#### The lack of dynamical theory in the traditional theory of games

At the end of the first chapter of Theory of Games and Economic Behavior, von Neumann and Morgenstern wrote:

"We repeat most emphatically that our theory is thoroughly static. A dynamic theory would unquestionably be more complete and therefore preferable. But there is ample evidence from other branches of science that it is futile to try to build one as long as the static side is not thoroughly understood."

#### **Application of Game Theory to Biology**

A long-standing puzzle in the study of animal behavior is the prevalence of conventional fights in the competition for mates. Conflicts are often settled by displays rather than all out fighting. There are many examples such as: birds fluff out their feathers, stags and bisons engage in pushing matches, snakes have wrestling matches. Maynard-Smith and Price (1973) modelled these conflicts as games to give an explanation. It also proposed a strengthen concept of strategic equilibrium, the Evolutionarily Stable Strategy.







# The Logic of Animal Conflict

#### J. MAYNARD SMITH

School of Biological Sciences, University of Sussex, Falmer, Sussex BN1 9QG

#### G. R. PRICE

Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE

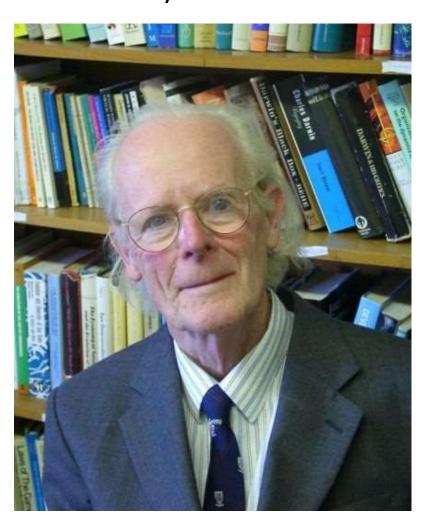
Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur<sup>13</sup> and of Hamilton<sup>14</sup> on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that

G.R. Price



John Maynard Smith



#### The Logic of Animal Conflict: Maynard Smith & Price

"Conflicts between animals of the same species are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behavior benefiting the species rather than individuals. Game Theory and computer simulation analyses show, however, that a "limited war" strategy benefits individuals as well as species."



### The Logic of Animal Conflict: Maynard Smith & Price

"In a typical combat between two male animals of the same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes.

Consequently, one might expect that natural selection would develop maximally effective weapons and fighting styles for a "total war" strategy of battles between males to the death.

But instead, intraspecific conflicts are usually of a "limited war" type, involving inefficient weapons or ritualized tactics that seldom cause serious injury to either contestant."



### **Evolutionarily Stable Strategies**

Individual members of a biological species have similar needs, and resources are limited, conflicts situations will often arise. There are many different behavior patterns for individuals to follow. What are the strategic choices? If we want to apply Game Theory we need to assume rationality and intelligence.

What takes the place of rationality and intelligence is evolutionary pressure - natural selection.

# Payoff: fitness of individuals

pure strategy: certain behavior determined by the gene mixed strategy:

- (i) a random mechanism that trigger off each of the behaviors or
- (ii) the proportion of population with certain behavior gene.

Remark on fitness as payoff: (John Maynard Smith): In human conflicts, strategies are chosen by reason to maximize the satisfaction of human desires-or at least it is in those terms that they are analyzed by game theorists.

Strategies in animal contests are naturally selected to maximize the fitness of the contestants. Thus apparently incommensurable outcomes can be placed on a single scale of utility according to the contribution they make to reproductive success. This equivalence between utility and contribution to fitness is the main justification for applying game theory to animal contests.

Example: Hawk & Dove

Hawk: keep fighting until you or your opponent is injured

Dove: run away

Winner gets a prize of V and injury means your fitness goes down by D.

	Hawk	Dove
Hawk	$(\frac{1}{2}(V-D), \frac{1}{2}(V-D))$	(V,0)
Dove	(0,V)	$(\frac{1}{2}V, \frac{1}{2}V)$

We are then studying the symmetric bimatrix game  $[A, A^T]$ .

$$A = \begin{pmatrix} \frac{1}{2}(V - D) & V \\ 0 & \frac{1}{2}V \end{pmatrix}$$

From Game Theory, we will arrive at the concept of finding a strategy p such that <p, p> is a SE i.e. p is a BR to p.

