Modelling Evolutionary Games

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Boxing Kangaroos

Stags

Mark Fellowes Nature Photography

The Problem

- How does ritualised fighting emerge in intra-species conflict?
- Why do individuals limit the use of their weaponry?
- Maynard Smith & Price (1973)

venemous

> How can one explain such oddities as snakes that wrestle with each other, deer that refuse to strike "foul blows", and antelope that kneel down to fight?

Games in Biology

- Fisher (1930) The Genetical Theory of Natural Selection “On the evolution of the sex-ratio”.
- Kalmus(1960) Games animals play.
- Maynard Smith & Price(1973) The logic of animal conflicts.

Evolutionary Conflicts

- 2 Player, symmetric.
- Suppose each individual has a set of available strategies S.
- There is a payoff function $f: S \times S \to R$, so if an individual plays strategy x and his opponent plays strategy y then that individual receives $f(x,y)$ ($\neq f(y,x)$ in general)

Additivity

- Payoffs are additive, so if an individual plays x in a population which has p(y) playing y then the expected payoff to x is

$$E(x,p)=\sum_{y} p(y) f(x,y)$$

Additivity

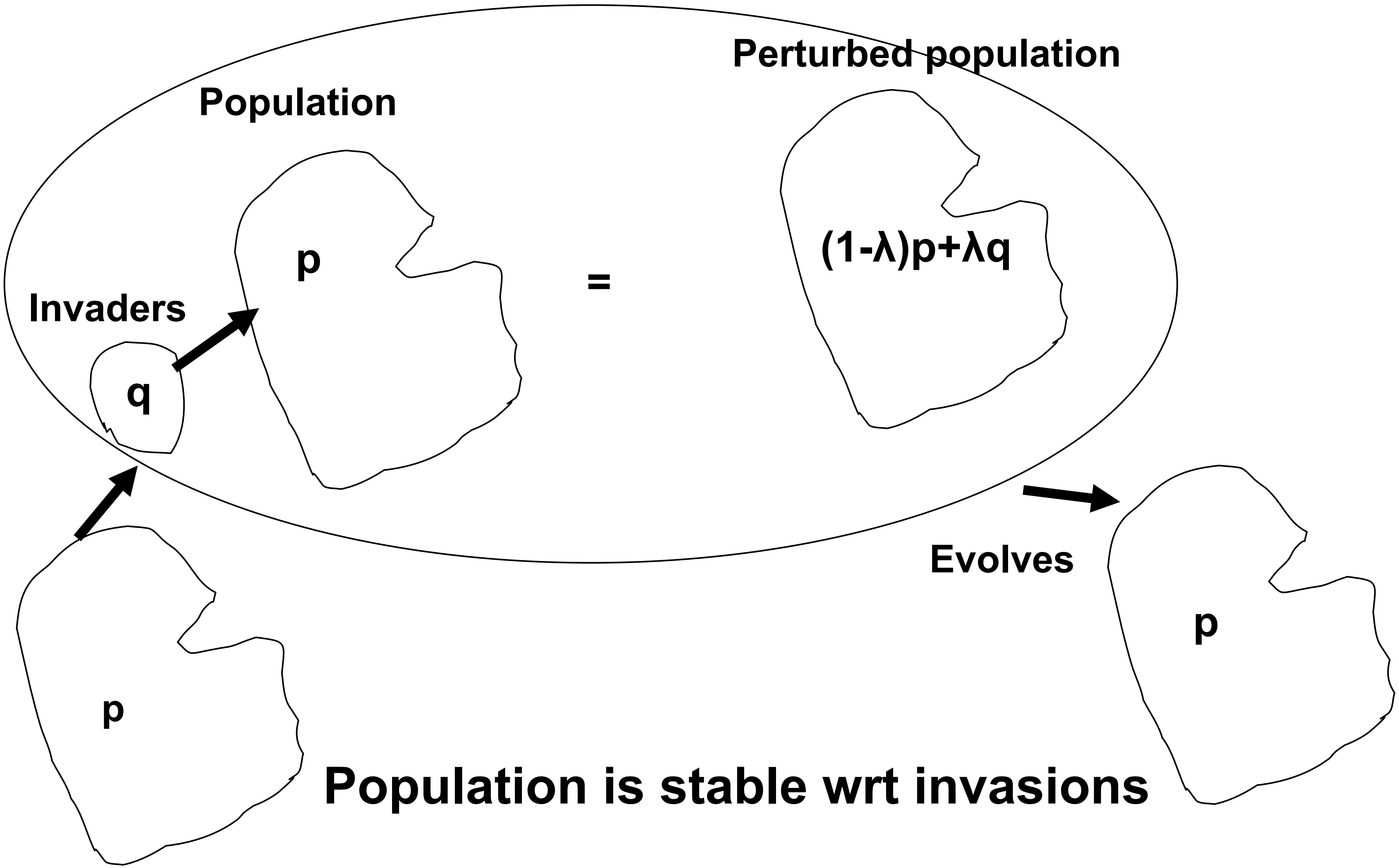
- Further if an individual or group of individuals plays x's with probabilities r(x), against a group playing y's with probabilities p(y) then their expected payoff is

$$E(r,p)=\sum_x r(x)E(x,p)=\sum_x\sum_y r(x)p(y)E(x,y)$$

Evolutionarily Stable Strategies

- Maynard Smith & Price (1973) introduced the idea of an ESS. They specified this as a strategy which if played by the population would be capable of resisting invasion by any alternative strategy.

Evolutionarily Stable Strategies



Population is stable wrt invasions

ES

- We say **p** is Evolutionarily Stable wrt **q** if

$$E(p,(1-\lambda)p+\lambda q) > E(q,(1-\lambda)p+\lambda q)$$

- Thus for λ small (mutations, fluctuations) require

(1) $$E(p,p) > E(q,p)$$

or

(2) $$E(p,p) = E(q,p) \,\&\, E(p,q) > E(q,q)$$

ESS

We say p is an ESS if, and only if, p is ES wrt every $q \neq p$.

Support and Equality

- U(p)={x; x ε S & p(x)>0} is the support of p.

- Define T(p)={x; x S & E(x,p)=E(p,p)}

ε

ESS is an equilibrium

-

An ESS must be an equilibrium

i.e. $E(x,p)=E(p,p)$ for (almost) all $x \in U$.

War of Attrition

- Two individuals each choose a time to display. When the lesser time elapses the corresponding individual departs. The other collects the reward V. The cost is the time.
- This is an all-pay auction!

Who fetches the beer?

The War of Attrition

$$S = [0, \infty)$$

$$E(x, y) = \begin{pmatrix} V - y & if & x > y \\ V/2 - y & if & x = y \\ -x & if & x < y \end{pmatrix}$$

“The War of Attrition”

$$S = [0, \infty)$$

$$E(x, y) = \begin{pmatrix} f(y) - y & if & x > y \\ f(y)/2 - x & if & x = y \\ -x & if & x < y \end{pmatrix}$$

The Unlabelled Ordinal Conflict

$$S = [0, \infty)$$

$$E(x,y) = \begin{pmatrix} f(y) - \boxed{g(y)} & if & x > y \\ f(y)/2 - \boxed{g(y)} & if & x = y \\ -\boxed{g(x)} & if & x < y \end{pmatrix}$$

The War of Attrition

$$S = [0, \infty)$$

$$E(x, y) = \begin{pmatrix} V - y & if & x > y \\ V/2 - x & if & x = y \\ -x & if & x < y \end{pmatrix}$$

War of Attrition

There can be no atoms in an ESS except at values v where it is not permitted to play in some non-zero interval (v, w].

If there were an atom p(s) at some s then playing s^+ (if that were possible) would have a higher payoff than s (actually by an approx. amount Vp(s)/2).

The War of Attrition

- Now an ESS p must be an equilibrium, thus for x in U(p) (the support of p) we must have

$$E(x,p) = E(p,p)$$

- So we examine

$$d(E(x,p))/dx = 0$$

The War of Attrition

$$E(x,p) = \int_0^x (V - y)\,p(y)\,dy - x\int_x^\infty p(y)\,dy$$

War of Attrition

$$E(x,p) = \int_0^x (V-y)\,p(y)\,dy - x\int_x^\infty p(y)\,dy$$

$$dE(x,p)/dx = (V-x)\,p(x) - (1-P(x)) + xp(x) = 0$$

War of Attrition

$$E(x,p) = \int_0^x (V-y)p(y)dy - x\int_x^\infty p(y)dy$$

$$\downarrow$$

$$dE(x,p)/dx = (V-x)p(x) - (1-P(x)) + xp(x) = 0$$

$$\downarrow$$

$$\boxed{Vp(x) = (1-P(x))}$$

War of Attrition

$$E(x,p)=\int_0^x (V-y)p(y)dy - x\int_x^\infty p(y)dy$$

$$\downarrow$$

$$dE(x,p)/dx=(V-x)p(x)-(1-P(x))+xp(x)=0$$

$$\downarrow$$

$$Vp(x)=(1-P(x))$$

$$\downarrow$$

$$p(x)=\exp(-x/V)/V$$

The War of Attrition

- For $S = [0, \infty)$ the only equilibrium is

$$p(x) = \exp(-x / V) / V$$

$$E(x, p) = 0$$

So effort is perfectly converted to reward.
No memory.

The War of Attrition

- Now it can be proved (Bishop & Cannings, 1976) that for all p and q

$$E((p-q),(p-q)) =$$

$$(E(p,p)-E(q,p))-(E(p,q)-E(q,q)) \leq 0$$

with equality only when p=q.

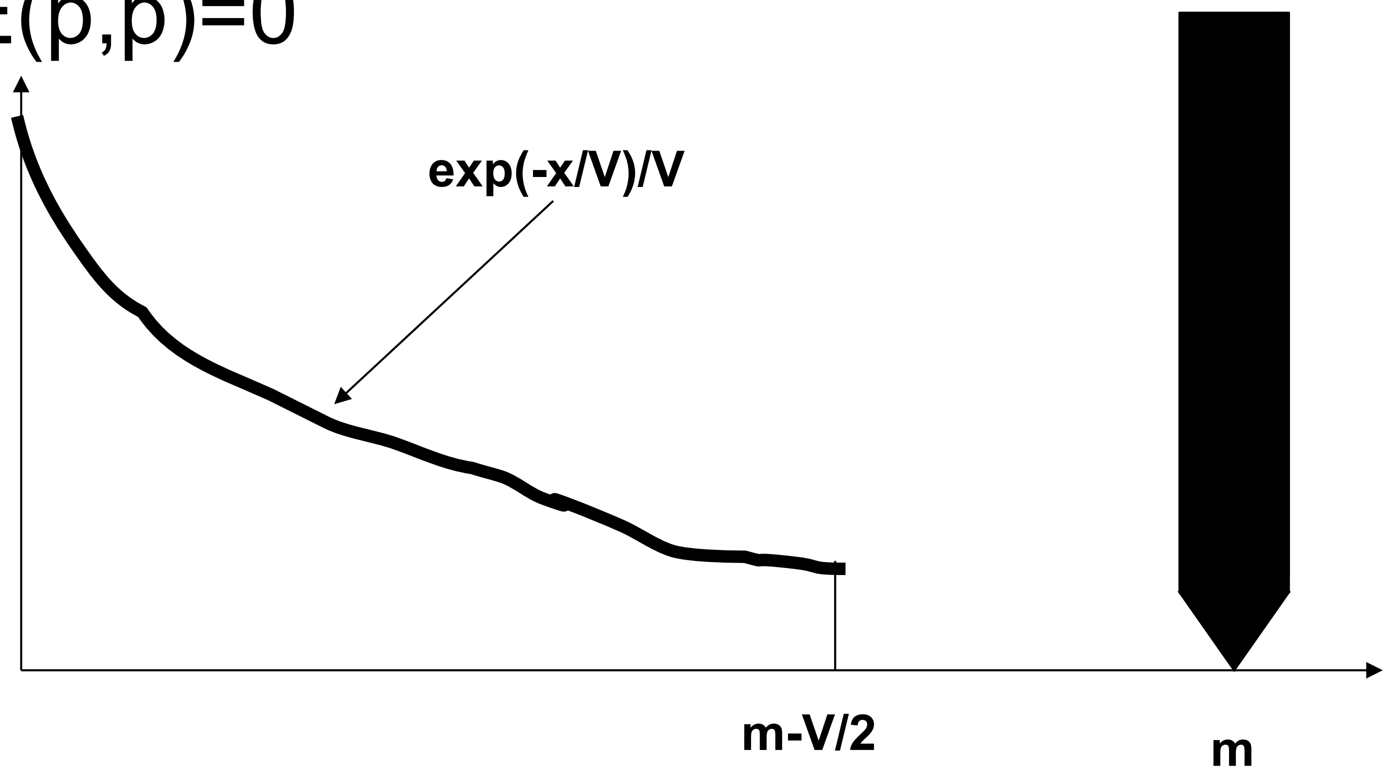
- So given the p (an equilibrium) above it follows that p is an ESS.

Finite Time

- In practice individuals may well be limited in how long they may play e.g. by the onset of sunset, etc.

