EVOLUTION AND THE THEORY OF GAMES

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17. An *evolutionarily stable strategy* (ESS) is a strategy such that, if adopted by a sufficiently large fraction of the population, then no other strategy can invade, i.e., increase in frequency.

We have seen that if the opponent of a player is selected randomly from the population, then x is evolutionarily stable, if and only if for every $x' \neq x$ we have

$$\pi_1(x', x) < \pi_1(x, x)$$

or

$$\pi_1(x', x) = \pi_1(x, x) \text{ and } \pi_1(x', x') < \pi_1(x, x')$$

commonly referred to as respectively the first and second ESS conditions.

For example, consider the *Prisoner's Dilemma* with payoff matrix

	C	D
C	R, R	S, T
D	T, S	P, P

with $T > R > P > S$. Then

$$\pi_1(\mathrm{C}, \mathrm{D}) = S < P = \pi_1(\mathrm{D}, \mathrm{D})$$

which satisfies the first ESS condition, and so D is an ESS. However,

$$\pi_1(\mathrm{D}, \mathrm{C}) = T > R = \pi_1(\mathrm{C}, \mathrm{C})$$

which violates both ESS conditions, and so C is not an ESS.

18. The ESS is a special kind of Nash equilibrium, and therefore the Bishop-Cannings theorem applies: if x is an ESS, then $\pi_1(x', x) = \pi_1(x, x)$ for every pure strategy x' in the support of x.

We use the Bishop-Cannings theorem to find possible mixed ESSs. For example, consider the question *Who takes care of the kids?* There are two strategies: stay (S) and run (R). A parent who stays contributes to the cost of protecting the brood and feeding the hatchlings. If both parents stay, the costs are equally divided. However, a parent who runs away has none of these costs, while the one who stays pays all. If both parents run away, the offspring does not survive.

Let C be the total cost of raising the offspring, and let V be the value of the offspring (in terms of 'fitness') per breeding pair. The payoff matrix then is

	S	R
S	$\frac{1}{2}V - \frac{1}{2}C$, $\frac{1}{2}V - \frac{1}{2}C$	$\frac{1}{2}V - C$, $\frac{1}{2}V$
R	$\frac{1}{2}V$, $\frac{1}{2}V - C$	0 , 0

We further assume that $V > 2C$ so that there is no pure ESS. To see whether there is a mixed ESS, write $x = (p, 1-p)$ where $p \in (0, 1)$ is the probability of staying. Applying the Bishops-Cannings theorem we get

$$\begin{cases} \pi_1(\mathrm{S}, x) &= p\big(\frac{1}{2}V - \frac{1}{2}C\big) + (1-p)\big(\frac{1}{2}V - C\big) &= \pi_1(x, x) \\ \pi_1(\mathrm{R}, x) &= p\,\frac{1}{2}V + (1-p)\,0 &= \pi_1(x, x) \end{cases}$$

and so

$$p\Big(\frac{1}{2}V - \frac{1}{2}C\Big) + (1-p)\Big(\frac{1}{2}V - C\Big) = p\,\frac{1}{2}V$$

from which we find

$$p = \frac{V - 2C}{V - C} \in (0, 1)$$

But is $x = (p, 1-p)$ an ESS? By construction (i.e., how we calculated p) the first ESS condition does not hold, and so we have to check the second condition. To this end the following proposition is quite useful:

Proposition. For the second ESS condition to hold it is necessary and sufficient that $\pi_1(\mathrm{S}, \mathrm{S}) < \pi_1(x, \mathrm{S})$ and $\pi_1(\mathrm{R}, \mathrm{R}) < \pi_1(x, \mathrm{R})$. In other words, we only have to check that the second ESS condition holds for *pure strategies*. $\square$

The proof is left as an exercise. Applying the proposition to $x = (p, 1-p)$ with $p = (V - 2C)/(V - C)$ gives

$$\pi_1(\mathrm{S}, \mathrm{S}) - \pi_1(x, \mathrm{S}) = -\frac{C^2}{2(V - C)} < 0$$

and

$$\pi_1(\mathrm{R}, \mathrm{R}) - \pi_1(x, \mathrm{R}) = -p\left(\frac{1}{2}V - C\right) < 0$$

and so x is an ESS indeed.