Let's define an Evolutionarily Stable Strategy p<sup>ESS</sup>.

Consider a large population of ESS players playing p<sup>ESS</sup>.



A mutation occurs, producing a small numbers of players with mutant strategy  $p^M$ ,  $p^M \neq p^{ESS}$ .



The proportion of the population with this mutant strategy is  $\in$ . Then for a player using  $p^{ESS}$  the expected payoff is

$$(1-\in)\pi(p^{ESS},p^{ESS})+\in\pi(p^{ESS},p^{M})$$

A player using p<sup>M</sup> the payoff is

$$\pi^{M} = (1 - \epsilon)\pi(p^{M}, p^{ESS}) + \epsilon \pi(p^{M}, p^{M})$$

# We want

$$\pi^{M} < \pi^{ESS}$$

$$(1-\epsilon)\pi(p^{M}, p^{ESS}) + \epsilon \pi(p^{M}, p^{M})$$

$$< (1-\epsilon)\pi(p^{ESS}, p^{ESS}) + \epsilon \pi(p^{ESS}, p^{M})$$

This is guaranteed if for  $p^{M} \neq p^{ESS}$ 

$$(i)\pi(p^{ESS},p^{ESS}) \ge \pi(p^M,p^{ESS})$$

$$(ii) \pi(p^{ESS}, p^{ESS}) = \pi(p^{M}, p^{ESS}) \implies \pi(p^{M}, p^{M}) < \pi(p^{ESS}, p^{M})$$

This is called an Evolutionarily Stable Strategy.

#### Pure strategy as ESS:

Theorem: Suppose the payoff matrix is  $(a_{ij}, a_{ji})$ .

Suppose for the  $j^{th}$  column of  $(a_{ij})$  is such that its diagonal element,  $a_{jj}$ , is the largest (strictly) of the column. Then playing the  $j^{th}$  strategy is an ESS.

Proof: The assumption is that  $a_{ij} < a_{jj}$  for  $i \neq j$ . Then, the  $j^{th}$  strategy is the BR to itself. To check condition (ii), let  $p^{M}=(p_{1},...,p_{n})\neq j^{th}$  strategy.

Then, 
$$\pi(j^{th}, j^{th}) = a_{jj}, \pi(p^{M}, j^{th}) = p_1 a_{1j} + ... + p_n a_{nj}$$

Therefore,  $\pi(j^{th}, j^{th}) \ge \pi(p^M, j^{th})$ . Condition (ii) is satisfied automatically as  $a_{ij} < a_{jj}$  for  $i \ne j$  and hence the  $j^{th}$  strategy is an ESS.

Remark: A column with such a property is called a diagonally dominant column. Since there may be n diagonally dominant columns. We see that there may be more than one ESS strategies.

Necessary and sufficient condition for an ESS.

Theorem: Let  $[A, A^T]$  be a given bimatrix game, where A is an nxn matrix. Let  $p=(p_1,...,p_n)$  be a mixed strategy. Then p is an ESS iff

(\*) p<sub>j</sub>>0 implies j<sup>th</sup> strategy is a BR row to p

(\*\*) Let B be the matrix  $(b_{ij})$  such that  $b_{ij}=a_{ij}$  if i, j are BR rows to p and  $b_{ij}=0$  otherwise. Then,  $Z^TBZ < 0$ 

where  $Z^T = (z_1, ..., z_n) \neq 0$  satisfies (i)  $z_i = 0$  if i is not a BR row to p and

(ii) 
$$z_1 + ... + z_n = 0$$
.

Example: For the following matrix A, verify whether p=(8/19, 6/19, 5/19) is an ESS for the bimatrix game  $[A, A^T]$ .

$$A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$$

Solution: Row 1, 2, 3 are BR rows to p. Therefore, Condition (i) is satisfied.