Finite Interval [0,m]

- Neg. Exp. over [0,m-v/2] and Atom at m.
- E(p,p)=0

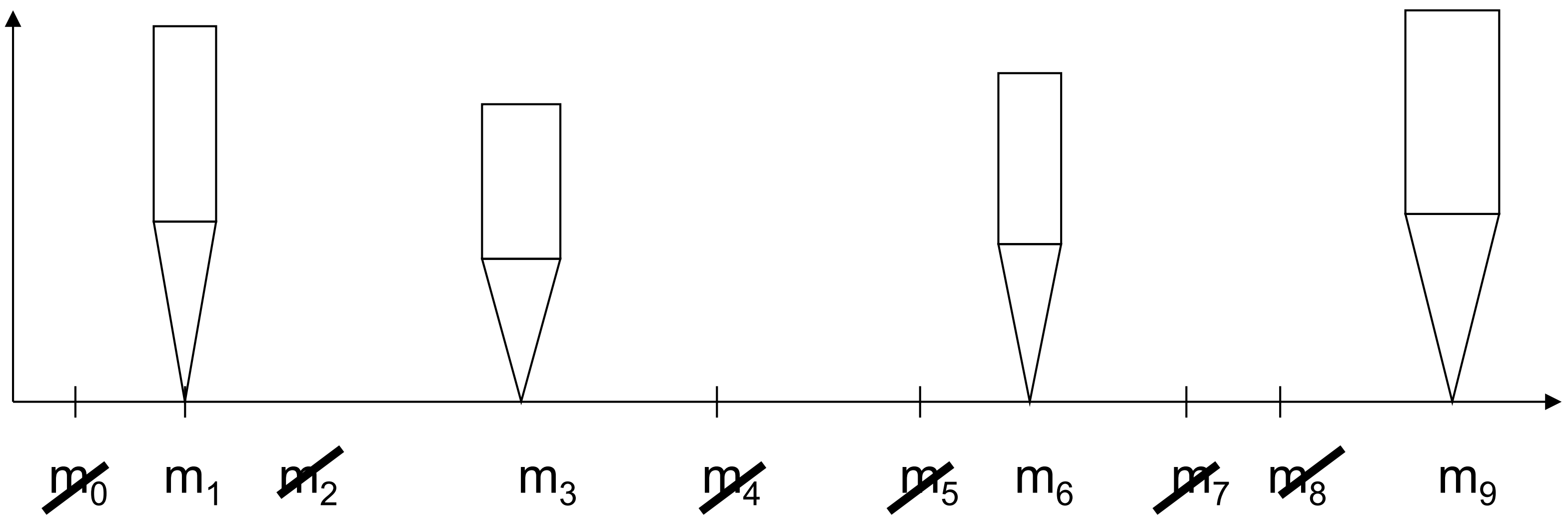


Discrete Plays

- Individuals may be constrained to always play the same (pure) strategy, e.g. they may need to “pick” the size of their weapons, as they will grow.

Discrete Space

- Suppose $S=\{m_0,m_1,m_2,\ldots\ldots\ldots,m_{k-1},m_k\}$ where $m_i<m_{i+1}$ all i. Then (we revisit later) obtain a unique ESS, with atoms on a subset of S, e.g.



Discrete S

- Suppose that T= $\{x_0, x_1, \ldots. x_n\} \subset S$. So we have vectors of frequencies over T.
- Suppose A is the payoff matrix i.e $a_{ij}=f(i,j)$ i,j $\in$ T, then we seek ESS which is equilibrium p, i.e. require

$$Ap = c\mathbf{1}$$

- so need

$$p = A^{-1}1/1^T A^{-1}1 > 0$$

p is an equilibrium

- For p an equilibrium over T to be an ESS we require that $E(x,p)<E(p,p)$ all $x \varepsilon S \backslash T$ and that $C=(c_{ij})=(a_{ij}-a_{in}-a_{nj}+a_{nn})$ is negative definite (see Haigh, 1975 & Abukucs, 1977)

NB. If we take a set of mixtures which span the space then the condition above is still sufficient even though the payoff matrix will be very different.

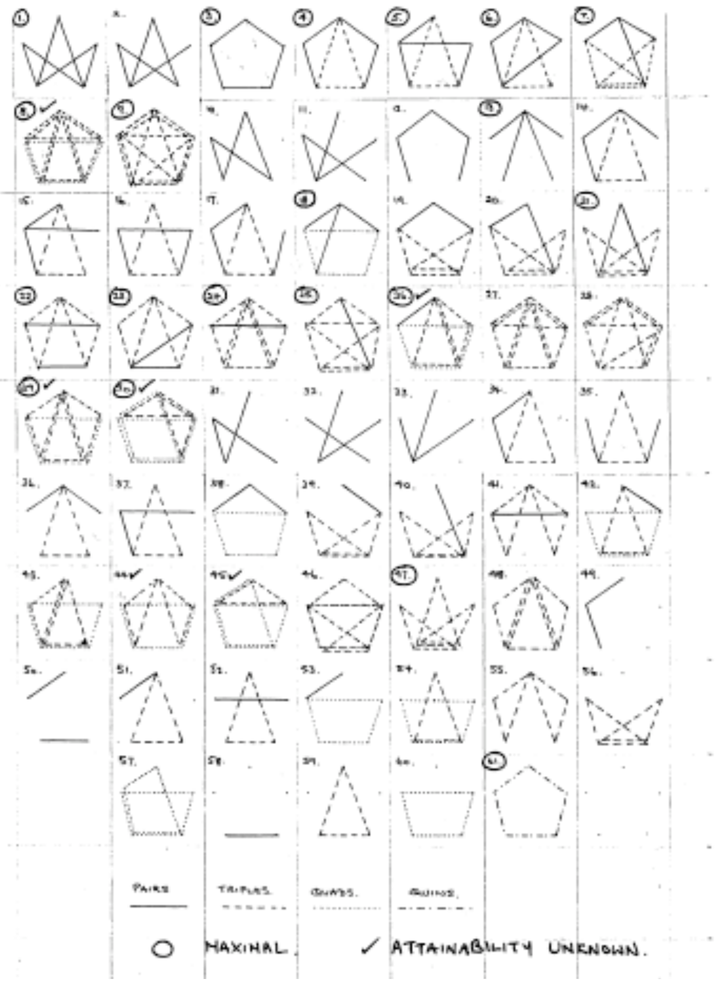
Discrete S

- Thus to find all ESS's we need to examine all the possible T i.e.($2^n - 1$) cases.
- However Bishop and Cannings proved that if there is an ESS on some T then there cannot be an ESS on a subset of T.

Discrete S

- Broom, Cannings,Vickers proved many other restrictions on the coexistence of ESS's for general matrix games.
- Example. Cannot have ESS's on {1,2}, {1,3} and {2,3} simultaneously.

Patterns of ESS's: n=5



Problems with the ESS concept

EVOLUTIONARILY

STABLE

STRATEGY

Problems with the ESS concept

EVOLUTIONARILY

STABLE

IT IS NOT A STRATEGY

~~STRATEGY~~

Problems with the ESS concept

- To be a strategy there must be a proper specification of what plays are available to the individuals.
- The ESS describes the overall play of the population (average).

Problems with the ESS concept

EVOLUTIONARILY

IT IS NOT STABLE

~~STABLE~~

~~STRATEGY~~

The Problem with the ESS concept

- To be stable a system needs a properly specified dynamic; i.e. a description of how the frequencies of the strategies change as a result of the conflicts.

The Replicator Dynamic

- The simplest dynamic supposes that the frequency of a strategy i (properly specified) at time (discrete) t , say, is given by x_t^i in p_t

$$x_{t+1}^i = x_t^i (c + E(i, p_t)) / (c + E(p_t, p_t))$$

$$= x_t^i \{\sum_{j=1}^n (c + a_{i,j} x_t^j)\} / \{\sum_{j=1}^n \sum_{k=1}^n (c + a_{j,k}) x_t^j x_t^k\}$$

Here A=($a_{i,j}$) is the payoff matrix, c is the constant background fitness, p_t is the population strategy frequency.

The Replicator Dynamic

- Note that the value of c does not affect the set of ESS's.
- It may affect the behaviour of the dynamic.

W of A

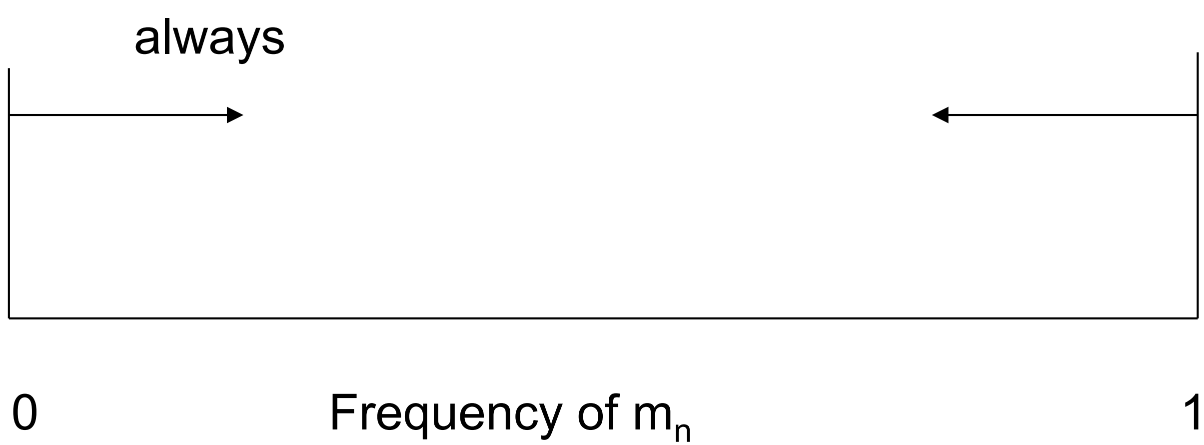
- In the War of Attrition on any S (of pure plays) in fact there is a unique ESS (ignoring sets of measure zero).
- Moreover under the replicator dynamic convergence is assured.
- The value of c is irrelevant to the dynamics.

War of Attrition; 2 strategies $m_{n-1}<m_n$

Payoff matrix

$$\begin{bmatrix} V/2 - m_{n-1} & -m_{n-1} \\ V - m_{n-1} & V - m_n \end{bmatrix}$$

If $(m_n - m_{n-1}) > V/2$ there is a polymorphic ESS
Otherwise only m_n present.



Convergence of the frequencies is monotone

War of Attrition

- Payoff Matrix

	0	1	2	…….	n-2	n-1	n
0	$V/2-m_0$	$-m_0$	$-m_0$	.....	$-m_0$	$-m_0$	$-m_0$
1	$V-m_0$	$V/2-m_1$	$-m_1$	.....	$-m_1$	$-m_1$	$-m_1$
2	$V-m_0$	$V-m_1$	$V/2-m_2$	.....	$-m_2$	$-m_2$	$-m_2$
	.	.	.	.....	.	.	.
	.	.	.	.....	.	.	.
n-2	$V-m_0$	$V-m_1$	$V-m_2$	.....	$V/2-m_{n-2}$	$-m_{n-2}$	$-m_{n-2}$
n-1	$V-m_0$	$V-m_1$	$V-m_2$	.....	$V-m_{n-2}$	$V/2-m_{n-1}$	$-m_{n-1}$
n	$V-m_0$	$V-m_1$	$V-m_2$	.....	$V-m_{n-2}$	$V-m_{n-1}$	$V/2-m_n$

War of Attrition: Discrete S

- Noting that the entries in the rows from i to n up to the (i-1)th position are identical we see that the equilibria over some T and some W $\supset$ T must have precisely the same relative frequencies over the set T.
- Thus we can find the ESS's by working sequentially from m_n to $\{m_n, m_{n-1}\}$ to $\{m_n, m_{n-1}, m_{n-1}\}$ and so on.

m_k vis-à-vis $\{m_{k+1}, m_{k+2}, \ldots\ldots, m_n\}$

- Suppose we have the ESS over the set of strategies $\{m_{k+1}, m_{k+2}, \ldots\ldots, m_n\}$ with frequencies $\{p_{k+1}, p_{k+2}, \ldots\ldots, p_n\}$, and consider m_k. Now
- $E(m_k;p)=-m_k$ and

  $E(m_{k+1},p)=E(p,p)= 0.5Vp_{k+1}-m_{k+1}$
- m_k invades if $W=(m_{k+1}-m_k) - Vp_{k+1}/2 > 0$ and its frequency converges monotonically to $p_k=W/(W+V/2)$, as the frequencies of the other strategies converge monotonically to

  $\{p_{k+1}, p_{k+2}, \ldots\ldots, p_n\}/(1-p_k)$

War of Attrition

- As we add new m_i's there is a requirement for gaps of sufficient sizes. For example if we have $m_2=10$ and $m_1=4$ then we obtain ESS $p_2=5/6$ and $p_1=1/6$ with $E(p,p)= -19/6$. Invaded by any $m_0<19/6$.
- In general a new strategy m_0 invades iff $m_0<$ where p is the ESS over the strategies in the population $> m$.