19. Every two-person game with finitely many strategies has a Nash equilibrium if mixed strategies are allowed. Does a similar thing also hold for the ESS? The answer is no, because the ESS is a stronger concept than the Nash equilibrium: every ESS corresponds to a Nash equilibrium, but the reverse is not true, because the definition of an ESS is more restrictive. However, we have the following result:

Proposition. Every two-person game with two pure strategies and payoff matrix

	x_1	x_2
x_1	a, a	b, c
x_2	c, b	d, d

has an ESS if mixed strategies are allowed and $a \neq c$ and $d \neq b$.

Proof. If $a > c$, then x_1 is an ESS, and if $d > b$, then x_2 is and ESS. Now suppose that $a < c$ and $d < b$. Then from the Bishop-Cannings theorem we find that $x = (p, 1 - p)$ with

$$p = \frac{b - d}{c - a + b - d} \in (0, 1)$$

is a candidate-ESS. Again by construction the first ESS condition fails, and so we check the second condition:

$$\pi_1(x_1, x_1) - \pi_1(x, x_1) = -\frac{(c - a)^2}{c - a + b - d} < 0$$

and

$$\pi_1(x_2, x_2) - \pi_1(x, x_2) = -\frac{(b - d)^2}{c - a + b - d} < 0$$

Conclusion: x is an ESS indeed. □

What about games with more than two pure strategies? Consider the Rock-Paper-Scissors game with the payoff matrix

	R	P	S
R	0 , 0	-1 , 1	1 , -1
P	1 , -1	0 , 0	-1 , 1
S	-1 , 1	1 , -1	0 , 0

We have seen that $x = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ corresponds to a Nash equilibrium. Is it also an ESS? The first ESS condition fails, and the second ESS condition fails too:

$$\pi_1(\mathrm{R}, \mathrm{R}) - \pi_1(x, \mathrm{R}) = 0$$

and so x is not an ESS.

20. The following proposition gives a necessary condition for the existence of a mixed ESS with a given support:

Proposition. **(a)** If there exists a mixed ESS $x \in \mathbb{R}^n$ with support $\mathrm{supp}(x) = \{x_{i_1}, \ldots, x_{i_m}\}$ for $m \leq n$, then necessarily

$$(*) \quad \pi_1(x_{i_k}, x_{i_k}) - \pi_1(x_{i_k}, x_{i_{k+1}}) - \pi_1(x_{i_{k+1}}, x_{i_k}) + \pi_1(x_{i_{k+1}}, x_{i_{k+1}}) < 0$$

for $k = 1, \ldots, m-1$, and where the ordering of the x_{i_k} is fixed but otherwise arbitrary. **(b)** If $x \in \mathbb{R}^n$ is a mixed strategy such that $\pi_1(x', x) = \pi_1(x, x)$ for all x' in the support of x and $\pi_1(x', x) < \pi_1(x, x)$ for all x‘ not in the support of x, then x is an ESS whenever $(*)$ is satisfied.

Proof. Without loss of generality we assume that $x_{i_k} = x_k$ for all k. Define the matrix

$$A \stackrel{\text{def}}{=} \begin{pmatrix} \pi_1(x_{i_1}, x_{i_1}) & \ldots & \pi_1(x_{i_1}, x_{i_m}) & 0 & \ldots & 0 \\ \vdots & & \vdots & \vdots & & \vdots \\ \pi_1(x_{i_m}, x_{i_1}) & \ldots & \pi_1(x_{i_m}, x_{i_m}) & 0 & \ldots & 0 \\ 0 & \ldots & 0 & 0 & \ldots & 0 \\ \vdots & & \vdots & \vdots & & \vdots \\ 0 & \ldots & 0 & 0 & \ldots & 0 \end{pmatrix} \in \mathbb{R}^{n \times n}$$

For arbitrary mixed strategies x and y with support in $\{x_{i_1}, \ldots, x_{i_m}\}$, we have

$$\pi_1(y, x) = y^{\mathrm{T}} A\, x$$

where the superscript $^{\mathrm{T}}$ denotes the transpose. If x is a mixed ESS with support $\{x_{i_1}, \ldots, x_{i_m}\}$, then by the second ESS condition

$$y^{\mathrm{T}} A\, x = x^{\mathrm{T}} A\, x \quad \& \quad y^{\mathrm{T}} A\, y < x^{\mathrm{T}} A\, y$$

for all $y \neq x$ with a support in $\{x_{i_1}, \ldots, x_{i_m}\}$. Taking the transpose, we get the equivalent conditions

$$x^{\mathrm{T}} A^{\mathrm{T}} y = x^{\mathrm{T}} A^{\mathrm{T}} x \quad \& \quad y^{\mathrm{T}} A^{\mathrm{T}} y < y^{\mathrm{T}} A^{\mathrm{T}} x$$