To check Condition (ii), B=A, Z= $(x, y, -x-y)^T \neq 0$ . Then,  $Z^TBZ = -5x^2 - 7xy - 5y^2$ 

Thus, the given p is an ESS.
$$= -5((x+7/10 \text{ y})^2 + 51/100 \text{ y}^2) < 0. \quad A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$$

Example: For the following matrix A, verify whether p=(0, 1/3, 2/3) is an ESS for the bimatrix game [A, A<sup>T</sup>].

$$A = \begin{pmatrix} 4 & 6 & 1 \\ 7 & 5 & 4 \\ 0 & 7 & 3 \end{pmatrix}$$

Solution: The BR rows are Row 2, Row 3. Thus, Condition (i) is satisfied. To check Condition (ii), let  $Z=(0, t, -t)^T \neq 0$ ,

$$B = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 5 & 4 \\ 0 & 7 & 3 \end{pmatrix}$$

$$Z^{T}BZ=(0, t, -t) (0, t, 4t)^{T}=-3t^{2}<0$$

Thus, p is an ESS.

Proof of Theorem: Condition (i) for ESS is equivalent to the condition that p is a BR to p. This is valid because every row used by p is a BR row to p (Condition (\*)).

To verify Condition (ii) for ESS, we assume  $q\neq p$  and q is also a BR to p.

We need to show that  $\pi(q, q) < \pi(p, q)$  is equivalent to condition (\*\*) on the matrix B.

Observation 1: Suppose  $p=(p_1,...p_n)^{T}$ . If  $p_i$ ,  $p_j>0$ , then  $i^{th}$  and  $j^{th}$  row are BR row to p.

Hence the ith and jth entry of Ap and hence Bp are equal.

We denote this value to be C.

Observation 2:  $q_j=0$  if  $j^{th}$  row is not a BR row to p.

 $\pi(q, q) = q^{T}Aq = q^{T}Bq,$   $\pi(p, q) = p^{T}Aq = p^{T}Bq.$ 

$$\pi(q, q) - \pi(p, q) = (q-p)^{T}Bq$$

$$= (q-p)^{T}B(q-p) + (q-p)^{T}Bp$$

Observation 1 says that  $(q-p)^TBp=C\sum(q_i-p_i)$ = $C(\sum_i q_i - \sum_i p_i)=C(1-1)=0$ 

Therefore, Condition (ii) of ESS which says that  $\pi(q, q) - \pi(p, q) < 0$  is equivalent to  $(q-p)^TB(q-p) < 0$ . This completes the proof of the Theorem.

Example: For the following matrix A, verify whether p=(1/4, 3/4, 0) is an ESS for the bimatrix game [A, A<sup>T</sup>].

$$A = \begin{pmatrix} 4 & 6 & 1 \\ 7 & 5 & 4 \\ 0 & 7 & 3 \end{pmatrix}$$

Solution: The BR rows to p are Row 1, Row2. Thus, Condition (i) is satisfied. To check Condition (ii),  $Z=(t, -t, 0)^T \neq 0$ ,

$$B = \begin{pmatrix} 4 & 6 & 0 \\ 7 & 5 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

 $Z^TBZ=(t, -t, 0)(-2t, 2t, 0)^T=-4t^2<0.$ Thus, p is an ESS.

## Example: Find an ESS for the Hawk and Dove Game.

(i) V > D Hawk Dove
Hawk Dove
$$(\frac{1}{2}(V-D), \frac{1}{2}(V-D))$$
 (V,0)
Dove
 $(0,V)$   $(\frac{1}{2}V, \frac{1}{2}V)$ 

In this case the Hawk strategy is diagonally dominant. It is then an ESS. It is the unique ESS.

In this case,  $\langle \text{Hawk}, \text{Hawk} \rangle$  is a SE. Now Dove is also a BR to Hawk. Then,  $\langle \text{Hawk}, \text{Dove} \rangle = V \rangle V/2 = \langle \text{Dove}, \text{Dove} \rangle$ . Therefore, Hawk is an ESS.

$$\begin{pmatrix} \frac{1}{2}(V-D) & V \\ 0 & \frac{1}{2}V \end{pmatrix}$$

In this case, there is no pure strategy as ESS. We first look for mixed strategy p=(x, 1-x) such that  $\langle p, p \rangle$  is an SE. This means that (x, 1-x) an equalizing strategy on the rows.

