

ESS and Replicator Dynamics

Tutorial

Pierre Bernhard

I3S

University of Nice-Sophia Antipolis and CNRS

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Bibliography

John Maynard-Smith and G.R. Price: “The logic of animal conflict”, *Nature* **246**, pp 15–18, 1973

John Maynard-Smith: *Evolution and the theory of games*, Cambridge University Press, Cambridge, U.K., 1982

Bibliography

John Glen Wardrop: “Some theoretical aspects of road traffic research” *Proceedings of the Institution of Civil Engineers*, pp 325–378, 1952.

John Maynard-Smith and G.R. Price: “The logic of animal conflict”, *Nature* **246**, pp 15–18, 1973

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John Glen Wardrop: “Some theoretical aspects of road traffic research” *Proceedings of the Institution of Civil Engineers*, pp 325–378, 1952.

John Maynard-Smith and G.R. Price: “The logic of animal conflict”, *Nature* **246**, pp 15–18, 1973

John Maynard-Smith: *Evolution and the theory of games*, Cambridge University Press, Cambridge, U.K., 1982

Taylor and Jonker: “Evolutionarily stable strategies and game dynamics”, *Mathematical Bioscience*, **40**, pp145–156, 1978

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Capture the interplay between individual and collective behaviour in a large population of identical agents.



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- ¿ Stock market ?

Strategies

Pure strategy

Individual behavior: choice of a *phenotype* or *trait* (evolution) or *strategy* (routing, sociology) x in a *trait* or *strategy space* X either **finite** or **infinite**.



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$$p, q, \dots \in \Delta(X)$$

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- individual
- population *monomorphic* or *polymorphic*

Generating function

An individual using strategy x in a population using p gets $G(x, p)$

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Fitness function A mixed strategy q yields a *fitness*

$$F(q, p) = \int_X G(x, p)q(dx) .$$

Generating function

An individual using strategy x in a population using p gets $G(x, p)$

Linear case G may be given via an *pairwise encounter* function $H(x, y)$

$$G(x, p) = \int_X H(x, y)p(dy).$$

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Interpret “fitness” as reproductive success. Assume most of the population behaves according to strategy p , while a small proportion ε behaves according to q . The overall population then behaves according to

$$q_\varepsilon := (1 - \varepsilon)p + \varepsilon q.$$

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$$F(p, p) \geq F(q, p),$$

and in the linear case

$$[F(p, p) = F(q, p)] \Rightarrow F(p, q) > F(q, q).$$

A menagerie of concepts

Other concepts, close to ESS, have been introduced : locally superior, evolutionarily robust (ERS), uninvadable, continuously stable, etc.

Definition A strategy p is locally superior if there exists a neighborhood $\mathcal{N}(p)$

$$\forall q \in \mathcal{N}(p), q \neq p, \quad F(p, q) > F(q, q).$$

In the infinite cases, depends on the topology used on $\Delta(X)$.

Definition A strategy is Evolutionarily Robust if it is locally superior in the weak topology of $\Delta(X)$.

Theorem In the linear case, $\text{ERS} \Rightarrow \text{ESS}$.

In the finite linear case, $\text{ESS} \Leftrightarrow \text{ERS}$.

Relation with Nash

Define a non zero sum two players game on $\Delta(X) \times \Delta(X)$ by

$$J_1(p, q) = F(p, q), \quad J_2(p, q) = F(q, p).$$

Then the first ESS condition (linear case) is equivalent to (p, p) being a Nash point of this game. As a consequence we get

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Theorem [Von Neuman 1944, Kuhn 1950, Wardrop 1952] Let p be an ESS.

1. $\forall x \in X, \quad G(x, p) \leq F(p, p),$
2. let $N = \{x \in X \mid G(x, p) < F(p, p)\},$ then, $p(N) = 0.$

Finite linear case

Let $X = \{x_i, i = 1, \dots, n\}$. $\Delta(X)$ is the simplex of \mathbb{R}^n .

Let $H(x_i, x_j) = a_{ij}$, $A = (a_{ij})$, $F(p, q) = \langle p, Aq \rangle$

$$\text{Wardrop} \Leftrightarrow p = \begin{pmatrix} p_1 \\ 0 \end{pmatrix}, \quad Ap = \begin{pmatrix} v\mathbf{1} \\ r_2 \end{pmatrix}, \quad r_2 < v\mathbf{1};$$

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The second condition is a second order condition. Partition A according to the partition of p . A sufficient condition is that the restriction of the quadratic form $\langle q_1, A_{11}q_1 \rangle$ to the orthogonal subspace of $\mathbb{1}$ be negative definite.

