157473$.

Comparisons

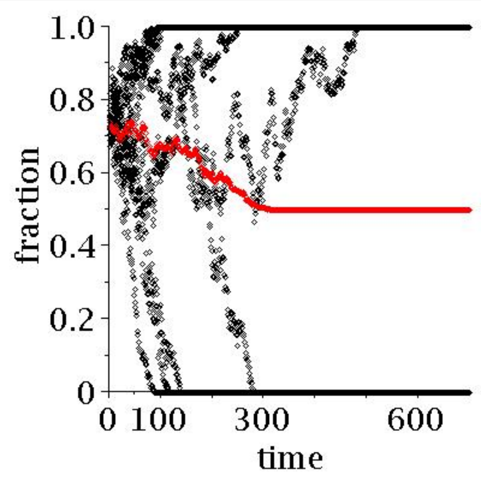
Fixation probability for homogeneous populations



Fixation probability for $N = 50$ and pay-off matrix $\begin{pmatrix} 9 & 4 \\ 2 & 2 \end{pmatrix}$. The red line indicates the function $\phi(x)$ for $\varepsilon = 0.04315862961$.

Comparisons

Time evolution in the Wright-Fisher process



Number of individuals of the first type, for the Wright-Fisher process with pay-off matrix given by $\begin{pmatrix} 10 & 5 \\ 5 & 15 \end{pmatrix}$, for ten simulations with initial conditions of 220/300 individuals of the first type. The red line indicates the evolution of the mean.

Continuous models

Rigorous asymptotic: the replicator-diffusion equation for two types

Let $\mathcal{BM}^+([0,1])$ denote the positive Radon measures in $[0,1]$.

Theorem

For a given $p^{\mathrm{I}} \in \mathcal{BM}^+([0,1])$, there exists a unique (weak) solution p, with $p \in L^\infty\left([0,\infty);\mathcal{BM}^+([0,1])\right)$ and such that p satisfies the conservations laws. The solution can be written as $p(x,t) = r(x,t) + a(t)\delta_0 + b(t)\delta_1$, where $r \in C^\infty\left(\mathbb{R}^+; C^\infty([0,1])\right)$ is a classical (regular) solution to the replicator diffusion equation without boundary conditions, and δ_y denotes the singular measure supported at y. We also have that $a(t)$ and $b(t)$, belong to $C([0,\infty)) \cap C^\infty(\mathbb{R}^+)$. For large time, we have that $\lim_{t\to\infty} r(x,t) = 0$, uniformly, and that $a(t)$ and $b(t)$, the transient extinction and fixation probabilities, respectively, are monotonically increasing functions. Moreover, we have that

$$\lim_{t\to\infty} p(\cdot,t) = \pi_0[p^{\mathrm{I}}]\delta_0 + \pi_1[p^{\mathrm{I}}]\delta_1,$$

with respect to the Radon metric. Finally, the convergence rate is exponential.

Continuous models

Rigorous asymptotic: the replicator-diffusion equation for two types

Theorem

Let $p(x,t,N,\Delta t)$ be the solution of the finite population dynamics (of population N, time step $\Delta t = 1/N$), with initial conditions given by $p^0(x,N,\Delta t) = p^0(x)$, $x = 0, 1/N, 2/N, \cdots, 1$, for p^0 as in the previous theorem. Assume also the weak-selection limit, with $\nu = \frac{1}{2}$. Let $p_{\mathrm{cont}}(x,t)$ be the solution of the continuous model, with initial condition given by $p^0(x)$. If we write p_i^n for the i-th component of $p(x,t,N,\Delta t)$ in the n-th iteration, we have, for any $t^* > 0$, that

$$\lim_{N\to\infty} p_{xN}^{tN^2} = p_{\mathrm{cont}}(x,t), \quad x \in [0,1], \quad t \in [0,t^*].$$

The Wright-Fisher process

From the discrete to the continuous

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This means that we look for a differential equation for the fraction of type i individuals. This equation should present two time-scales associated to two different phenomena:

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   Diffusion to the vertexes of the simplex (*pure states*)

   Let the $n-1$-dimensional simplex be

$$S^{n-1} := \{\mathbf{x} \in \mathbf{R}^n | |\mathbf{x}| := \sum_{i=1}^{n} x_i = 1, x_i \geq 0, \forall i = 1, \cdots, n\} .$$

The Wright-Fisher process

From the discrete to the continuous

We consider the discrete evolution ($|\mathbf{y}| = \sum_i y_i$)

$$p_N(\mathbf{x}, t+\Delta t) = \sum_{|y|=1} \Theta_N(\mathbf{y} \to \mathbf{x}) p_N(t, \mathbf{y}) = \sum_{|y|=0} \Theta_N(\mathbf{x}-\mathbf{y} \to \mathbf{x}) p_N(t, \mathbf{x}-\mathbf{y}) \,.$$

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We assume the weak selection principle $\phi^{(i)}(\mathbf{y}) = 1 + \frac{\psi^{(i)}(\mathbf{y})}{N}$, and then $\bar{\phi}(\mathbf{y}) = 1 + \frac{\bar{\psi}(\mathbf{y})}{N}$.