Solving x/2(V-D) + (1-x)V = (1-x)V/2, we get x = V/D.

Now we still have to check Condition (ii) of the Theorem. For this we note that

$$(t -t) \begin{pmatrix} (V-D)/2 & V \\ 0 & V/2 \end{pmatrix} \begin{pmatrix} t \\ -t \end{pmatrix} = -Dt^2/2 < 0$$

Example: Suppose A is the payoff matrix for Scissor-Rock-Paper. Is p=(1/3, 1/3, 1/3) an ESS? Solution: p equalizes on all rows and hence all rows are BR rows. Thus, Condition (i) is satisfied. As for Condition (ii), Z=(x, y, -x-y)<sup>T</sup>, B is the original Scissor-Rock-Paper payoff matrix. Then, Z<sup>T</sup>BZ=0 because B is skew-symmetric. Condition (ii) is then not satisfied.

So (1/3. 1/3, 1/3) is NOT an ESS.

We are interested in the question of existence of ESS. We should then address the following question first. Question: Given a symmetric bimatrix game [A, A<sup>T</sup>], does there exist p such that <p, p> is a SE?

Theorem: Let  $[A, A^T]$  be a symmetric bimatrix game. There exists a mixed strategy p such that  $\langle p, p \rangle$  is a SE.

Sketch of Proof: We follow Nash's argument of applying Kakutani Fixed Point Theorem in proving existence of SE for n-person games.

Let  $X^*$  be the set of mixed strategies. For  $p \in X^*$ , the set  $\{q \in X^*: q \text{ is a BR to } p\}$  is a compact convex subset of  $X^*$ .

The set-valued mapping sending  $p \in X^*$  to  $\{q \in X^*: q \text{ is a BR to } p\}$  has a closed graph and hence continuous.

The Kakutani Fixed Point Theorem then asserts the existence of p such that  $p \in \{q \in X^*: q \text{ is a BR to p}\}$ , i.e.  $\langle p, p \rangle$  is a SE.

Example: For the symmetric game  $[A, A^T]$ , where A is given below, we have shown that (8/19, 6/19, 5/19) is an ESS. Are there any ESS that uses only one or two pure strategies?  $A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$ 

Solution: Using one strategy: <Row 1, Col 1>, <Row 2, Col 2>, <Row 3, Col 3> are not SE because they are not largest in its column. Therefore, no ESS using just one pure strategy.

Using two strategies:

Then we study 
$$\begin{pmatrix} 3 & 2 \\ 5 & 1 \end{pmatrix}$$

$$A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$$

There is a saddle point in this game and hence no SE using only Row 1 and Row 2.

(ii) Using Row 1, Row 3:

Then, we study 
$$\begin{pmatrix} 3 & 5 \\ 4 & 1 \end{pmatrix}$$

$$A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$$

(4/5, 1/5) equalizes on the rows. Then, we should check whether < (4/5, 0, 1/5), (4/5, 0, 1/5) > is an SE. Note that Row 1 and Row 2 are not BR to Player II's (4/5, 0, 1/5). Hence it is not an SE.

Therefore, there is no ESS using only Row 1 and Row 3.

Using Row 2, Row 3:

Then, we study 
$$\begin{pmatrix} 1 & 3 \\ 4 & 1 \end{pmatrix}$$

$$A = \begin{pmatrix} 3 & 2 & 5 \\ 5 & 1 & 3 \\ 4 & 4 & 1 \end{pmatrix}$$

Note that (2/5, 3/5) equalizes on the rows. Then, we should check whether <(0, 2/5, 3/5), (0, 2/5, 3/5)> is a SE. Note that Row 2, and Row 3 are not BR to Player II's strategy of (0, 2/5, 3/5).

Hence, <(0, 2/5, 3/5), (0, 2/5, 3/5)> is not a SE.