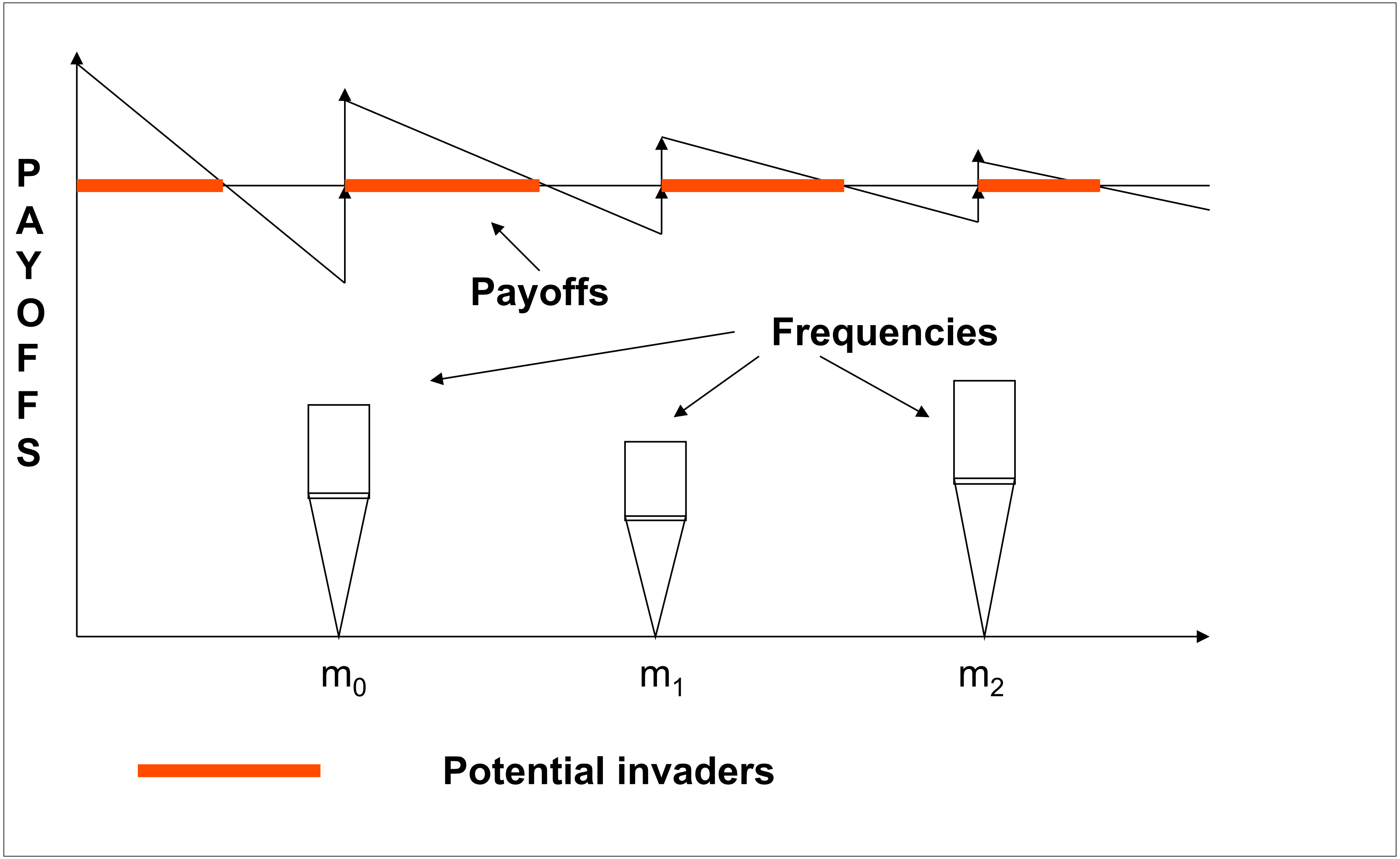
W of A: 3 strategies

- Example. m_0=3.5, m_1=4, m_2=10, V=10
  ESS p=(0, 5, 25)/30

- Example. m_0=2, m_1=4, m_2=10, V=10
  ESS p=(7, 5, 25)/37

- Example. m_0=1, m_1=4, m_2=10, V=10
  ESS p=(17, 5, 25)/47

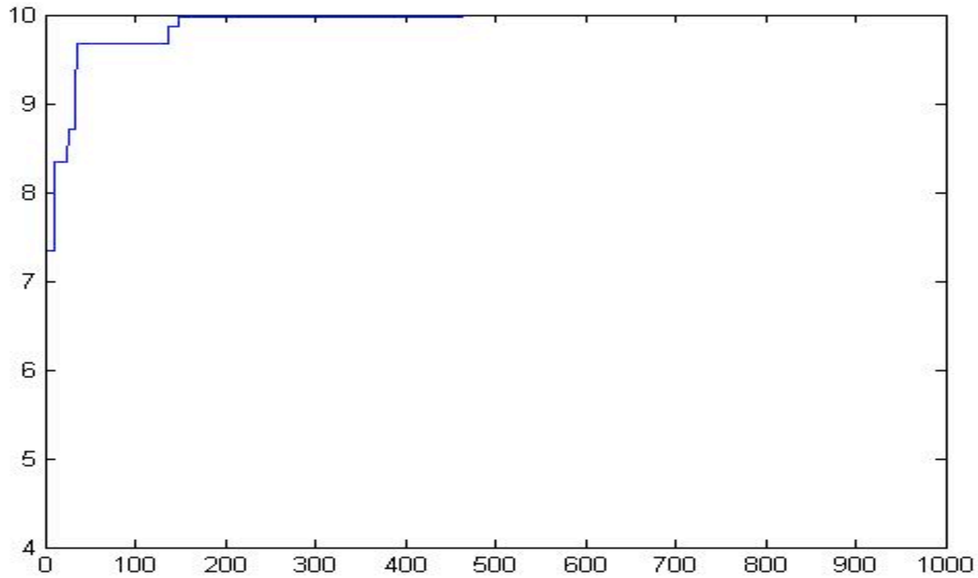
Payoffs: Discrete S={$m_0<m_1<m_2$}



Invasions; V=10 & range [0,10]

- We start with a single strategy {0} and then allow strategies to occur randomly, and if they invade they reach equilibrium before a new mutation occurs.
- Convergence is monotone