Combining these expressions, we find

$$y^{\mathrm{T}}(A + A^{\mathrm{T}})\, y - y^{\mathrm{T}}(A + A^{\mathrm{T}})\, x - x^{\mathrm{T}}(A + A^{\mathrm{T}})\, y + x^{\mathrm{T}}(A + A^{\mathrm{T}})\, x < 0$$

which can be rewritten as

$$(y - x)^{\mathrm{T}}(A + A^{\mathrm{T}})\,(y - x) < 0$$

or, equivalently, as

$$\Delta^{\mathrm{T}}(A + A^{\mathrm{T}})\,\Delta < 0$$

for every non-zero $\Delta \in \mathbb{D} \overset{\text{def}}{=} \{(\Delta_1, \dots, \Delta_m, 0, \dots, 0) \in \mathbb{R}^n : \sum_{i=1}^m \Delta_i = 0\}$. The set $\mathbb{D}$ is an m-dimensional linear subspace of $\mathbb{R}^n$ for which we can choose a basis: $\{e_i - e_{i+1}\}_{i=1}^{m-1}$ where e_i is the i^{th} unit vector. Hence, the condition

$$\Delta^{\mathrm{T}}(A + A^{\mathrm{T}})\,\Delta < 0 \quad \forall\, \Delta \in \mathbb{D} \neg \{0\}$$

is equivalent to

$$(e_i - e_{i+1})^{\mathrm{T}}(A + A^{\mathrm{T}})\,(e_i - e_{i+1}) < 0$$

for $i = 1, \dots, m-1$, which, using the definition of the matrix A is easily shown to be equivalent to

$$\pi_1(x_{i_k}, x_{i_k}) - \pi_1(x_{i_k}, x_{i_{k+1}}) - \pi_1(x_{i_{k+1}}, x_{i_k}) + \pi_1(x_{i_{k+1}}, x_{i_{k+1}}) < 0$$

for $k = 1, \dots, m-1$. This proves the first part of the proposition, i.e., the above is a necessary condition for the existence of an ESS with support $\{x_{i_1}, \dots, x_{i_m}\}$. If $m = n$, then the condition is not only necessary but also sufficient for the existence of an ESS with full support, because all steps above are reversible. □

For example, consider the modified Rock-Paper-Scissors game with payoff matrix

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

with $\varepsilon > 0$. We have

$$\pi_1(\mathrm{R}, \mathrm{R}) - \pi_1(\mathrm{R}, \mathrm{P}) - \pi_1(\mathrm{P}, \mathrm{R}) + \pi_1(\mathrm{P}, \mathrm{P}) < 0$$
$$\pi_1(\mathrm{P}, \mathrm{P}) - \pi_1(\mathrm{P}, \mathrm{S}) - \pi_1(\mathrm{S}, \mathrm{P}) + \pi_1(\mathrm{S}, \mathrm{S}) < 0$$

and so there exists a mixed ESS with full support.

21. The following is a handy little proposition that will save you the trouble of having to check for the existence of certain ESSs.

Proposition. If a game has two ESSs, then the support of the one cannot be a subset of the other.

Proof. Let $\hat{x}_1$ and $\hat{x}_2$ be two evolutionarily stable strategies. To reach a contradiction, suppose that the support of $\hat{x}_1$ is a subset of the support of $\hat{x}_2$. Then, by the Bishop-Cannings theorem, $\pi_1(\hat{x}_1, \hat{x}_2) = \pi_1(\hat{x}_2, \hat{x}_2)$, and so the first ESS condition fails for $\hat{x}_2$. Hence, the second ESS condition should hold, i.e., $\pi_1(\hat{x}_1, \hat{x}_1) < \pi_1(\hat{x}_2, \hat{x}_1)$. But this contradicts that $\hat{x}_1$, too, is an ESS. □

For example, in the Prisoner's Dilemma the strategy D is evolutionarily stable, and therefore there cannot be a mixed ESS as well. Also, whenever in a given game there is an ESS with full support, then that ESS is the only one possible for that game. For example, the modified Rock-Paper-Scissors game in the previous section has an ESS with full support, which necessarily is the only ESS of the game.