Therefore, there is no ESS using only Row 2 and Row 3.

Summing up all three case, there is no ESS using only one or two pure strategies.

Question: Do all symmetric bimatrix games admit an ESS?

Theorem: Let A be the Scissor-Rock-Paper payoff matrix. Then [A, A<sup>T</sup>] does not have an ESS.

#### Proof:

Let p be a mixed strategy such that  $\langle p, p \rangle$  is a SE.

- 1. p uses only one strategy i.e. a pure strategy: As no diagonal entry is dominant in its column. There is no pure strategy as ESS.
- 2. p uses two strategies: Suppose <p, p> is a SE and p uses only Paper and Scissor. Then, as Scissor dominates Paper. Scissor will be a SE contradicting the result in (1).
- 3. p uses 3 strategies: Then, p must be equalizing on all rows. p must then be (1/3, 1/3, 1/3). While <p, p> is an SE, it does not satisfy the second condition for ESS.

In summary, the Scissor-Rock-Paper game has no ESS.

T.R. Malthus: Through the animal and vegetable kingdom, nature has scattered the seeds of life abroad with the most profuse and liberal hand; but has been comparatively sparing in the room and nourishment necessary to rear them.

Charles Darwin: Fifteen months after I had begun my systematic enquiry, I happened to read for amusement "Malthus on Population"... it at once struck me that... favorable variations would tend to be preserved, and unfavorable ones to be destroyed. Here, then, I had at last got a theory by which to work.

# Replicator Dynamics

An evolutionary process has two basic elements: mutation and selection mechanism. The ESS concept highlights mutation. Replicator dynamics highlights the role of selection.

Replicator dynamics is formalized as a system of ODE that does not include any mutation mechanism. Instead robustness against mutation is indirectly taken care of by dynamic stability criteria.

The usual replicator dynamics presumes that individuals can only be programmed to pure strategies. Then, one interprets a mixed strategy  $x=(x_1,...,x_n)$  as a population state such that each  $x_i$  represents the proportion of population programmed to the pure strategy i.

We still assume random pairwise matching in a large population where payoffs represent fitness, measured as the number of offspring, and each offspring inherits its single parent's strategy. The replicators are here the pure strategies that can be copied without error from parent to child.

## Replicator Dynamics

Let  $p=(p_1,...p_n)^T$  be a mixed strategy for a symmetric bimatrix game [A, A<sup>T</sup>].  $p_i$  denotes the proportion of population using the i<sup>th</sup> strategy.

Payoff to strategy i against p is  $\sum_{j} a_{ij} p_{j}$ .

Payoff to strategy p against p is  $\sum_{i} \sum_{j} a_{ij} p_{i} p_{j}$ .

We assume the growth rate of the population using strategy i is proportional to the advantage of that strategy over the whole population. For simplicity, we assume the constant is 1.

Therefore, growth rate of the population playing strategy i is

 $\sum_{j} a_{ij} p_{j.} \text{-} \sum_{k,j} p_k a_{kj} p_{j.}$ 

# Replicator Dynamics Equations:

$$dp_i/dt = [\sum_j a_{ij}p_j - \sum_{k,j} p_k a_{kj}p_j]p_i,$$
  $i=1,...n.$ 

Remark: An equilibrium point of the set of Replicator Dynamics Equations is the point such that RHS= 0 for all i.

RHS=0 for all i iff  $\sum_{j} a_{ij} p_{j} = \sum_{k,j} p_{k} a_{kj} p_{j}$  for  $p_{i} \neq 0$ . This is true when p is a BR to p.

Therefore, p is an equilibrium point of Replicator Dynamics Equations when <p, p> is a SE.

A geometric approach to study solutions of ODE is to study the motions (flow) generated by the orbits of the ODE.

Vector field defined by Replicator Dynamics Equations: For  $p=(p_1,\ldots,p_n)\in\mathbb{R}^n$ , let X be the vector field such that its  $i^{th}$  component  $X_i=[\sum_j a_{ij}p_j-\sum_{k,j} p_k a_{kj}p_j]p_i$ . X generates a flow (local diffeomorphism) on  $\mathbb{R}^n$ .