Top m-value

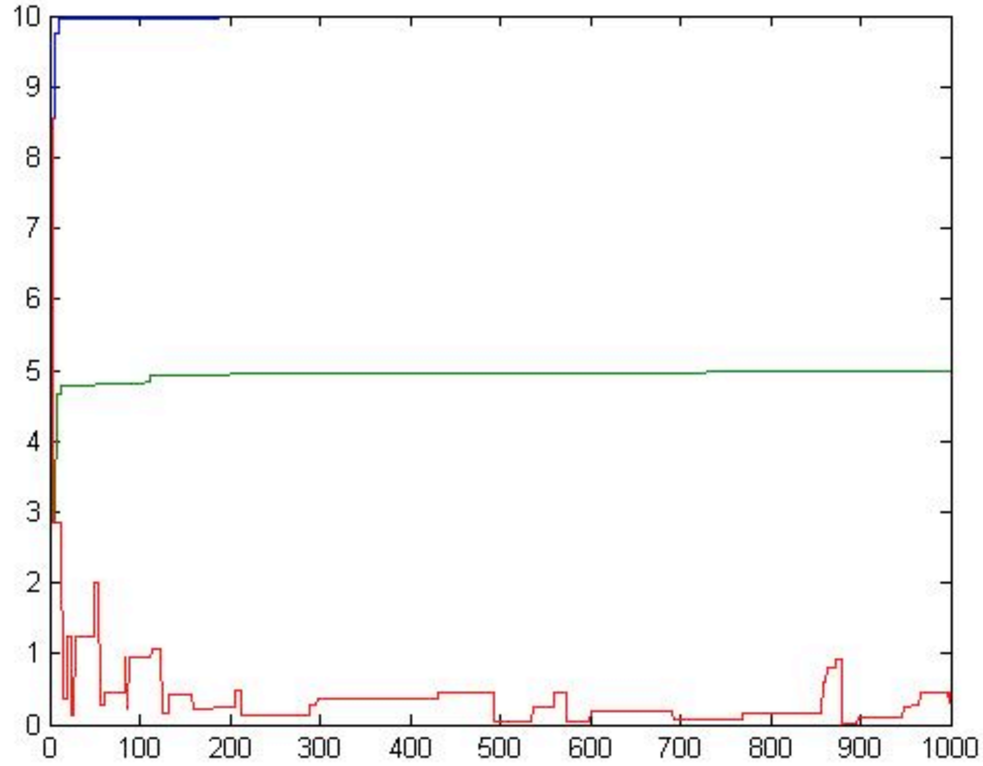


Greatest strategy

Time

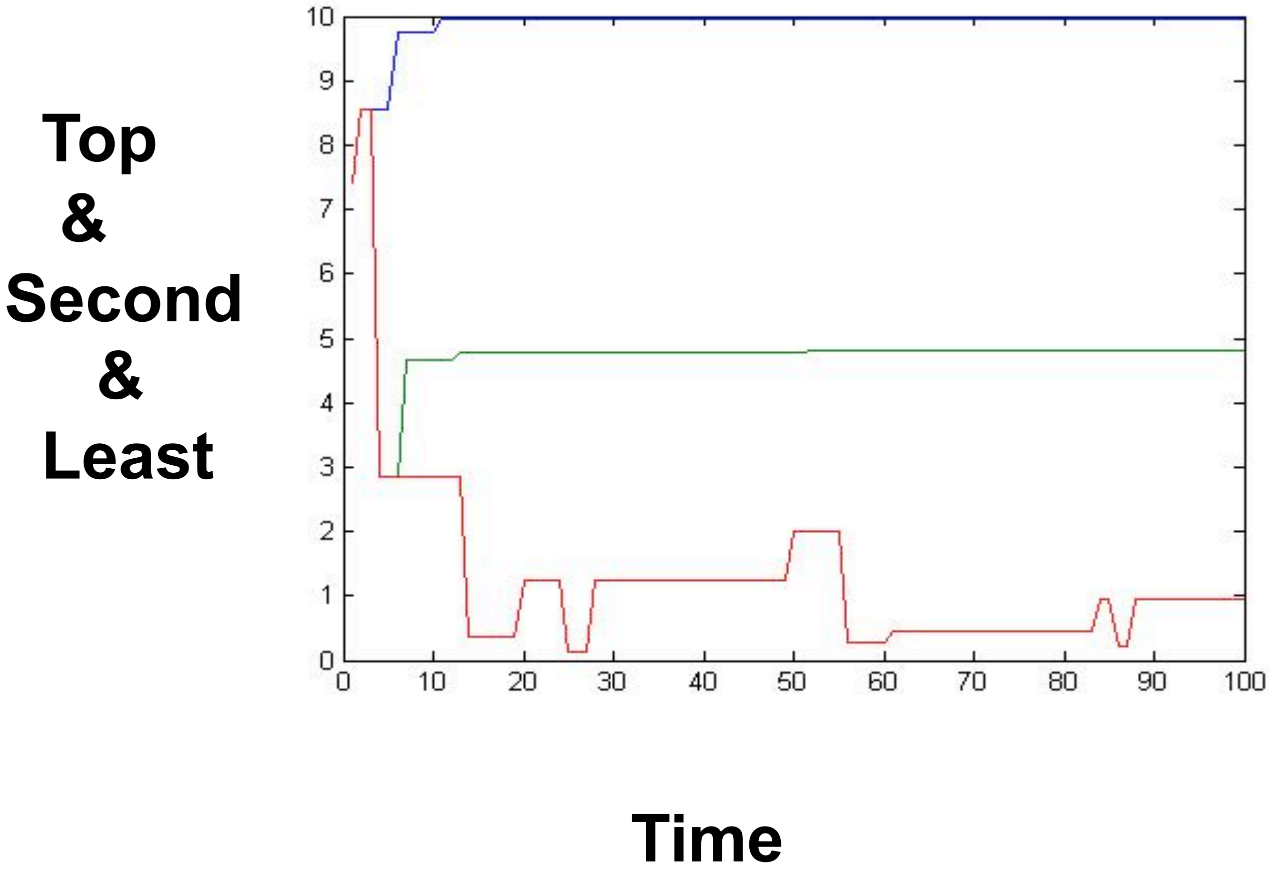
Top, Second & Least: V=m=10

Top
&
Second
&
Least

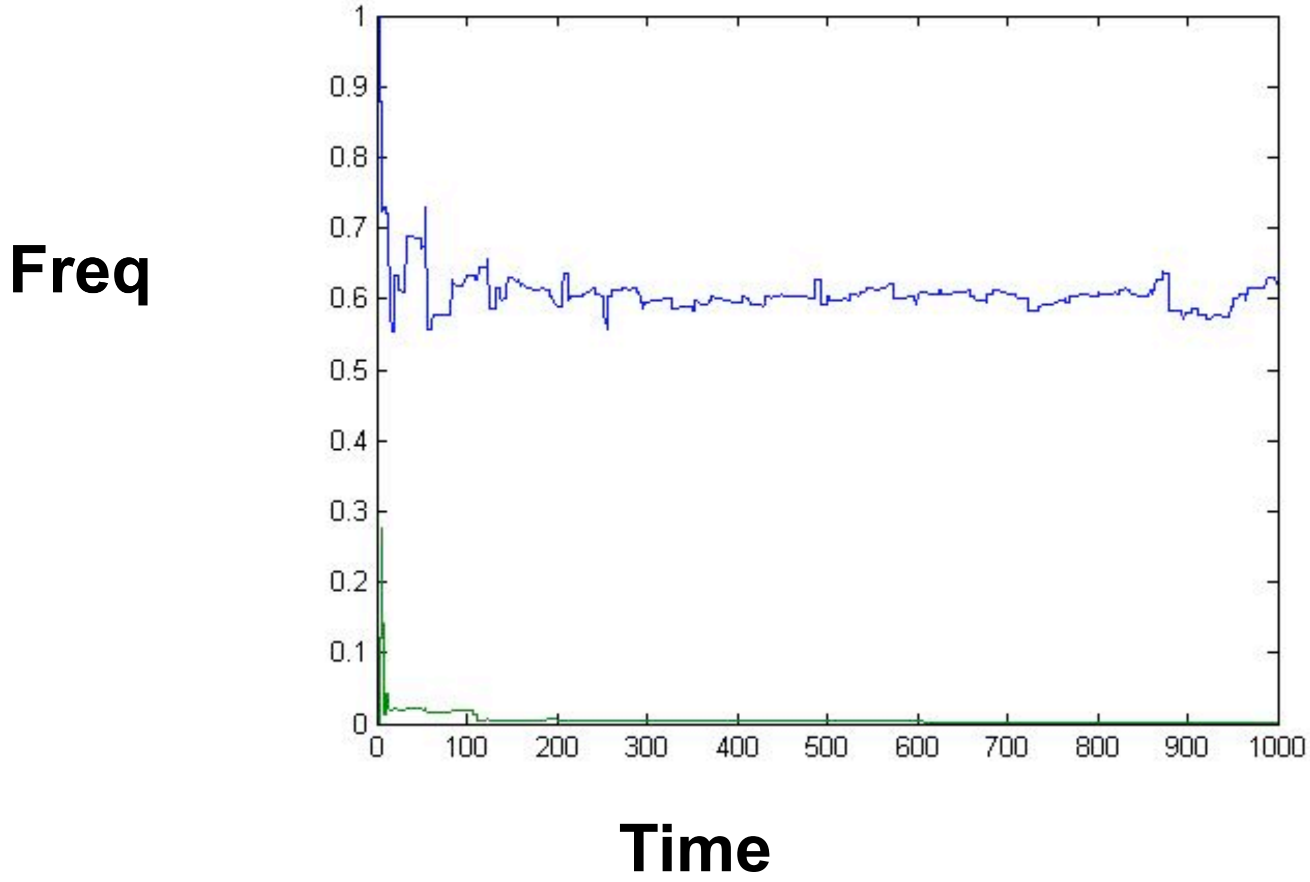


Time

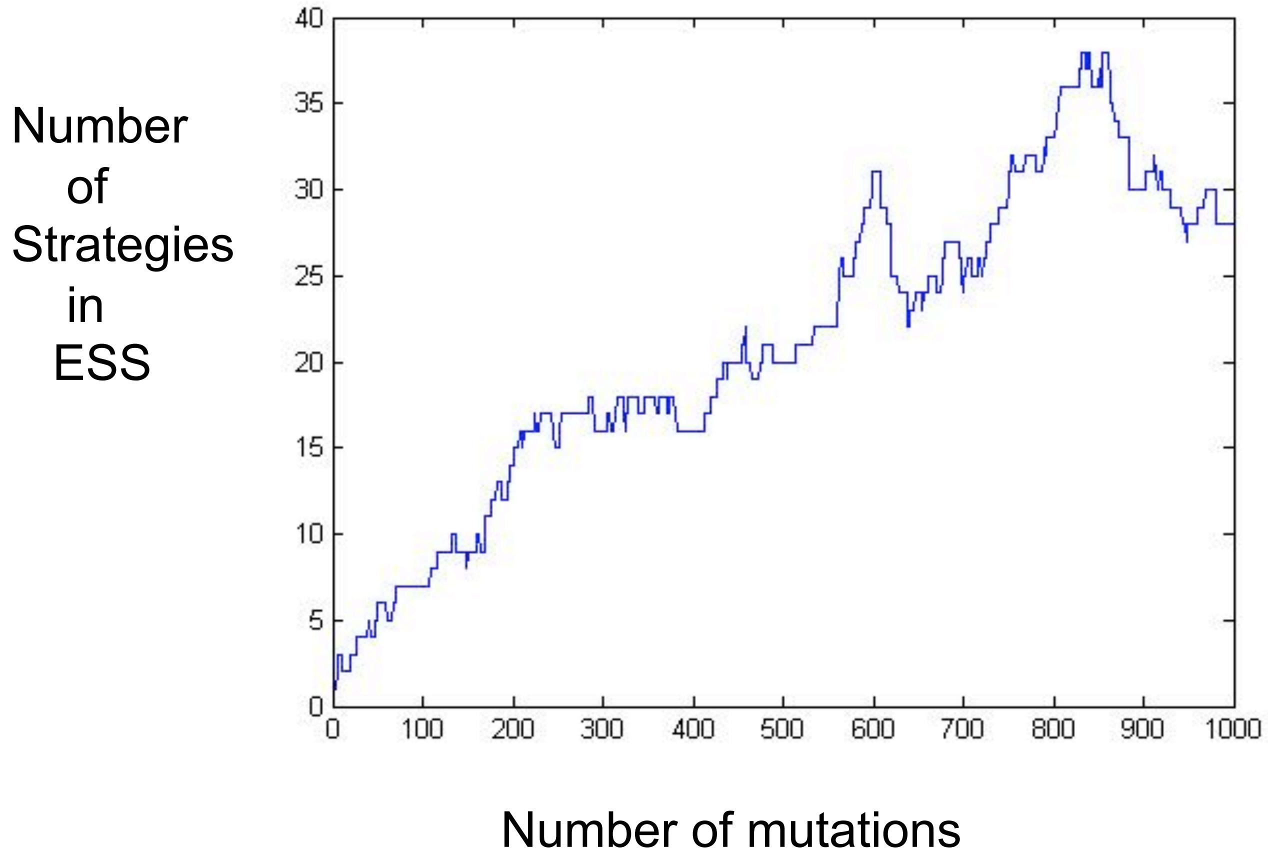
Top, Second, Least V=m=10



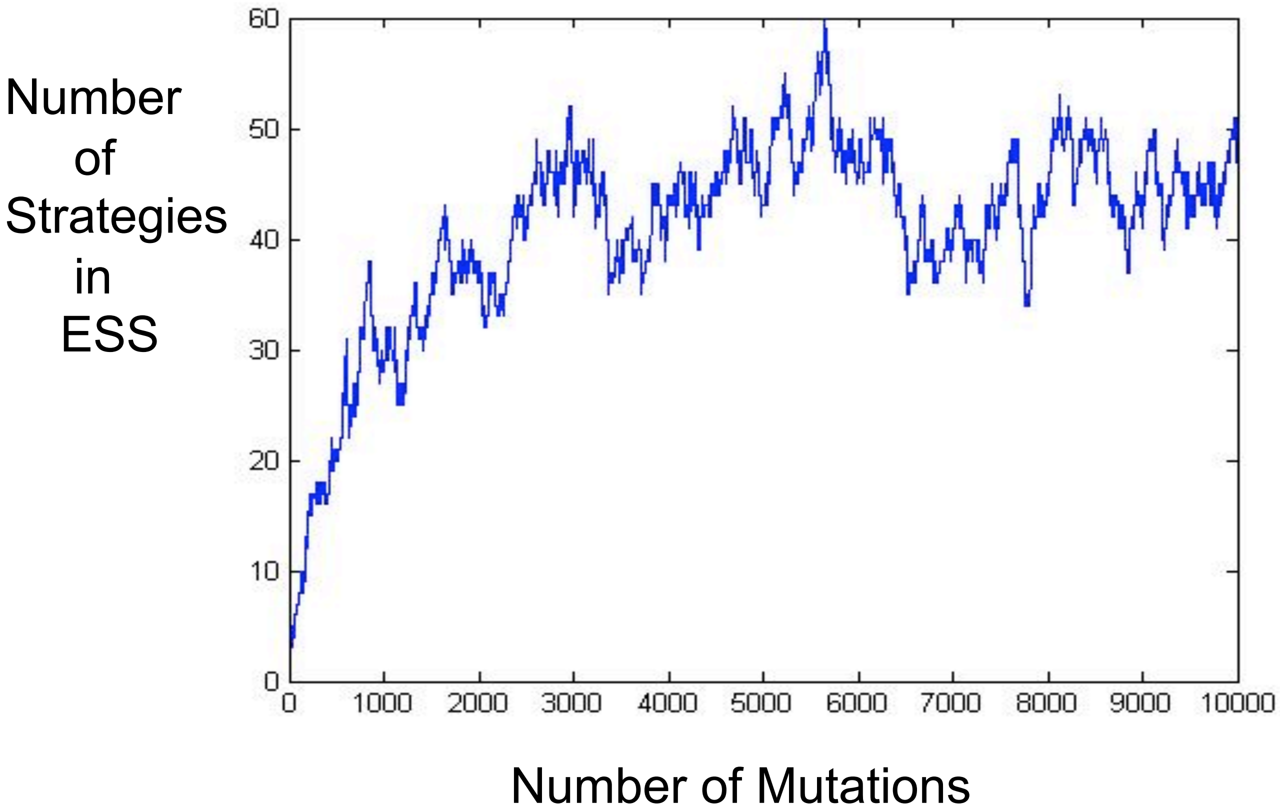
Frequencies of largest strategy



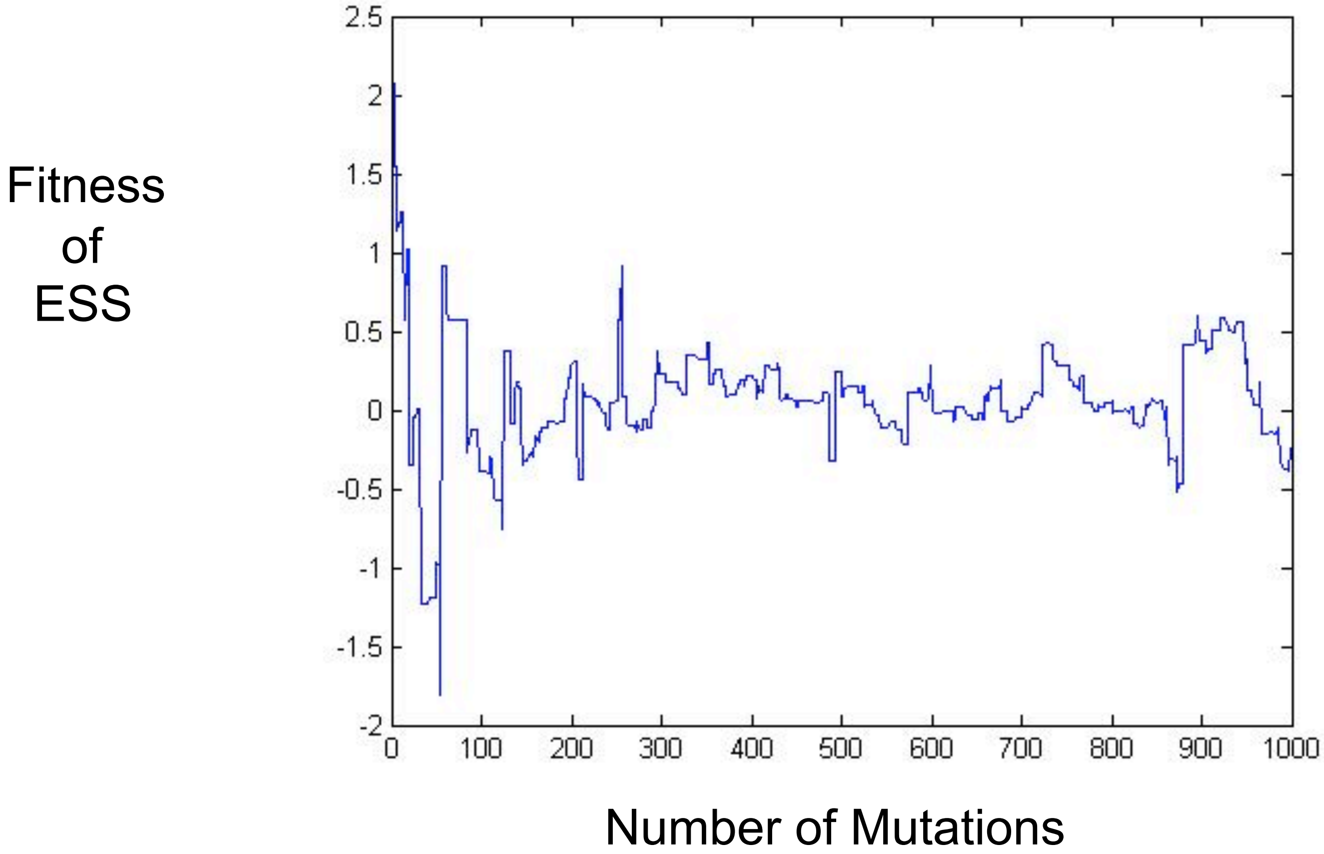
Number of Strategies



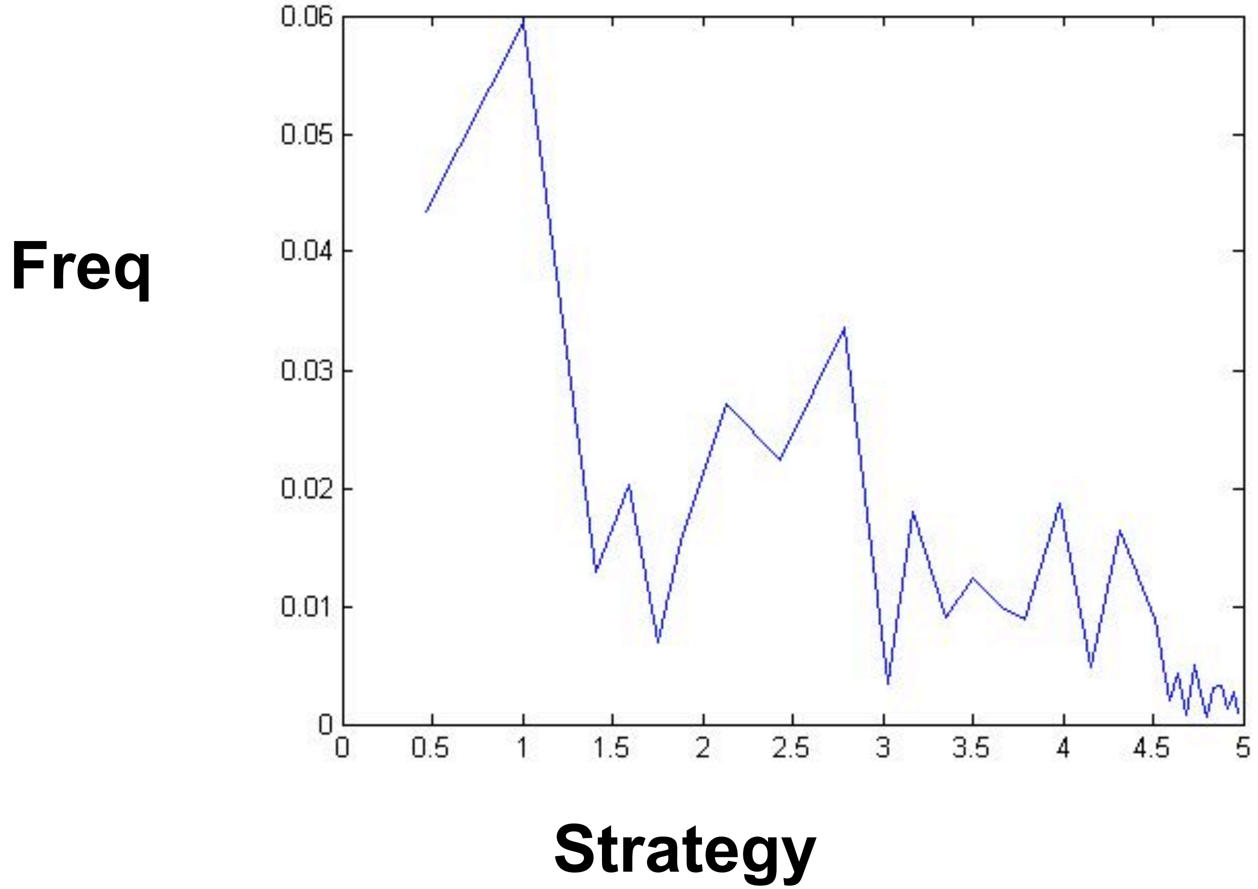
Number of Strategies



E(p,p) through Time

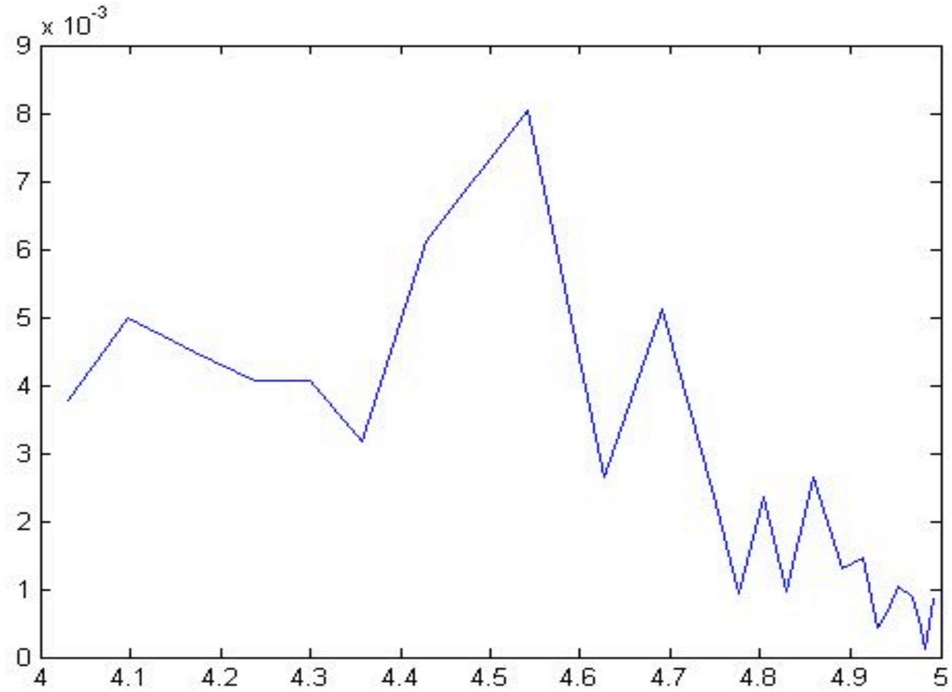


Frequencies of strategies after 1,000 steps (V=m=10)



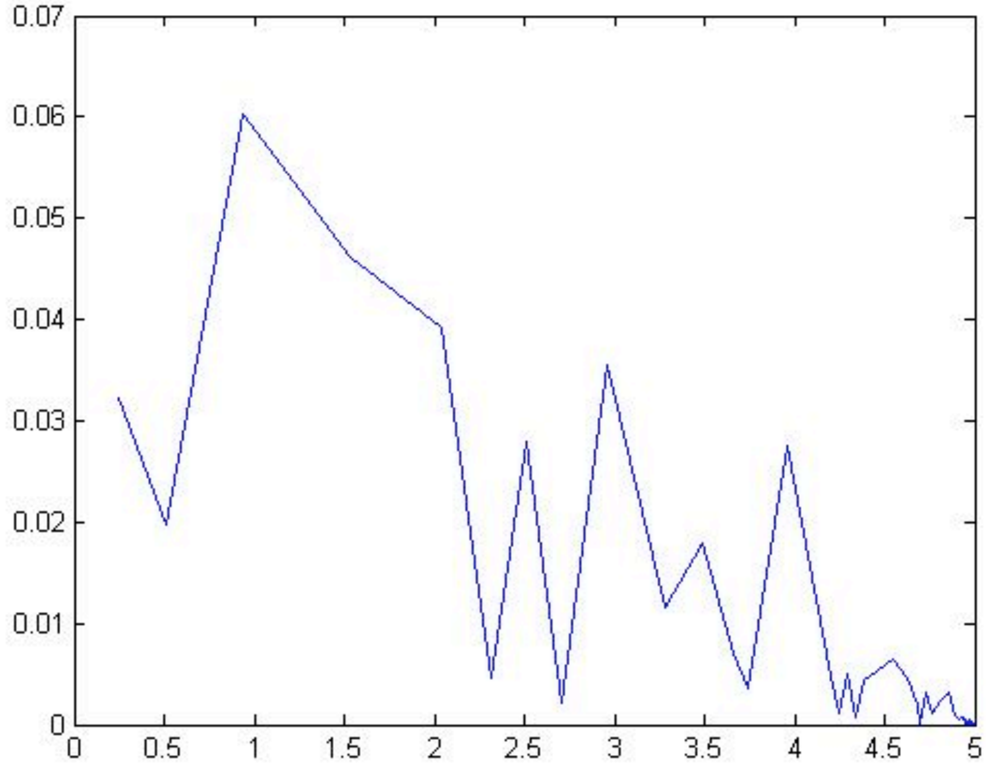
Frequency of strategies>4 after 10,000 steps (V=m=10)