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A necessary condition is that the same restricted quadratic form for the submatrix A_{22} of A corresponding to the strictly positive elements of p_1 be nonpositive definite.

A second order criterion

Given a 2×2 matrix

$$M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

define its *symmetric difference* $\sigma(M) = a - b - c + d$.

Given an $n \times n$ matrix M , define the $(n-1) \times (n-1)$ matrix $\sigma(M)$ by replacing each block of four adjacent numbers in M by their symmetric difference.

The sufficient condition is that $\sigma(A_{11}) + \sigma(A_{11})^t < 0$.

The necessary condition is that $\sigma(A_{22}) + \sigma(A_{22})^t \leq 0$.

Example

A **rare** example of a non trivial ESS in a continuous setting.

$$X = [0, 1], H(x, y) = \max\{x - y, \lambda(y - x)\}, \lambda \in (0, 1).$$

Theorem p is a global ERS:

$$p = \frac{\lambda}{1 + \lambda} \delta_0 + \frac{1}{1 + \lambda} \delta_1.$$

For a given $q \in \Delta(X)$, define x_0 [...] such that $q([0, x_0]) = \lambda/(1 + \lambda)$, and $a = \int_0^{x_0} xq(dx)$, x_1 and b symmetrically in the neighborhood of 1. We show

$$F(p, q) - F(q, q) \geq (1 + \lambda) \left(\frac{a^2}{x_0} + \frac{b^2}{1 - x_1} \right).$$

Hawk and Doves

Sharing a prey

| | | |
|-----------------|----------|-----------|
| <i>Opponent</i> | <i>D</i> | <i>H</i> |
| <i>Him</i> | | |
| <i>D</i> | 1/2 | 0 |
| <i>H</i> | 1 | $-\theta$ |

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| <i>Population</i> | p | $1 - p$ |
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Wardrop condition:

$$0.5p = p - \theta(1 - p) \quad \Rightarrow \quad p = \frac{\theta}{\theta + 0.5}$$

Replicator Dynamics

If $G(x, q)$ measures the excess of births over deaths, like begets like, and q is interpreted as the distribution of strategies among the population, it follows that

$$\dot{q}(t, x) = q(t, x)[G(x, q(t)) - F(q(t), q(t))].$$

This is called the *replicator dynamics*.

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$$\dot{q}(t, x) = q(t, x)[G(x, q(t)) - F(q(t), q(t))]. \quad (1)$$

This is called the *replicator dynamics*. “Evolutionary game ?”

Theorem In the finite linear case, every locally stable point of (1) is a Nash point. Every ESS is a locally asymptotically stable point of (1) and its attraction basin contains a neighborhood of the relative interior of the lowest dimensional face of $\Delta(X)$ it lies on.

Proof

Use the Lyapunov function

$$V(q) = \sum_i p_i \ln \left(\frac{p_i}{q_i} \right) .$$

$\ln x \leq 1 + x \Rightarrow V(q) > 0$ if $q \neq p$ and

$$\dot{V}(q) = F(q, q) - F(p, q) .$$

Stability in the infinite case

with A. J. Shaiju

We are investigating the stability of a differential equation over a space of measures. The Lyapunov function used to prove the above theorem is not continuous in the weak topology in the infinite case. **We do not know** whether an ERS (even global) is necessarily a stable point of (1).

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Theorem If $H(x, y) = H(y, x)$, an ERS is locally asymptotically stable.

Proof: use the Lyapunov function $F(p, p) - F(q, q)$.

Two by two case

Players have only two pure strategies (two phenotypes in the population).
The game is described by a 2×2 matrix

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

Let $\sigma = a - b - c + d$, (assume here $\sigma \neq 0$.)

Candidate Nash (via Wardrop condition) $p^* = \frac{d-c}{\sigma}$. Is an ESS iff $\sigma < 0$.

Example : for Hawk and Dove, $\sigma = -0.5 - \theta < 0$.