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We assume the weak selection principle $\phi^{(i)}(\mathbf{y}) = 1 + \frac{\psi^{(i)}(\mathbf{y})}{N}$, and then $\bar{\phi}(\mathbf{y}) = 1 + \frac{\bar{\psi}(\mathbf{y})}{N}$. This implies that

$$\begin{aligned} \left(\frac{y_i \phi^{(i)}}{\bar{\phi}}\right)^{N x_i} &\approx \exp\left\{ N x_i \left[\log y_i + \log\left(1 + \frac{\psi^{(i)}(\mathbf{y})}{N}\right)\left(1 - \frac{\bar{\psi}(\mathbf{y})}{N} + \frac{\bar{\psi}^2(\mathbf{y})}{N^2}\right)\right]\right\} \\ &\approx y_i^{N x_i} \exp\left[x_i \left(\psi^{(i)}(\mathbf{y}) - \bar{\psi}(\mathbf{y})\right) + \frac{x_i \bar{\psi}}{N}\left(\bar{\psi}(\mathbf{y}) - \psi^{(i)}(\mathbf{y})\right)\right] \, . \end{aligned}$$

The Wright-Fisher process

From the discrete to the continuous

Using the Stirling formula $x! \approx \sqrt{2\pi x}x^x\mathrm{e}^{-x}$ we write

$$\frac{N!}{(Nx_1)!(Nx_2)!\cdots(Nx_n)!} \approx \frac{(2\pi)^{\frac{1-n}{2}}}{N^{n-1}} \frac{N^{\frac{n-1}{2}}}{(x_1x_2\cdots x_n)^{\frac{1}{2}}x_1^{x_1N}x_2^{x_2N}\cdots x_n^{x_nN}} \ .$$

The Wright-Fisher process

From the discrete to the continuous

Finally, we have

$$\Theta_N(\mathbf{y} \to \mathbf{x}) \approx \frac{1}{N^{n-1}} \Lambda(\mathbf{y}, \mathbf{x}, N^{-\frac{1}{2}}) \left(1 + \Xi(\mathbf{y}, \mathbf{x}, N^{-\frac{1}{2}}) + o(N^{-1})\right) \ ,$$

where

$$\Lambda(\mathbf{y}, \mathbf{x}, z) := \frac{(2\pi)^{\frac{1-n}{2}} z^{1-n}}{(x_1 x_2 \cdots x_n)^{\frac{1}{2}}} \prod_{i=1}^{n} \left(\frac{y_i}{x_i}\right)^{\frac{x_i}{z^2}}$$

$$\Xi(\mathbf{y}, \mathbf{x}, z) := \sum_{i=1}^{n} \left[x_i \left(\psi^{(i)}(\mathbf{y}) - \bar{\psi}(\mathbf{y}) \right) + z^2 x_i \bar{\psi}(\mathbf{y}) \left(\bar{\psi}(\mathbf{y}) - \psi^{(i)}(\mathbf{y}) \right) \right] \ .$$

Note that Ξ is associated to the drift generated by the fitness; i.e., if $\psi^{(i)}(\mathbf{y})$ is constant, then $\Xi(\mathbf{y}, \mathbf{x}, N) = 0$.

The Wright-Fisher process

We introduce the new variables $\tau_i = y_i\sqrt{N}$ and $z = \frac{1}{\sqrt{N}}$.

Lemma

For large N (and then small z) the neutral transition probability Λ scales as

$$\Lambda(\mathbf{x} - z\boldsymbol{\tau}, \mathbf{x}, z) \approx \frac{(2\pi)^{\frac{1-n}{2}} z^{1-n}}{(x_1 x_2 \cdots x_n)^{\frac{1}{2}}} \exp\left(-\frac{1}{2}\mathcal{Q}(\boldsymbol{\tau}, \boldsymbol{\tau})\right) ,$$

where $\mathcal{Q}$ is a quadratic form with associated eigenvalues $\lambda_1, \cdots, \lambda_{n-1}$. These eigenvalues are the eigenvalues of the matrix $\mathbf{F} = (F_{ij})$, $i, j = 1, \cdots, n-1$, such that $F_{ii} = x_i^{-1} + x_n^{-1}$ and $F_{ij} = x_n^{-1}$, for $i \neq j$, i.e., $\lambda_1 \cdots \lambda_{n-1} = (x_1 \cdots x_n)^{-1}$. This implies that

$$\int_{\mathbb{R}^{n-1}} \exp\left(-\frac{1}{2}\mathcal{Q}(\boldsymbol{\tau}, \boldsymbol{\tau})\right) \mathrm{d}\boldsymbol{\tau} = (2\pi)^{\frac{n-1}{2}} \sqrt{x_1 \cdots x_n} \ .$$