Note that: (i) For  $p \in \{(p_1, ..., p_n) : \sum_i p_i = 1\}$  X is tangent to  $\{(p_1, ..., p_n) : \sum_i p_i = 1\}$  because  $\sum_i X_i = 0$ .

(ii)  $p_i$ =0 implies  $X_i$  =0. Hence, X is tangent to the hyperplane  $\{(p_1,...,p_n): \sum_i p_i =1, p_i$ =0 for  $i \in S\}$ , where  $S \subseteq \{1,...n\}$ 

Let 
$$\mathbf{P}_n = \{(p_1, ..., p_n) : \sum_i p_i = 1, p_i \ge 0 \text{ for } i = 1, ..., n\}$$

Theorem: The orbits of the Replicator Dynamics Equations stay in  $\mathbf{P}_n$ .

As the Replicator Dynamics Equations are nonlinear, it is not easy to find the orbits of X. The following shows that the orbits of the Replicator Dynamics Equation for Scissor-Rock-Paper payoff matrix are closed.

We can rewrite the Replicator Dynamics Equations as

$$\frac{p_i}{p_i} = (Ap)_i - p^T Ap, i = 1,...,n$$

For Scissor-Rock-Paper A is skew symmetric,

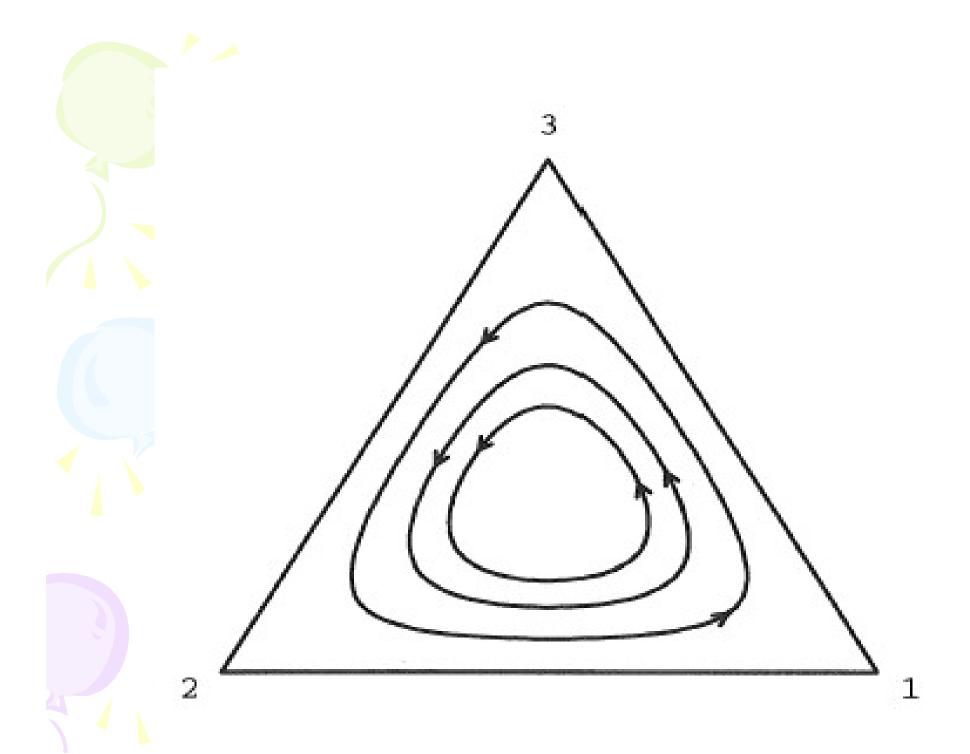
$$\frac{p_i}{p_i} = (Ap)_i$$
, the i<sup>th</sup> component of  $Ap$ ,  $i = 1, 2, 3$ ,

$$\frac{d}{dt}[p_1p_2p_3] = (\frac{d}{dt}p_1)p_2p_3 + (\frac{d}{dt}p_2)p_1p_3 + (\frac{d}{dt}p_3)p_1p_2$$

$$= [(Ap)_1 + (Ap)_2 + (Ap)_3]p_1p_2p_3 = [(1,1,1)Ap]p_1p_2p_3 = 0$$

The orbits of the Replicator Equations are the intersection of  $x_1 + x_2 + x_3 = 1$  with  $x_1x_2x_3 = C$ .