22. As a sort of intermezzo, to get an idea of another of population dynamical embedding of the notion of ESS, we have a brief look at a kind of game situation called "playing the field" where individuals are not involved in pair-wise contest but instead interact with the population as a whole.

The example we give is that of the evolution of the sex ratio: this is the ratio of the expected numbers of sons and daughters produced per female. In most species this ratio is close to one, but why is this so?

Mammals have the XY sex-determination system which more or less predisposes them to a sex ratio close to one, but notable exceptions are know, e.g., in chimpanzees (Boesch & Boesch-Achermann (2000) Oxford University Press, page 86), both towards a lower and towards a higher sex ratio.

Other sex-determination systems are more flexible, e.g., temperature sex-determination (most prominently in reptiles) or change of sex as in sequential hermaphrodites, which is quite common in fish and snails.

The upshot is that the sex-determination system in itself provides insufficient explanation for sex ratios observed in nature. Here we attempt to give a simple evolutionary explanation.

Let n and n' denote the population densities of the resident and the invader strategies. As strategies, however, we do not take the sex ratios themselves but rather the proportions x and x' of sons among the offspring; the sex ratios then are $x/(1-x)$ and $x'/(1-x')$. We further write $N = n + n'$ for the total population density and $\varepsilon = n'/N$ for the fraction of invaders.

We assume that all females are mated. In this way the 'fitness' of a given sex ratio strategy only depends on the success of males in finding a mate. We also assume that the expected number of children per female is independent of the sex ratio strategy. As a measure of 'fitness' of the strategy x', we therefore take the number $g_1(x', x, \varepsilon)$ of grandchildren produced per female.

Let λ denote the expected number of children per female. The number of daughters of a female with strategy x' then is $(1-x')\lambda$. Each of these daughters produces another λ children, and so the number of grandchildren produced via the daughters is $(1-x')\lambda^2$.

The number of grandchildren produced via the sons is equal to the number of sons (i.e., $x'\lambda$) times the number of females available per son (i.e., the total number of females in the population divided by the total number of males) times the number of children per female (i.e., λ), which is

$$x'\lambda^2 \, \frac{(1-\varepsilon)(1-x)N\lambda + \varepsilon(1-x')N\lambda}{(1-\varepsilon)xN\lambda + \varepsilon x' N\lambda}$$

The total number $g_1(x', x; \varepsilon)$ of grandchildren produced via sons and daughters then is

$$g_1(x', x; \varepsilon) = (1-x')\lambda^2 + x'\lambda^2 \, \frac{(1-\varepsilon)(1-x) + \varepsilon(1-x')}{(1-\varepsilon)x + \varepsilon x'}$$

Likewise, for the number of grandchildren produced per female with strategy x we find The total number $g_1(x', x; \varepsilon)$ of grandchildren produced via sons and daughters then is

$$g_2(x', x; \varepsilon) = (1-x)\lambda^2 + x\lambda^2 \, \frac{(1-\varepsilon)(1-x) + \varepsilon(1-x')}{(1-\varepsilon)x + \varepsilon x'}$$

Embedding the ESS definition into the present context gives that a sex ratio strategy x is evolutionarily stable if, and only if for every $x' \neq x$ there exists an $\varepsilon_0 > 0$ such that $g_1(x', x; \varepsilon) < g_2(x', x; \varepsilon)$ whenever $\varepsilon < \varepsilon_0$.

Expanding into terms of different order in ε, we get

$$g_1(x', x; \varepsilon) - g2(x, x; \varepsilon) = -\lambda^2\Big(1 - 2x + 2x' - \frac{x'}{x}\Big) - \lambda^2 \frac{(x-x')^2}{x^2}\varepsilon + \mathrm{O}(\varepsilon^2)$$

It follows that x is evolutionarily stable if for every $x' \neq x$

$$1 - 2x + 2x' - \frac{x'}{x} > 0$$

or

$$1 - 2x + 2x' - \frac{x'}{x} = 0 \quad \& \quad \frac{(x-x')^2}{x^2} > 0$$

Only $x = 1/2$ satisfies the conditions, i.e., the first condition fails, but the second condition is satisfied. Conclusion: $x = 1/2$ (which corresponds to a sex ration of one) is an ESS.

(Note: an earlier version of this example was wrong. This is the correct version.)