The Wright-Fisher process

From the discrete to the continuous

Lemma

For large N (and then small z) the neutral transition probability Λ has the following first moments:

$$z^{n-1}\int \Lambda(\mathbf{x},\mathbf{x}+z\boldsymbol{\tau},z)\mathrm{d}\boldsymbol{\tau} = \int \Lambda(\mathbf{x},\mathbf{x}+\mathbf{y},z)\mathrm{d}\mathbf{y} = 1\ ,$$

$$z^{n}\int \tau_i\Lambda(\mathbf{x},\mathbf{x}+z\boldsymbol{\tau},z)\mathrm{d}\boldsymbol{\tau} = 0\ ,$$

$$z^{n+1}\int \tau_i\tau_j\Lambda(\mathbf{x},\mathbf{x}+z\boldsymbol{\tau},z)\mathrm{d}\boldsymbol{\tau} = \mathrm{o}(z^3) + z^2\times\begin{cases} (-x_ix_j) & \text{if } i\neq j\ ,\ i,j\leq n-1\ ,\\ x_i(1-x_i) & \text{if } i=j\leq n-1\ .\end{cases}$$

The Wright-Fisher process

From the discrete to the continuous

We write the following equation for an appropriate test function g:

$$\int p(\mathbf{x}, t+\Delta t) g(\mathbf{x}) \mathrm{d}\mathbf{x} \approx \iint \Theta_N(\mathbf{x}-\mathbf{y} \to \mathbf{x}) p(\mathbf{x}-\mathbf{y}, t) N^{n-1} g(\mathbf{x}) \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}$$

$$\approx \frac{1}{z^{n-1}} \iint \Theta_{\frac{1}{z^2}}(\mathbf{x}-z\boldsymbol{\tau} \to \mathbf{x}) p(\mathbf{x}-z\boldsymbol{\tau}, t) g(\mathbf{x}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x}$$

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$$\approx z^{n-1} \iint \left[1 + \Xi(\mathbf{x}-z\boldsymbol{\tau}, \mathbf{x}, z)\right] \Lambda(\mathbf{x}-z\boldsymbol{\tau}, \mathbf{x}, z) p(\mathbf{x}-z\boldsymbol{\tau}, t) g(\mathbf{x}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x}$$

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$$= z^{n-1} \iint \left[1+\Xi(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z)\right] \Lambda(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z) p(\mathbf{x}, t) g(\mathbf{x}+z\boldsymbol{\tau}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x}$$

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\int p(\mathbf{x}, t+\Delta t) g(\mathbf{x}) \mathrm{d}\mathbf{x} &\approx \iint \Theta_N(\mathbf{x}-\mathbf{y} \to \mathbf{x}) p(\mathbf{x}-\mathbf{y}, t) N^{n-1} g(\mathbf{x}) \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y} \\
&\approx \frac{1}{z^{n-1}} \iint \Theta_{\frac{1}{z^2}}(\mathbf{x}-z\boldsymbol{\tau} \to \mathbf{x}) p(\mathbf{x}-z\boldsymbol{\tau}, t) g(\mathbf{x}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x} \\
&\approx z^{n-1} \iint \left[1+\Xi(\mathbf{x}-z\boldsymbol{\tau}, \mathbf{x}, z)\right] \Lambda(\mathbf{x}-z\boldsymbol{\tau}, \mathbf{x}, z) p(\mathbf{x}-z\boldsymbol{\tau}, t) g(\mathbf{x}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x} \\
&= z^{n-1} \iint \left[1+\Xi(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z)\right] \Lambda(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z) p(\mathbf{x}, t) g(\mathbf{x}+z\boldsymbol{\tau}) \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x} \\
&\approx z^{n-1} \iint \left[1+z\sum_{i=1}^{n} \tau_i \left(\psi^{(i)}(\mathbf{x})-\bar{\psi}(\mathbf{x})\right)+\mathrm{o}(z^3)\right] \Lambda(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z) p(\mathbf{x}, t) \\
&\quad \times \left[g(\mathbf{x}, t)+z\sum_{j=1}^{n-1} \tau_j \partial_{x_j} g(\mathbf{x})+\frac{z^2}{2}\sum_{k,l=1}^{n-1} \tau_k \tau_l \partial^2_{x_k x_k} g(\mathbf{x})\right] \mathrm{d}\boldsymbol{\tau}\mathrm{d}\mathbf{x}
\end{aligned}
$$