Then, all orbits are closed.



As remarked above, when <p, p> is a SE it is an equilibrium point for the Replicator Dynamics Equation. Then, does ESS possess further properties w.r.t. the Replicator Dynamics Equation?

Recall that ESS is a SE that cannot be invaded by mutant strategy. ESS concept should be related to stability of equilibrium points of the Replicator Equation. In fact, Taylor and Jonker (1978) proved that every ESS is an asymptotic stable point of the Replicator Equation.

Example (Asymptotic stable point):

Hawk & Dove with V=2, D=4.

$$\begin{pmatrix} -1 & 2 \\ 0 & 1 \end{pmatrix}$$

We write a mixed strategy as  $p = \begin{pmatrix} x \\ 1-x \end{pmatrix}$ 

$$\begin{pmatrix} x & 1-x \end{pmatrix} \begin{pmatrix} -1 & 2 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ 1-x \end{pmatrix} = 1-2x^2$$

The Replicator Equation is  $\frac{dx}{dt} = [2x^2 - 3x + 1]x$ .

Integrating,  $dt = ([2x^2-3x+1]x)^{-1}dx$  we get

$$t = \ln[|x(x-1)|(2x-1)^{-2}] + C.$$

It is easy to see that when x(0) stays close to 0.5, x(t) goes to 0.5 as t goes to infinity. This property of equilibrium point is called asymptotically stability in ODE. In Game Theory, we see that (0.5, 0.5) will not be invaded by mutation. Thus, (0.5, 0.5) is an ESS.

In the following we will sketch the proof that Replicator Dynamics Equations leads to ESS.

Let  $s=(s_1,...,s_n)$  be an ESS in the interior of the set of mixed strategies, i.e.  $s_i>0$ , for all i.

Consider, 
$$V(p) = (p_1)^{s_-1} \dots (p_n)^{s_-n}$$
.  
Then,  $V_i(p) = (s_i/p_i)V$ . Let  $\nabla V = (V_1, \dots, V_n)$ .  
 $\nabla V \cdot (s-p) = V \sum_i (s_i^2 - s_i p_i)/p_i = V [\sum_i s_i^2/p_i - 1]$   
 $= V [\sum_i s_i^2/p_i - 2 \sum_i s_i p_i/p_i + \sum_i p_i^2/p_i]$   
 $= V \sum_i (s_i - p_i)^2/p_i > 0$  for  $p \neq s$ .

$$\begin{aligned} dV/dt &= \nabla V \cdot (dp/dt) = \sum_{i} [\sum_{j} a_{ij} p_{j.} - \sum_{k,j} p_{k} a_{kj} p_{j.}] s_{i} \\ &= s^{T} A p - p^{T} A p > 0 \end{aligned}$$

Thus, we have

(i) 
$$\nabla V \cdot (s-p) > 0$$

(ii) 
$$dV/dt > 0$$

By (i) we know that V has a unique maximum at s.

By (ii) the orbits of the replicator dynamics tend to s.

Remark: We have shown that an ESS is an attractor of the replicator Dynamics when the ESS is in the interior of mixed strategies. We can extend this proof to the general cases because the vector field corresponding to the replicator dynamics equations is tangent to all the faces of the set of mixed strategies.

Remark: The introduction of Replicator Dynamics in game theory allows us to use concepts in dynamical system such as structural stability to game theory.

# Principle of Elimination of Dominated Strategy in the context of Replicator Dynamics Equation

Theorem: Suppose Row h strictly dominates Row k for the symmetric bimatrix game [A,  $A^T$ ] i.e.  $a_{hj} > a_{kj}$  for all j.