Freq



Strategy

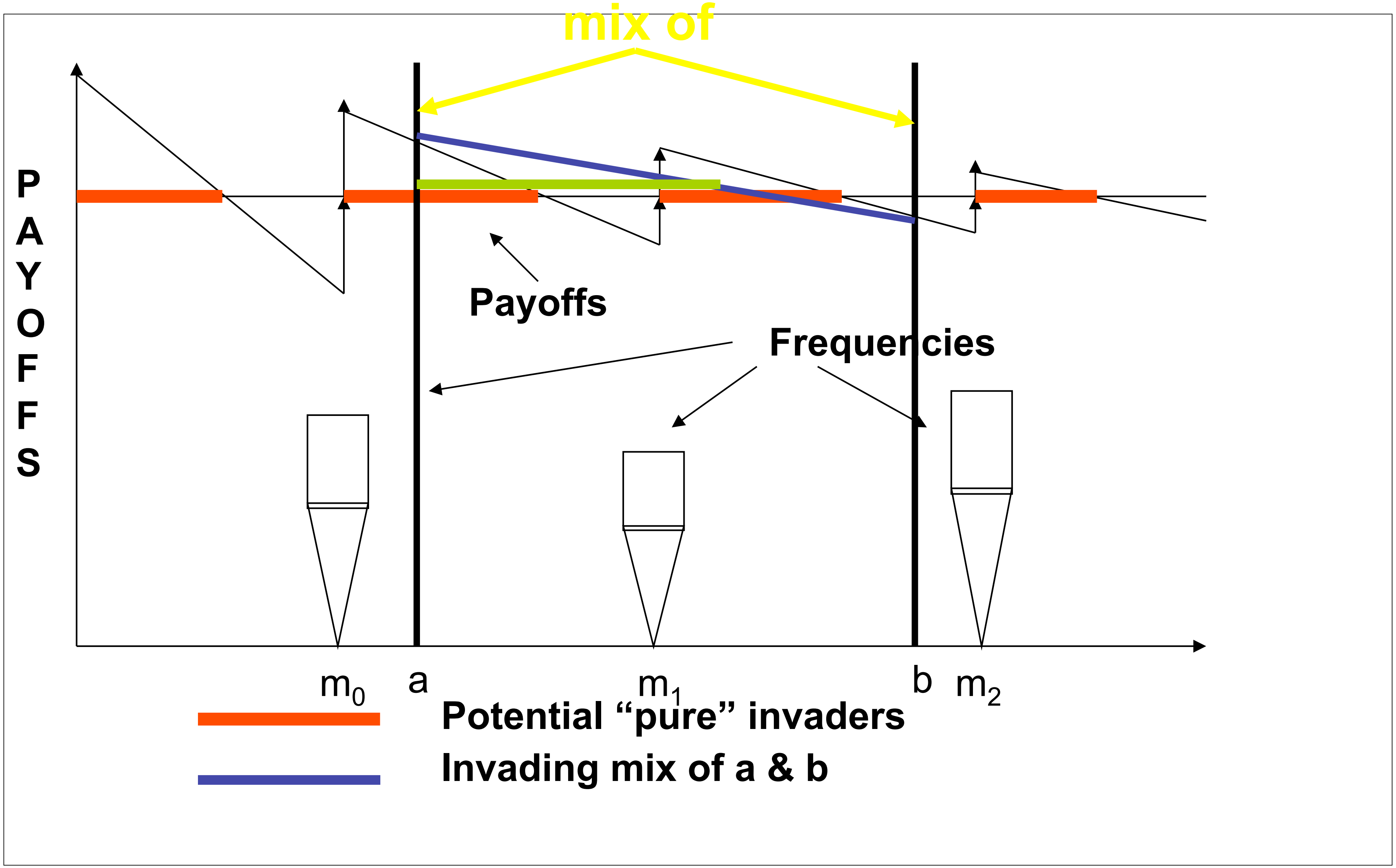
Frequencies of strategies after 100,000 steps (V=m=10)



Mixed Strategies

- How is the dynamic affected by including the possibility of mixed strategies (i.e. individuals play a variety of values)?

Payoffs: Discrete $S=\{m_0<m_1<m_2\}$



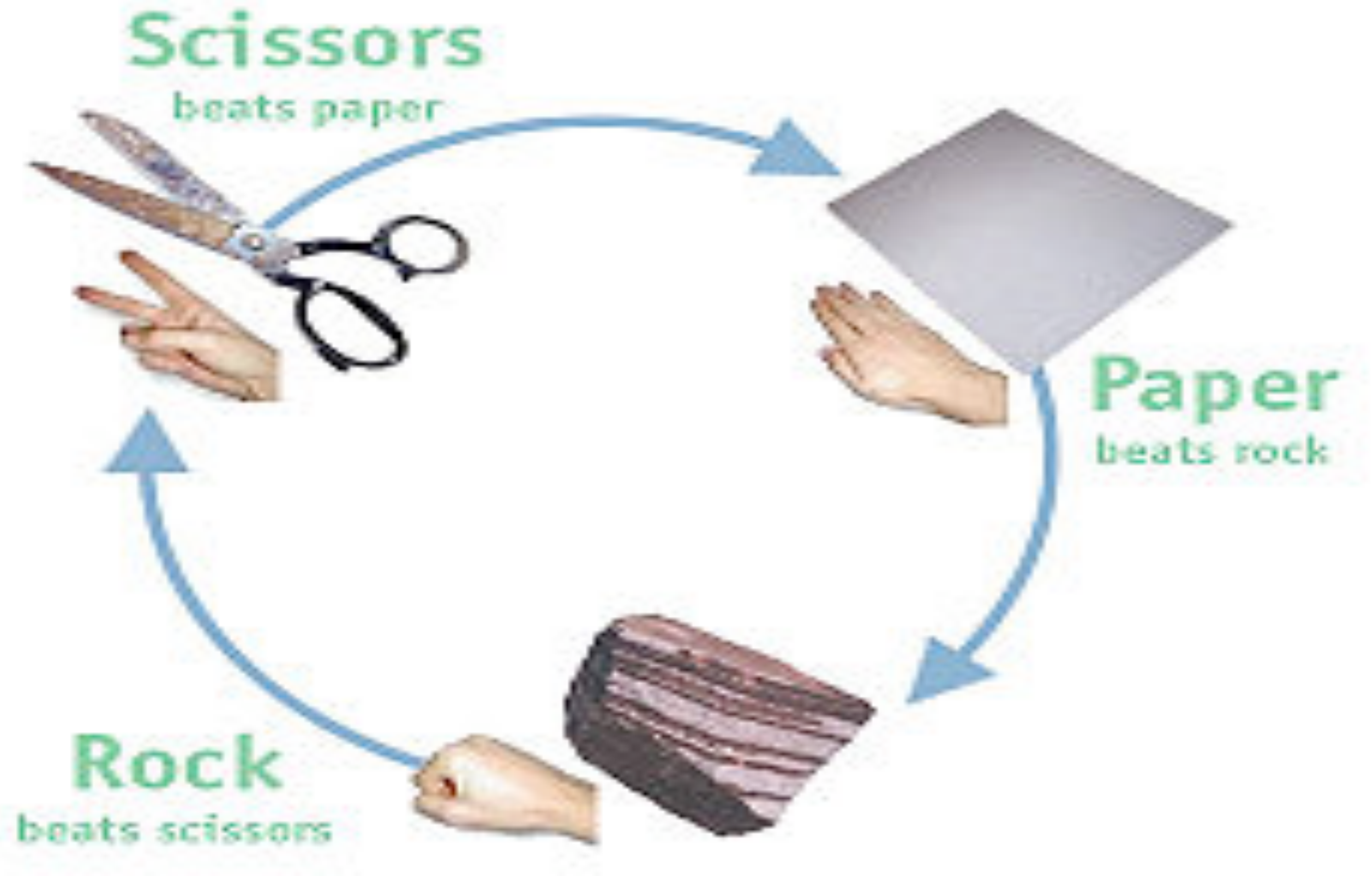
Mixed Strategies

- Strategies may invade which as pures could not, but cannot persist permanently if they contain a component from within the (m-V/2,m) range, since at some stage the better components will begin to give lower payoffs.
- Unless there is a cost associated with playing mixtures they will be neutral with respect to the ESS.