The Wright-Fisher process

From the discrete to the continuous

$$
\begin{aligned}
&\int p(\mathbf{x}, t+\Delta t) g(\mathbf{x}) \mathrm{d}\mathbf{x} \\
&\quad \approx z^{n-1} \iint \Lambda(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z) p(\mathbf{x}, t) g(\mathbf{x}) \mathrm{d}\boldsymbol{\tau} \mathrm{d}\mathbf{x} \\
&\qquad + z^{n} \iint p(\mathbf{x}, t) \left[\sum_{i=1}^{n} \left(\psi^{(i)}(\mathbf{x}) - \bar{\psi}(\mathbf{x}) \right) \tau_i + \sum_{j=1}^{n-1} \tau_j \partial_{x_j} g(\mathbf{x}) \right] \Lambda(\mathbf{x}, \mathbf{x}+z\boldsymbol{\tau}, z) \mathrm{d}\boldsymbol{\tau} \mathrm{d}\mathbf{x} \\
&\qquad + z^{n+1} \iint p(\mathbf{x}, t) \left[\sum_{k,l=1}^{n-1} \frac{\tau_k \tau_l}{2} \partial^2_{x_k x_l} g(\mathbf{x}) + \sum_{i=1}^{n} \sum_{j=1}^{n-1} \partial_{x_j} g(\mathbf{x}) (\psi^{(i)}(\mathbf{x}) - \bar{\psi}(\mathbf{x})) \tau_i \tau_j \right] \\
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$$+ z^{n+1} \iint p(\mathbf{x}, t) \left[\sum_{k,l=1}^{n-1} \frac{\tau_k \tau_l}{2} \partial^2_{x_k x_l} g(\mathbf{x}) + \sum_{i=1}^{n} \sum_{j=1}^{n-1} \partial_{x_j} g(\mathbf{x}) (\psi^{(i)}(\mathbf{x}) - \bar{\psi}(\mathbf{x})) \tau_i \tau_j \right]$$

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&\qquad + z^2 \int g(\mathbf{x}) \left[\frac{1}{2} \sum_{k=1}^{n-1} \partial^2_{x_k} \left(x_k (1 - x_k) p(\mathbf{x}, t) \right) - \frac{1}{2} \sum_{k,l=1, k\neq l}^{n-1} \partial^2_{x_k x_l} \left(x_k x_l p(\mathbf{x}, t) \right) \right. \\
&\qquad\quad \left. - \sum_{j=1}^{n-1} \partial_{x_j} \left(x_j \left(\psi^{(j)}(\mathbf{x}) - \bar{\psi}(\mathbf{x}) \right) p(\mathbf{x}, t) \right) \right] \mathrm{d}\mathbf{x} \; .
\end{aligned}
$$

The Wright-Fisher process

From the discrete to the continuous

Imposing $\Delta t = z^2 = \frac{1}{N}$, we have

$$\begin{aligned}\partial_t p &= \frac{1}{2}\sum_{k=1}^{n-1}\partial^2_{x_k}\left(x_k(1-x_k)p(\mathbf{x},t)\right) - \frac{1}{2}\sum_{k,l=1,k\neq l}^{n-1}\partial^2_{x_k x_l}\left(x_k x_l p(\mathbf{x},t)\right)\\ &\quad -\sum_{j=1}^{n-1}\partial_{x_j}\left(x_j\left(\psi^{(j)}(\mathbf{x})-\bar{\psi}(\mathbf{x})\right)p(\mathbf{x},t)\right)\end{aligned}$$

We call this equation the replicator-diffusion equation:

$$\partial_t p = \frac{1}{2}\sum_{i,j=1}^{n-1}\partial^2_{x_i x_j}\left(D_{ij}p\right) - \sum_{i=1}^{n-1}\partial_{x_i}\left(\Omega_i p\right) .$$

Short-term dynamics

The replicator equation appears...

The replicator-diffusion equation is given by

$$
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$$\frac{1}{\varepsilon}\partial_t p = \frac{1}{2}\sum_{k=1}^{n-1}\partial^2_{x_k}\left(x_k(1-x_k)p(\mathbf{x},t)\right)$$
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This equation is equivalent to the replicator dynamics.