Let p(t) be a solution for the Replicator Dynamics Equation

$$dp_i/dt = \left[\sum_j a_{ij}p_j - \sum_{k,j} p_k a_{kj}p_j\right]p_i$$

$$i=1,...n.$$

Then,  $\lim_{t\to\infty} p_k(t)=0$ .

## Proof:

Suppose  $a_{hj}$ - $a_{kj}$ > $\in$ >0.

From the Replicator Dynamics Equation we have  $dp_h/dt = [\sum_j a_{hj}p_j - \sum_{r,j} p_r a_{rj}p_j]p_h$ 

$$dp_k/dt = \left[\sum_j a_{kj} p_j - \sum_{r,j} p_r a_{rj} p_j\right] p_k$$

Thus,  $dlnp_h/dt - dlnp_k/dt = \sum_j (a_{hj} - a_{kj}) p_j > \sum_j \in p_j = \in.$ 

So  $\lim_{t\to\infty} \ln[p_h(t)/p_k(t)] = \infty$ . Hence,  $\lim_{t\to\infty} p_k(t)=0$ .

John Maynard Smith, "The games lizard play", Nature Vol 380, 21 March 1996:

In the side-blothed lizard, Uta stansburiana, males have one of three throat colors, each associated with a different behavior. The difference between color morphs is highly heritable. Orange-throated males establish large territories, within which live several females. A population of such males can be invaded by males with yellow-striped throats, these "sneaker" males do not defend territory, but steal copulations. The orange males cannot successfully defend all their females. However, a population of yellow-striped males can be invaded by blue-throated males, which defend territories large enough to hold one female, which they can defend against sneakers. Once, sneakers become rare, it pays to defend a large territory with several females. Orange males invade, and we are back where we started from.

The empirical support for these conclusions is as follows. The frequencies of the three morphs were followed for a complete cycle, lasting six years.

Aggressive: defends large territory

ish large territories, v

Orange-throated males establish large territories, within which live several females. A population of such males can be invaded by males with yellow-striped throats, these "sneaker" males do not defend territory, but steal copulations. The orange males cannot successfully defend all their females.

Less aggressive: defends smaller territory

Blue-throated males, which defend territories large enough to hold one female, which they can defend against sneakers. Once, sneakers become rare, it pays to defend a large territory with several females.

Sneakers:



These "sneaker" males have yellow-striped throat and do not defend territory, but steal copulations. The orange males cannot successfully defend all their females. A population of yellow-striped males can be invaded by blue-throated males, which defend territories large enough to hold one female, which they can defend against sneakers.

According to Karl Sigmund, John Maynard Smith gleefully greeted the discovery that male lizards of the species Uta stansburia were engaged in a game with rock-paper-scissor structure. Maynard Smith joked that "They have read my book."

### Escherichia coli:

Three types of E Coli

- Normal "Wild-Type"
- Toxic Strain produces both a toxin and an antidote to the toxin
- Resistant Strain produces only the antidote

The toxin kills the wild-type bacteria, and so the toxic strain can invade the wild-type.

When the population consists entirely of toxic bacteria, there is no advantage to producing the toxin (which requires energy).

The resistant strain can invade the toxic bacteria.

Once the population consists only of resistant strain, there is no reason to produce the antidote (which also requires energy). The wild-type strain can then invade the resistant strain.

### Criticisms of Maynard-Smith and Price Theory:

- 1. Assumption of an infinite random-mixing population: In fact, (a) opponents will have some degree of relatedness, (b) an individual may have a succession of contests against the same opponent, (c) the population we consider may be small.
- 2. Assumption of asexual reproduction.
- 3. Assumption of symmetric contests: most actual contests ate asymmetrical.
- 4. Assumption of pairwise contests.

John Maynard Smith's view of mathematics: (Karl Sigmund) "But mathematics was, in his hands, essentially a way of secure the results of his biology intuition: 'If the mathematical analysis of some system predicts that it will behave in a particular way, one usually tries to gain some insight into why it should do so...If I cannot gain such an insight, I check the algebra, or the computer program, and expect to find a mistake.' He added: 'mathematics without natural history is sterile, but natural history without mathematics is muddled'"