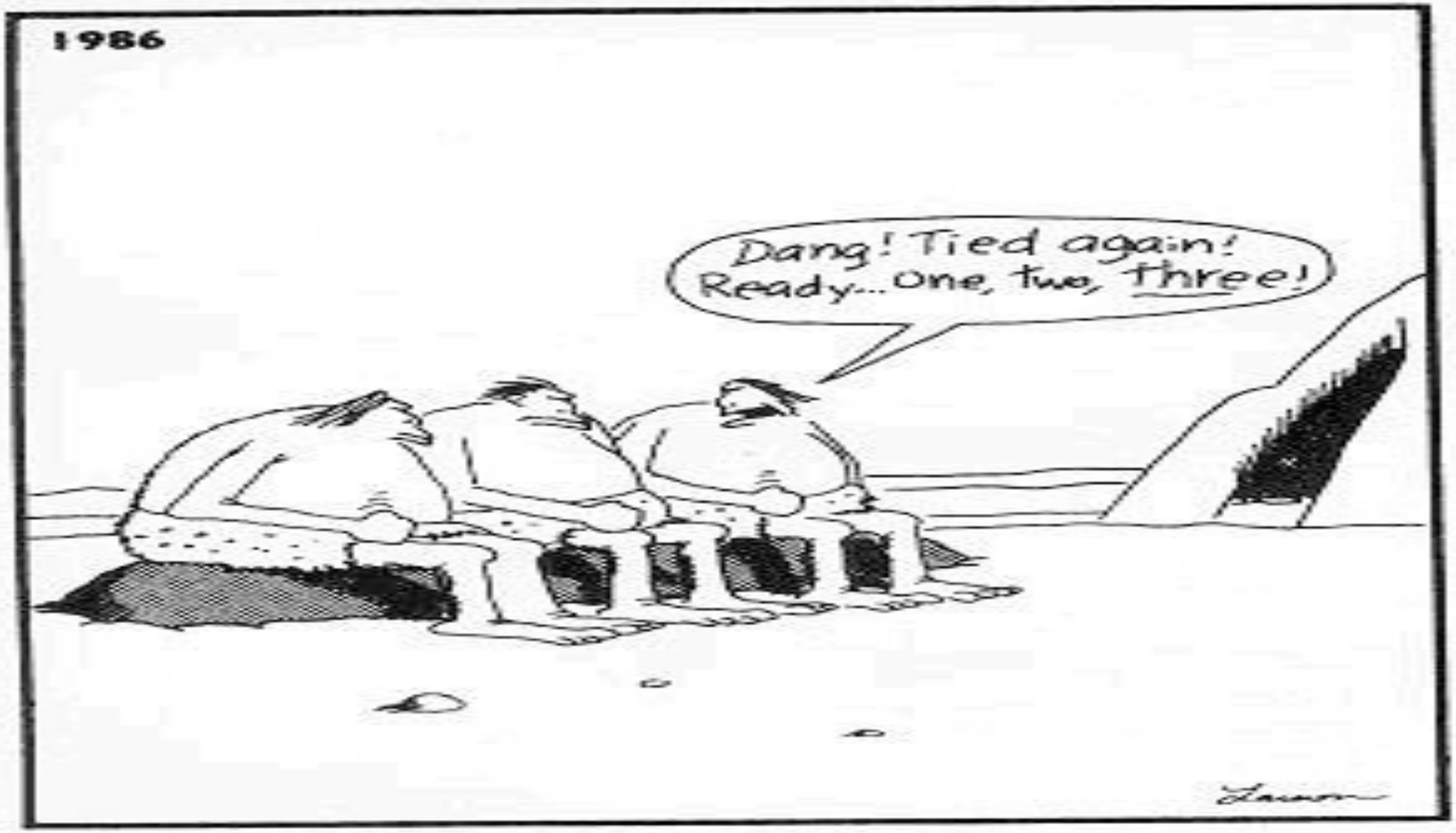
War of Attrition

- The simplicity of the W of A arises from the ordinal nature of the payoffs.
- We change now to another conflict which has symmetric strategies, but radically different behaviour.

Papier-Caillon-Ciseaux



RRR (from Gary Larson)



Before paper and scissors

Common Side-Blotched Lizard

http://en.wikipedia.org/wiki/Common_Side-blotched_Lizard

Beats

Papier-Caillon-Ciseaux

- rock-scissors-paper
-

$$A = cU + \begin{pmatrix} -\varepsilon & 1 & -1 \\ -1 & -\varepsilon & 1 \\ 1 & -1 & -\varepsilon \end{pmatrix}$$

	R	S	P
R	$-\varepsilon$	1	-1
S	-1	$-\varepsilon$	1
P	1	-1	$-\varepsilon$

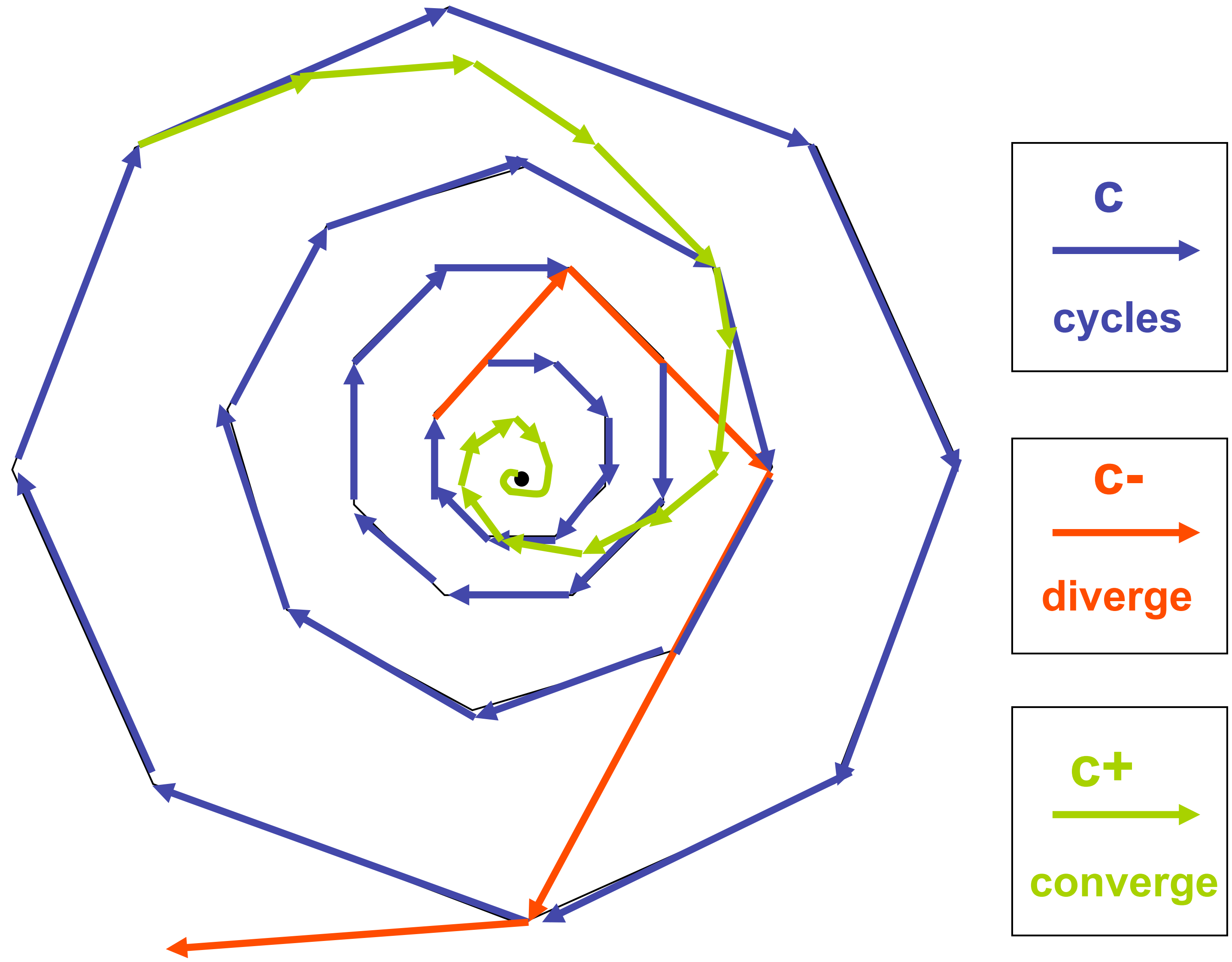
C is the background fitness, ε is a cost of a tie,
U **is the matrix of 1's**

Theory

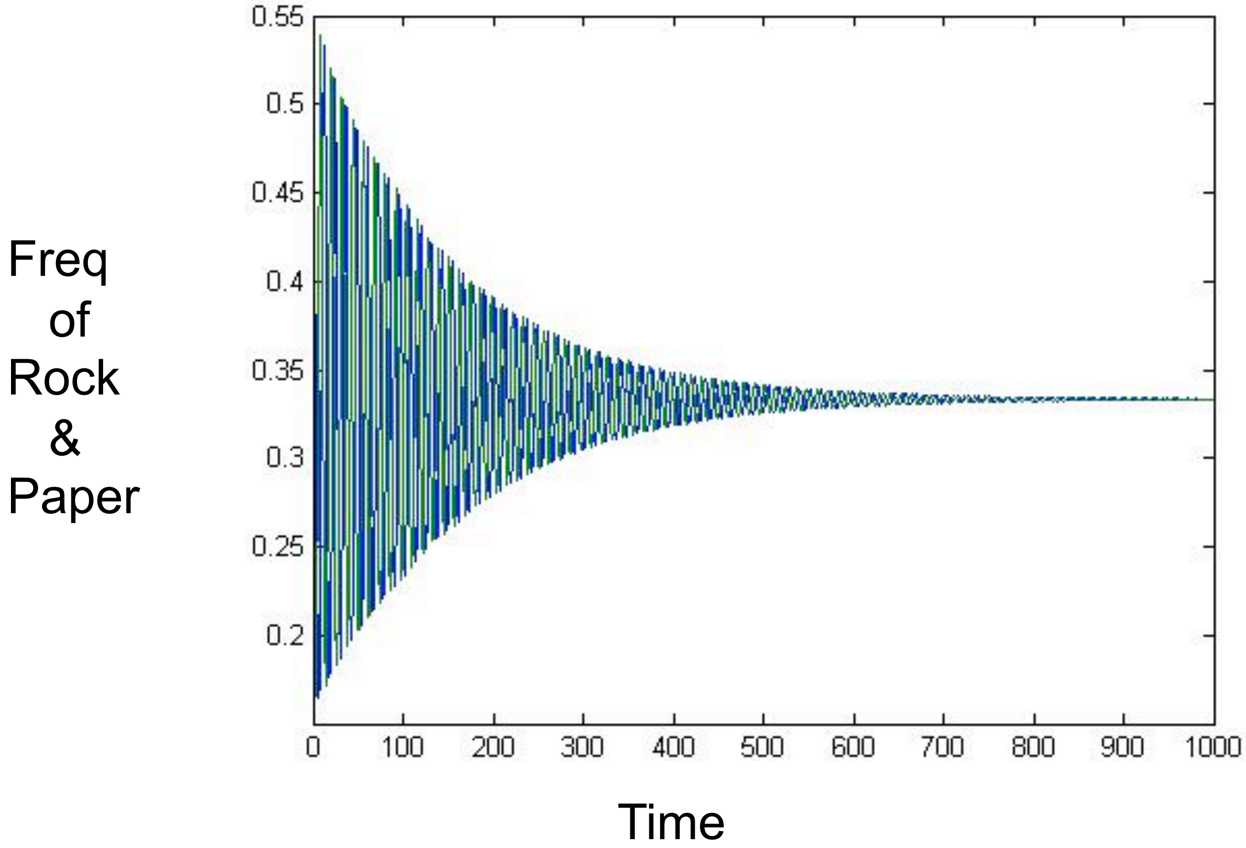
- The only possible ESS is **p**=(1,1,1)/3.
- If ε > 0 ESS at p.
- For the replicator dynamics with S={R,S,P}, the system converges to p only if