2 × 2 ESS

In this most simple context,

Definition p is an ESS if

1. (p, p) is Nash, \iff

$$\forall q \in [0, 1], \quad (p - q \quad q - p)A \begin{pmatrix} p \\ 1 - p \end{pmatrix} \geq 0,$$

and

2. If $p \notin \{0, 1\}$, then necessarily $p = p^*$ and the above is 0,

$$\forall q \neq p^*, \quad (p^* - q \quad q - p^*)A \begin{pmatrix} q \\ 1 - q \end{pmatrix} > 0.$$

2 × 2 ESS continued

Corollary If $a \neq c$ and $b \neq d$, there always exists an ESS

1. If $\sigma = 0$ or $\sigma \neq 0$, but $p^* \notin (0, 1)$, the unique ESS is pure,
2. If $\sigma \neq 0$ and $p^* \in (0, 1)$,
 - (a) If $\sigma < 0$, p^* is the only ESS,
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Proof

$$(p^* - q \quad q - p^*)A \begin{pmatrix} p^* \\ 1 - p^* \end{pmatrix} = -\sigma(q - p^*)^2.$$

Replicator equation

If “fitness” measures the reproductive efficiency, i.e. the rate of the excess of births over deaths (possibly negative), p evolves accordingly to the simple replicator equation which becomes here

If $\sigma \neq 0$,

$$\dot{p} = \sigma p(1 - p)(p - p^*)$$

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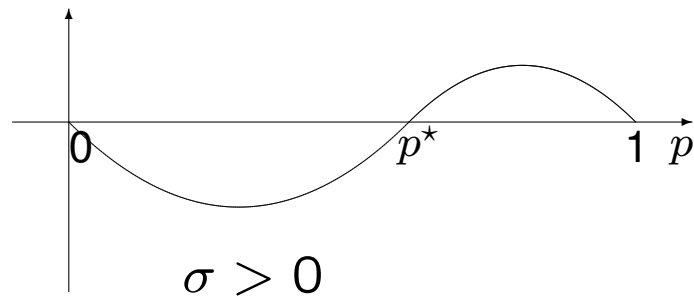
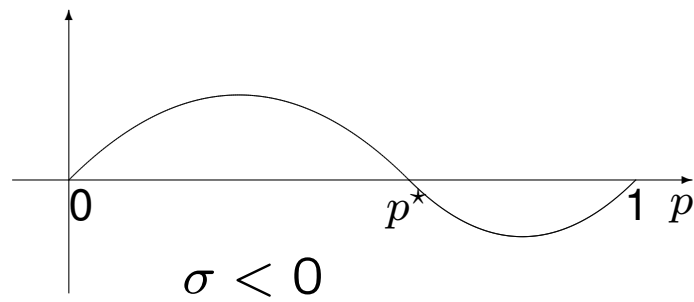
If $\sigma \neq 0$,

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If $\sigma = 0$,

$$\dot{p} = (b - d)p(1 - p)$$

Elementary replicator equation analysis



Population game

Two populations, with two behaviors each, interacting with each other. States p_1 and p_2 , proportions of individuals using the first behavior.

Fitness accrued by an individual of population i using its first behavior $a_i p_j + b_i(1 - p_j)$, and with its second behavior $c_i p_j + d_i(1 - p_j)$.

Replicator equations become

$$\dot{p}_i = \sigma_i p_i (1 - p_i) (p_j - p_j^*).$$

Phase portrait

1. Unique (pure) Nash equilibria are stable,
2. If $(p_1^*, p_2^*) \in (0, 1) \times (0, 1)$,
 - (a) If $\sigma_1 \sigma_2 < 0$, the unique Nash equilibrium (p_1^*, p_2^*) is a center, and all trajectories are periodic.
 - (b) If $\sigma_1 \sigma_2 > 0$, the Nash equilibrium (p_1^*, p_2^*) is a saddle, the two pure Nash are stable.

Proof The following function is a first integral:

$$V(p_1, p_2) = \sum_{i=1}^2 (-1)^i \sigma_i \left[p_i^* \ln \frac{p_i^*}{p_i} + (1 - p_i^*) \ln \frac{1 - p_i^*}{1 - p_i} \right]$$

Lynxes and wolves

| | | | |
|-------------|-----------------|---------------|-------------|
| | $I \setminus W$ | <i>cow.</i> | <i>agr.</i> |
| <i>cow.</i> | λ | $1 - \lambda$ | 0 |
| <i>agr.</i> | $1 - \mu$ | 0 | $1 - \nu$ |

$$\lambda + \mu > 1 > \nu$$

$$\sigma_1 = \lambda + \mu - \nu, \quad p_2^* = (1 - \nu) / (\lambda + \mu - \nu),$$
$$\sigma_2 = -\lambda - \theta, \quad p_1^* = \theta / (\lambda + \theta).$$