Long-term dynamics

Mixed states fade away...

Theorem

Let p be the solution of replicator-diffusion equation. Then, $p^{\infty} := \lim_{t\to\infty} p(\cdot, t)$*, is a linear combination of Dirac-deltas supported at the vertexes of the simplex.*

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We change variables and re-write the replicator-diffusion equation as

$$\partial_t u = \frac{1}{\omega}\nabla\cdot\left[\omega\left(\frac{1}{2}D\nabla u - \mathbf{B}u\right)\right] ,$$

where $u = \mathrm{e}^{-\theta}p/\lambda$, $\omega = \mathrm{e}^{\theta}/\lambda$, with $\lambda = x_1x_2\cdots x_n$ and $\nabla\theta$ and $\mathbf{B}$ are associated to the Hodges decomposition of the drift part.

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$$\frac{1}{2}\partial_t \int u^2 \omega \mathrm{d}V = \int_{S^n} \nabla \cdot \left[\omega\left(\frac{1}{2}D\nabla u - \mathcal{B}u\right)\right] u \, \mathrm{d}V < -\alpha \int_{S^n} u^2 \omega \, \mathrm{d}V.$$

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$$\int p^2 \mathrm{e}^{-\theta} \lambda \mathrm{d}x = \int u^2 \omega \mathrm{d}x \overset{t \to \infty}{\to} 0 \; ,$$

and, together with the conservation laws $\partial_t \int \phi_i p \mathrm{d}x = 0$, $i = 1, \ldots, n$ we have that p concentrates on the zeros of λ, i.e., the boundary of the simplex.

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$$p^\infty = \sum_{v\in V} c_v \delta_v \ ,$$

where V is the set of all vertexes of the simplex S^n.

Short-term dynamics

The replicator equation appears...

Theorem

Let p_0 be the solution of the replicator-diffusion equation, with $\varepsilon = 0$ and let p_ε be a solution to replicator-diffusion equation, with $\varepsilon > 0$. Then, there exits a C such that, for $\tau \leq C$, we have

$$\|p_\varepsilon(\cdot,\tau) - p_0(\cdot,\tau)\|_\infty \leq C\varepsilon.$$

Thus p_0 is the leading order asymptotic approximation to p_ε, for $t < \varepsilon C$.

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Define $w_\varepsilon = p_\varepsilon - p_0$, and

$$\partial_t w_\varepsilon = \frac{\varepsilon}{2}\sum_{i,j=1}^{n-1}\partial_{ij}\left(D_{ij}w_\varepsilon\right) - \sum_{i=1}^{n-1}\partial_{x_i}\left(\Omega_i w_\varepsilon\right) + \frac{\varepsilon}{2}\sum_{i,j=1}^{n-1}\partial_{x_i x_j}\left(D_{ij}p_0\right) \ , \quad w_\varepsilon|_{t=0} = 0$$

Generalizing Kimura Equation

General fitness function and n types

The dual of the replicator-diffusion equation generalizes the Kimura equation for n types and general fitness:

$$\partial_t f = \frac{\varepsilon}{2}\sum_{k=1}^{n-1} x_k(1-x_k)\partial_k^2 f - \frac{1}{2}\sum_{k,l=1;k\neq l}^{n-1} x_k x_l \partial_{kl}^2 f + \sum_{j=1}^{n-1} x_j\left(\psi^{(j)}(\mathbf{x}) - \bar{\psi}(\mathbf{x})\right)\partial_j f$$

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The function f gives the fixation probability of a given type. The precise type will be fixed by the boundary conditions imposed to f.

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Generalizing Kimura Equation

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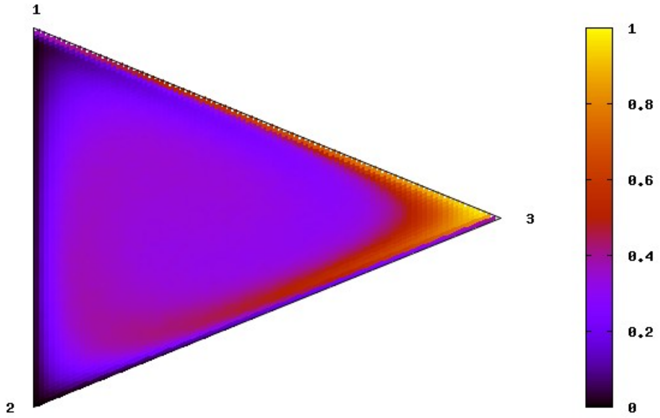
Fixation probability of a *Paper* in the Rock-Scissor-Paper game.



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THE END