$$c > (1 + \varepsilon^2) / 2\varepsilon$$

The effect of c

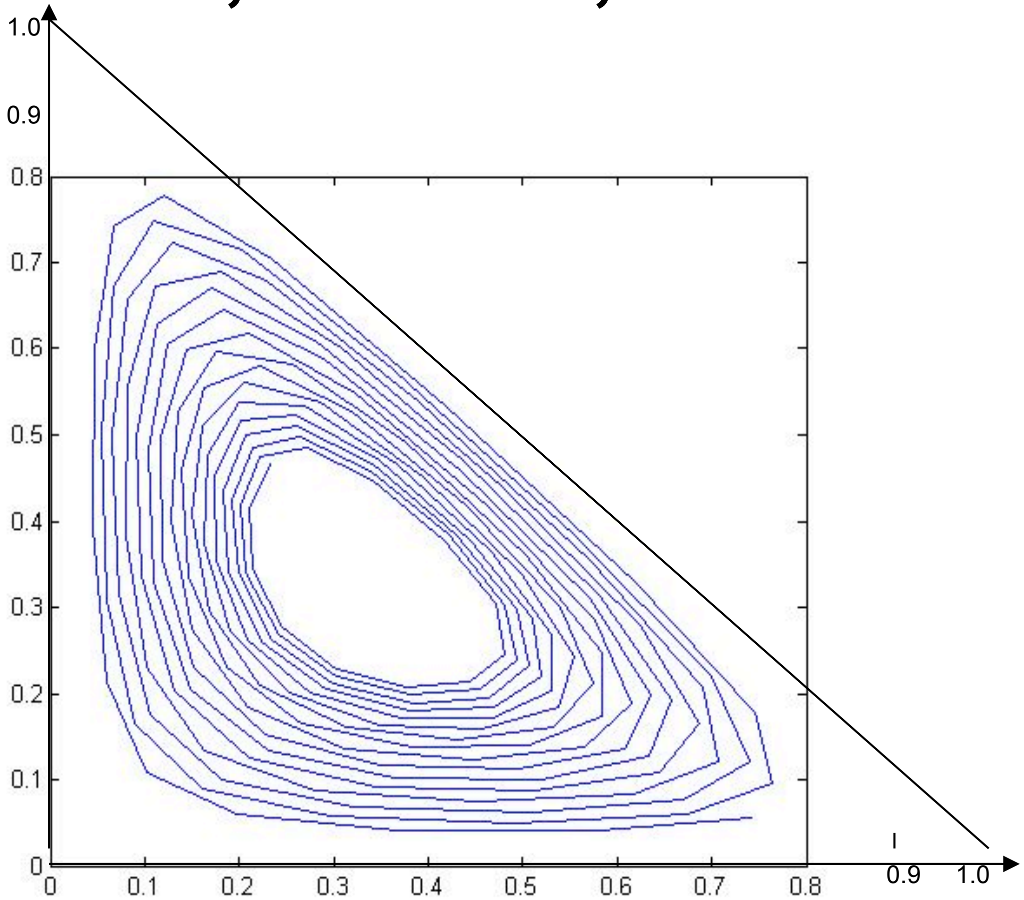


RSP, c=1.3,ε=0.5


Freq of Rock & Paper
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0
100
200
300
400
500
600
700
800
900
1000
Time

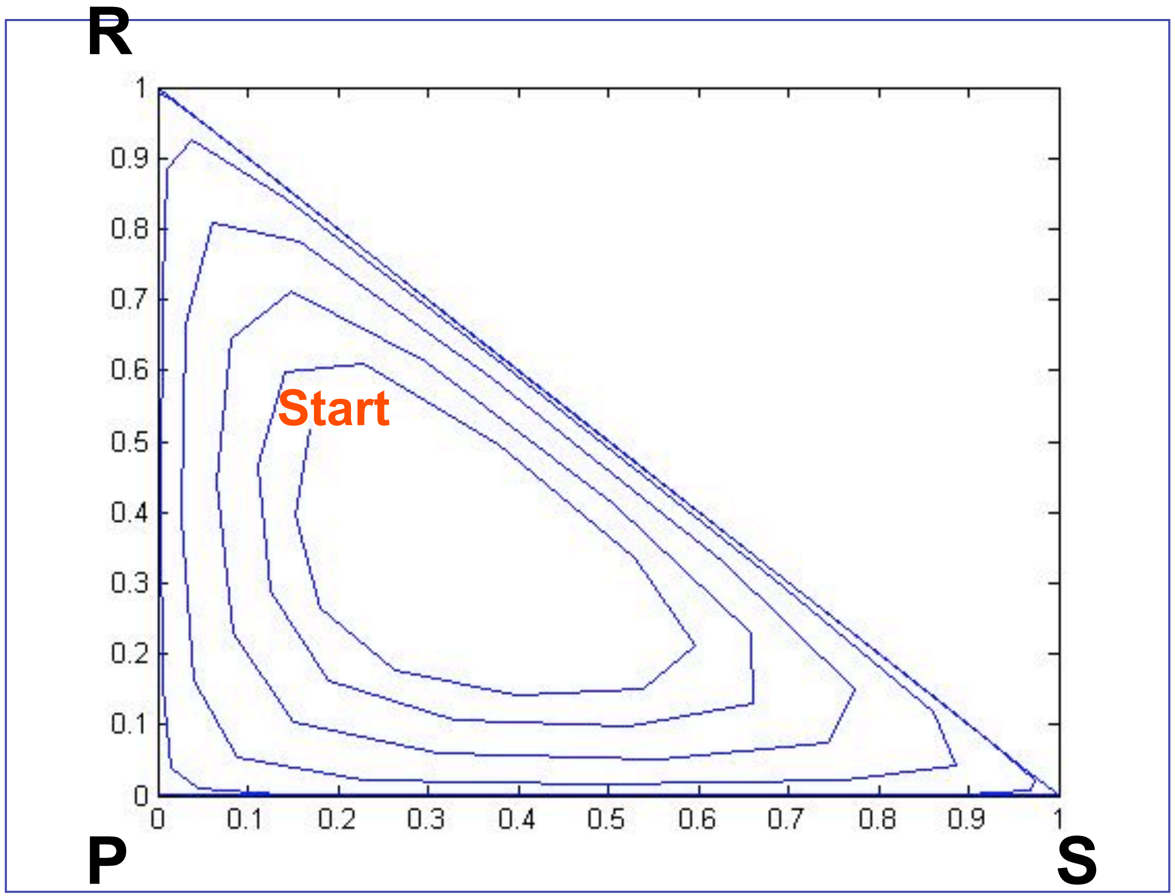
RSP, c=1.3,ε=0.5

Spirals in



RSP, c=1.1,ε=0.5

Spirals out



Cyclic Mixtures

- If we take three mixtures (x,y,z), (y,z,x) and (z,x,c) then the payoff matrix is just

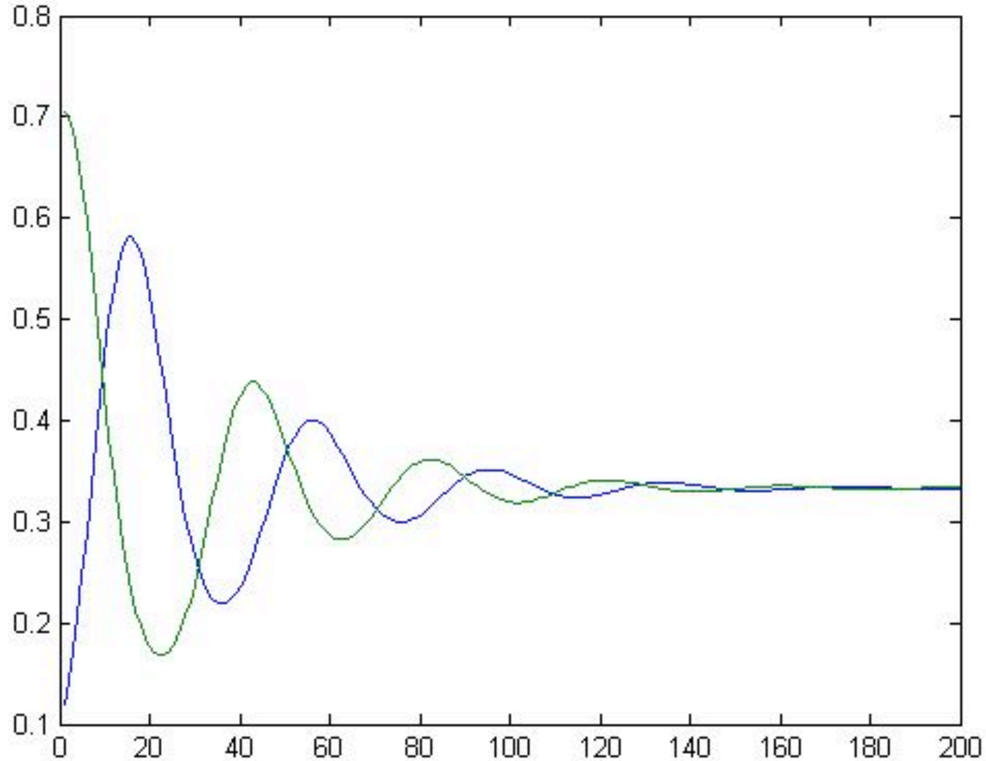
  $A^* = \lambda(A + dU)$

  where d>0, U is matrix of 1's, λ is a constant (has no effect).

  Thus taking such mixture may switch from divergent to convergent dynamic.

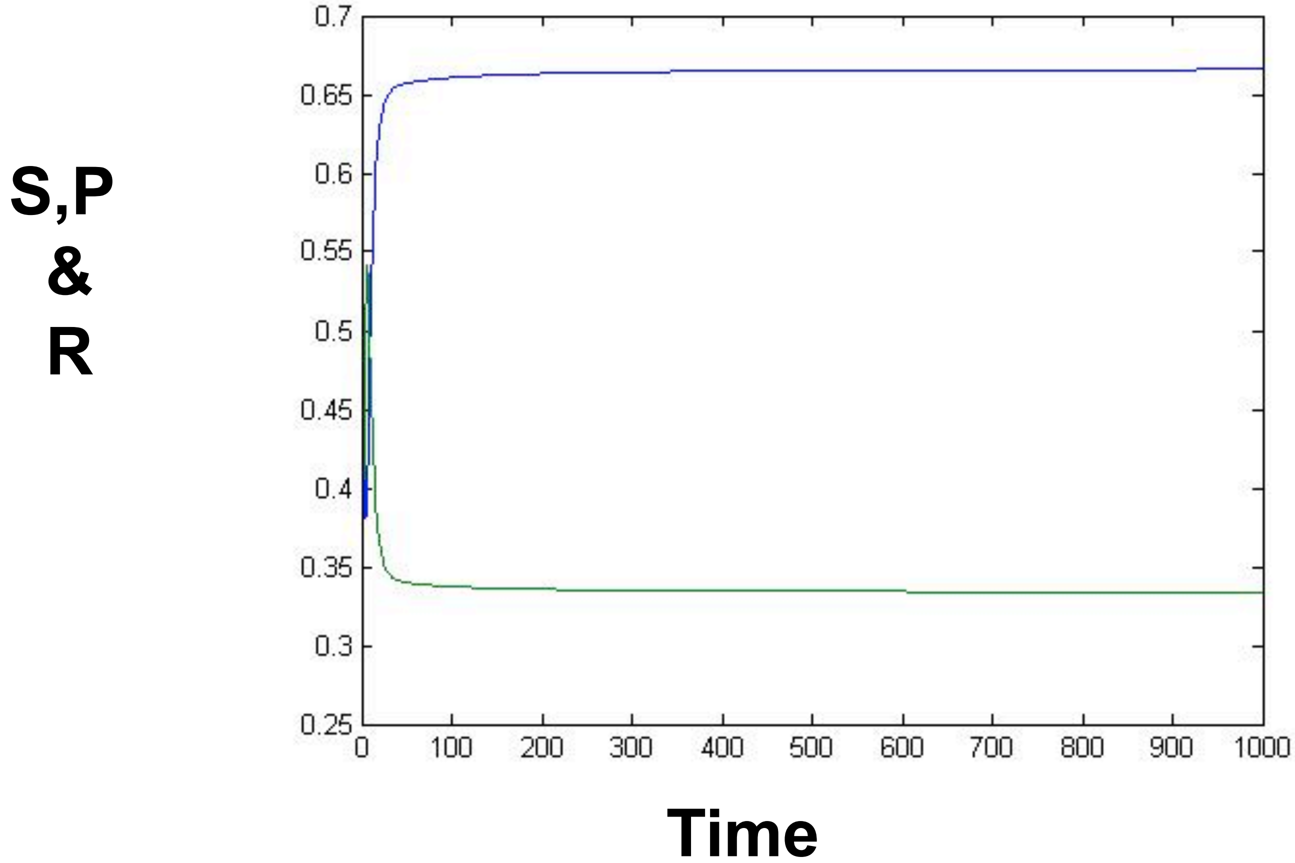
(RS*), (R*P), & (*SP); c=1.1,ε=0.5

Freq of RS* & R*P



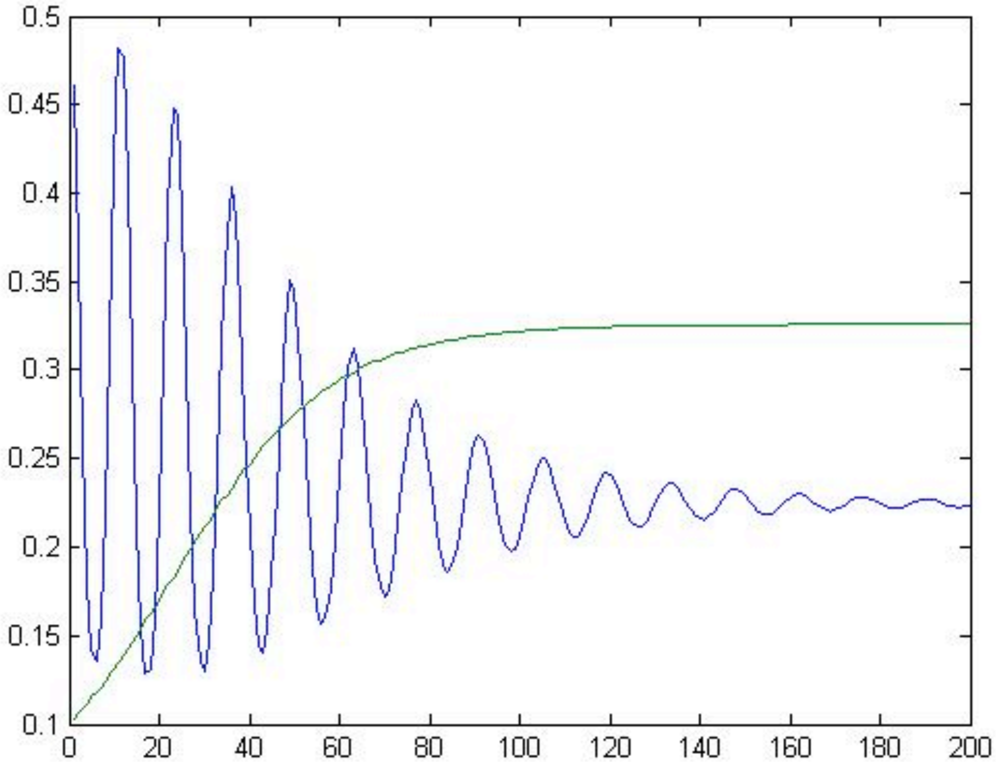
Time

{S,P},R,S k=1.1,ε=0.5


S,P
&
R
0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0
100
200
300
400
500
600
700
800
900
1000
Time