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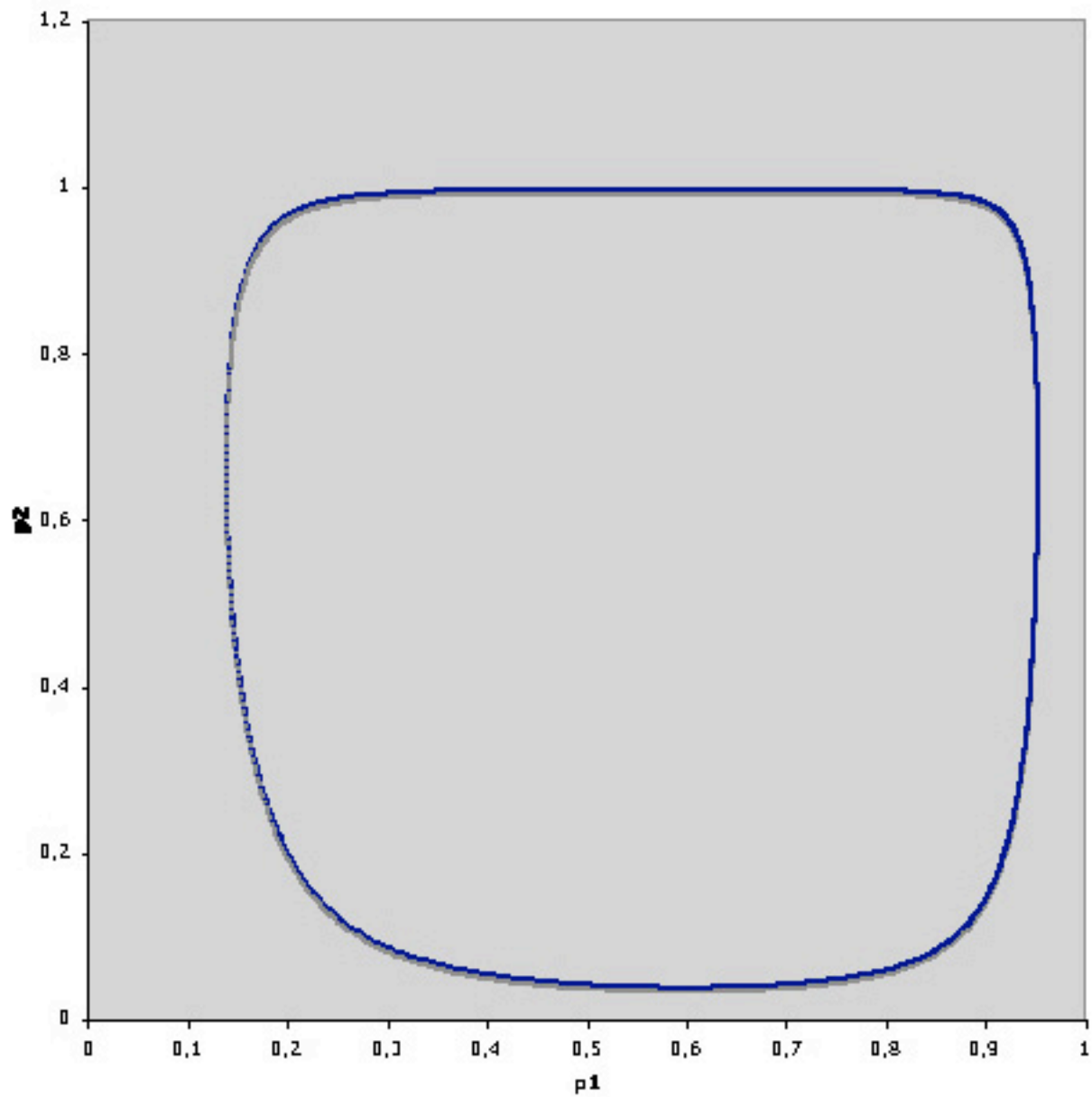
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$$\sigma_1 = \lambda + \mu - \nu, \quad p_2^* = (1 - \nu) / (\lambda + \mu - \nu),$$

$$\sigma_2 = -\lambda - \theta, \quad p_1^* = \theta / (\lambda + \theta).$$

Draw case $\lambda = \nu = 0,5, \quad \mu = 0,75, \quad \theta = 1,5.$

Wolves and Lynxes



Two identical populations

Two identical but distinct populations. Potentially, $p_1 \neq p_2$.

But $A_1 = A_2$, hence $\sigma_1 = \sigma_2$. Assume further that $\sigma_i < 0$. The single population replicator equation is stable at p^* , but $\sigma_1\sigma_2 > 0$ hence (p^*, p^*) is *not* stable.

The diagonal $p_1 = p_2 = p$ represents the solution of the one-population game. Highly unstable in the two-population game.

Two identical populations