Pures & (R,S,P)/3 , k=1.1,ε=0.5

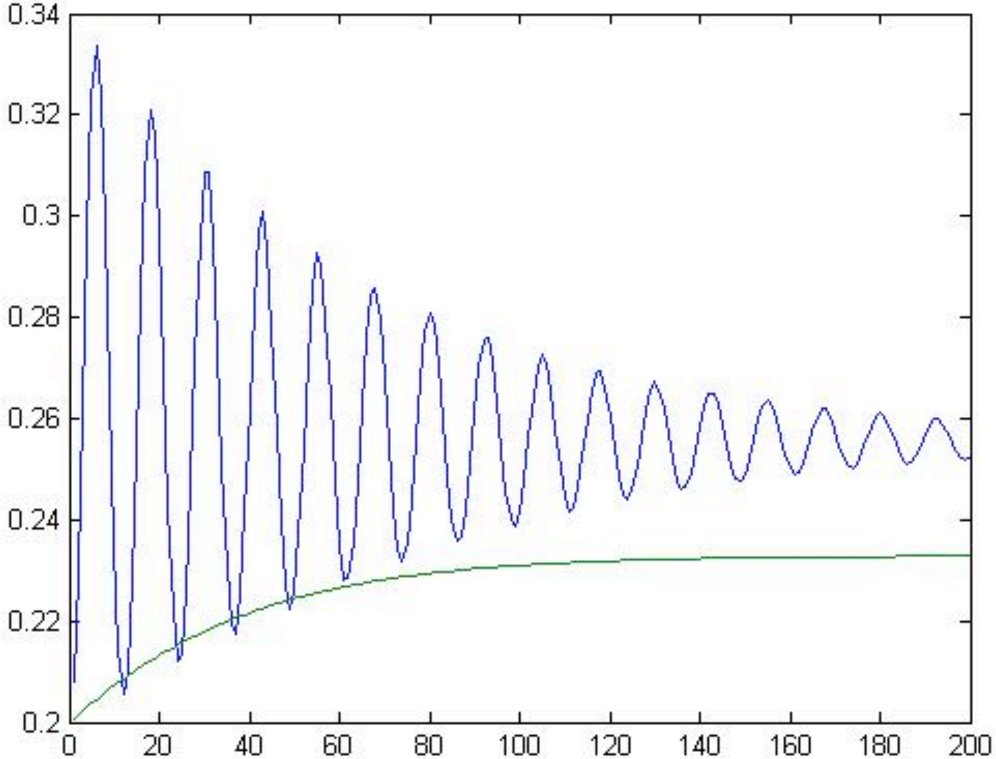
Freq of Rock & (R,S,P)/3



Time

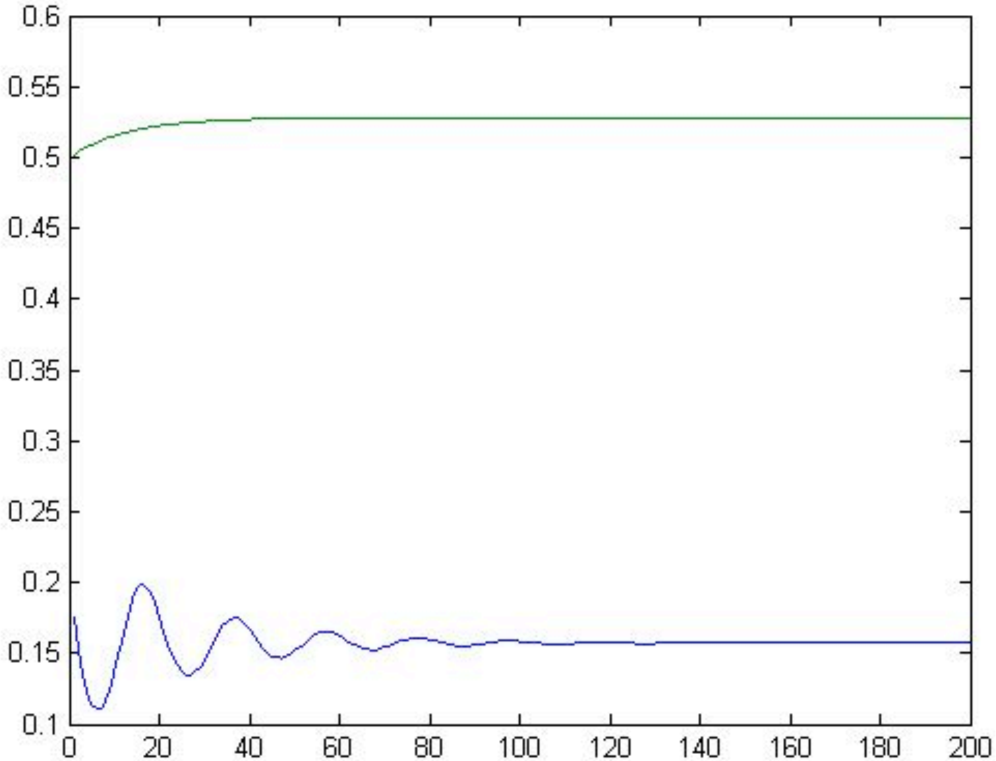
Pures & (R,S,P)/3 , k=1.1,ε=0.5

Freq of Rock & (R,S,P)/3



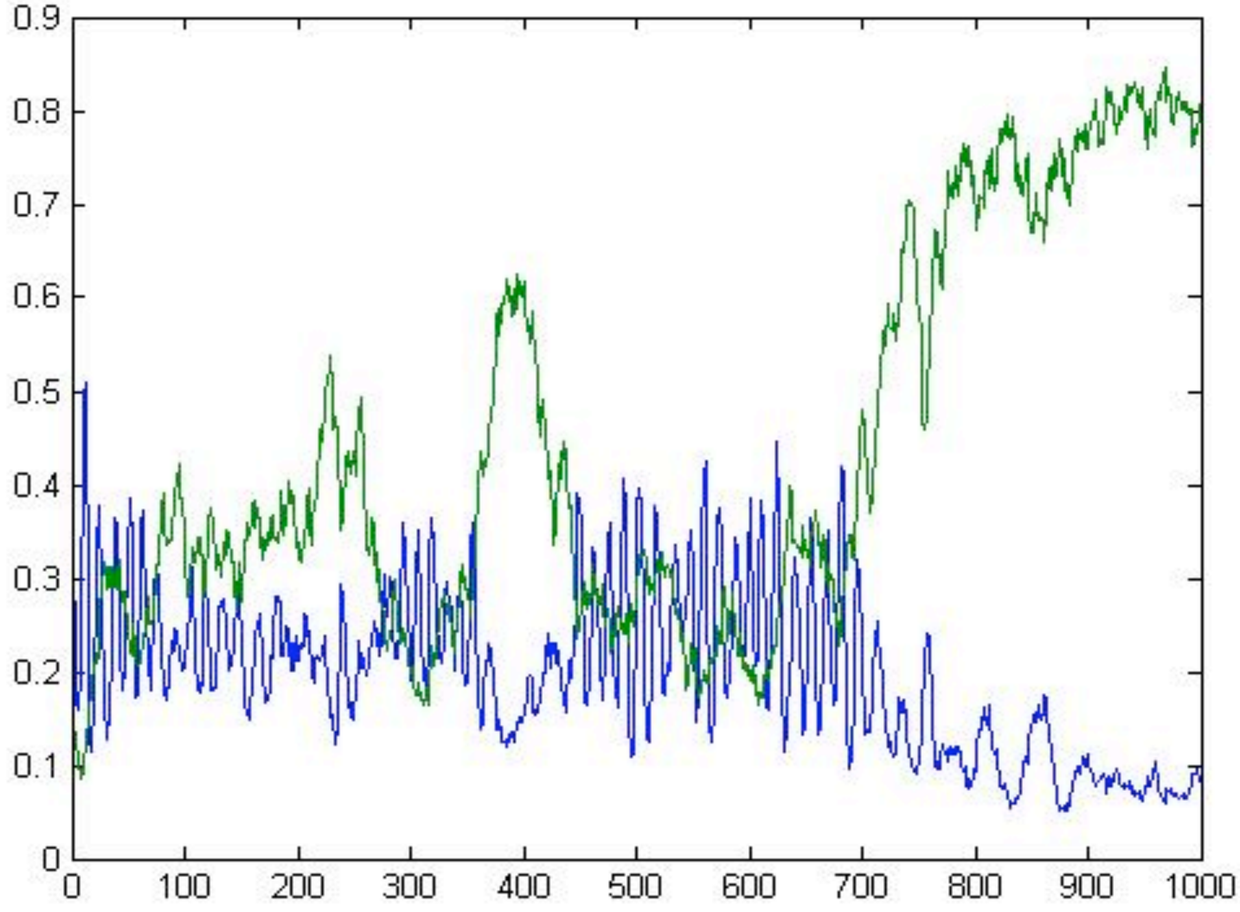
Time

Pures & (R,S,P)/3 , k=1.1,ε=0.5



Pures +(R,S,P)/3 , k=1.1,ε=0.5, Random perturbations

Freq of Rock —— **& (R,S,P)/3** ——



Time

Pures+**(R,S,P)**/3, k=1.1,ε=0.5, Random Perturbations

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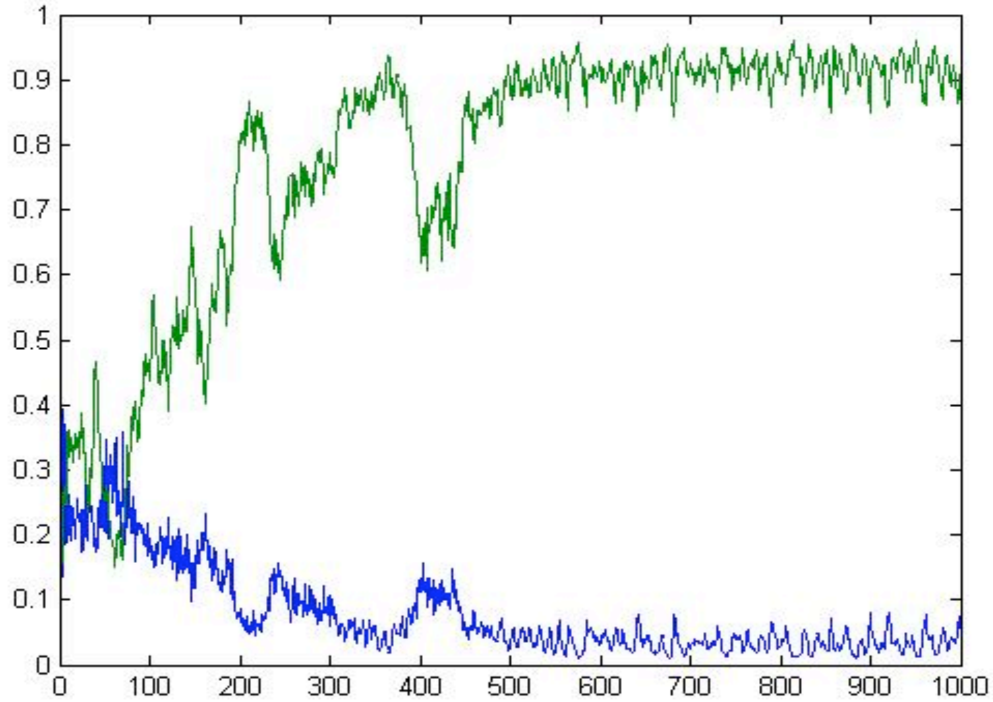
Freq of Rock & (R,S,P)/3



Time / 10

The ESS over S is “globally stable” under every (sensible) dynamic

- Suppose we have an ESS p over the whole S. If the population frequency is q then the population fitness is c+E(q,q). Now for p we have that for every q E(q,p)=E(p,p) and E(p,q)>E(q,q). Any dynamic for which $freq^{t+1}(r)>freq^{t}(r)$

  if E(r,q) >E(q,q) therefore has that the frequency of individuals playing the ESS strategy will increase.

Questions

Can we specify, for a system with an ESS over the whole space, the region W ε n-simplex within which there is convergence to the ESS?

Hypotheses: W is simply connected;

W is an open set (unless whole of n-simplex);