Evolutionary game theory

Slides taken from Lilach Hadany
Course: Population Genetics and Evolutionary Theory

Adi Shabi
The simplest model

- Adults
- Gametes
- Mating
- Newborns
- Selection
- Adults

One generation
The concept of fitness

Fitness of genotype $G$: the expected number of offspring of an individual of type $G$.

Components of fitness:
- Probability of survival to adulthood (viability selection)
- Mating success (sexual selection)
- Expected number of offspring given survival and mating (fecundity selection)
The concept of fitness

Fitness is specific to an environment

Example: Industrial melanism

Pollution
Lichens die
Soot makes trees dark
Light form becomes much more visible...
Frequency dependant selection

A situation where the fitness of a genotype is a function of genotype frequencies

Examples: host-parasite
            predator-prey
Frequency dependant selection

Perissodus microlepis, a cichlid fish feeding on scales (partial predator). The frequency of left-jawed fishes oscillates around 0.5. The prey learns to look more often towards the side that more predators come from...
Game theory

Economics
- Assumes that “players” behave rationally and attempt to maximize some criterion of self interest, e.g. profit

Evolution
- Natural selection replaces rationality
- Fitness replaces profit
When do we need game theory to model evolution?

Game theory is needed for situations in which the success of a particular strategy depends on the strategies of other individuals in the population – i.e., when selection is frequency dependent.
Modeling animal fights
Hawk and dove

A 'hawk' (H) fights until someone is injured or the opponent retreats.

A 'dove' (D) displays, and retreats if the opponent escalates.

The contest can be over food, territory, or a mate.

The winner gets a gain in fitness, $G$

Injury reduces fitness by $C$
Hawk and dove

If it meets a hawk

If it meets a dove

A hawk receives

A dove receives
Hawk and dove

If it meets a hawk

If it meets a dove

A hawk receives $(G-C)/2$

A dove receives

- When two hawks meet one is injured and the other gets the resource: on average they get $(G-C)/2$
Hawk and dove

If it meets a hawk

A hawk receives $(G-C)/2$

A dove receives $G$

If it meets a dove

- When a hawk and a dove meet, the dove retreats and the hawk receives a gain $G$
**Hawk and dove**

<table>
<thead>
<tr>
<th></th>
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<td>(G)</td>
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<td>A dove receives</td>
<td>0</td>
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Hawk and dove

If it meets a hawk
A hawk receives
\[ \frac{(G-C)}{2} \]
A dove receives
\[ 0 \]

If it meets a dove
\[ G \]
\[ \frac{G}{2} \]

- When two doves meet they display until one of them retreats: on average they get \( \frac{G}{2} \)
Definitions

Assume two strategies, I and J, with frequencies $p(I)$ and $p(J)$.

$E(I,J)$ is the payoff of individual of type I from interaction with individual of type J.

The fitness of an individual is composed of a constant, $K$, plus a payoff: the change in fitness resulting from the interaction.

$W(I) = K + p(I)E(I,I) + p(J)E(I,J)$

$W(J) = K + p(I)E(J,I) + p(J)E(J,J)$
Definitions

After interaction, individuals reproduce their kind (I produce I’s and J produce J’s) in proportion to their fitness, and then die.

We could find the frequency of each strategy in the next generation:

\[ p(I)' = \frac{p(I)W(I)}{W}, \]

Where \( W = p(I)W(I) + p(J)W(J) \)

But what we are most interested in is **Equilibria**
Nash equilibrium

If each player has chosen a strategy and no player can benefit by changing his or her strategy while the other players keep theirs unchanged, then the current set of strategy choices and the corresponding payoffs constitute a Nash equilibrium.
Evolutionary Stable Strategy

Consider a strategy $I$ of the majority of the population and $M$ is a rare mutant with frequency $p$, with $p<<1$. From our definitions

$$W(I) = K + (1-p)E(I,I) + pE(I,M)$$

$$W(M) = K + (1-p)E(M,I) + pE(M,M)$$

Definition: The strategy $I$ is an evolutionarily stable strategy (ESS) if, for any alternative strategy $M$, $W(I) > W(M)$. That is, either:

$$E(I,I) > E(M,I)$$

or

$$E(I,I) = E(M,I) \text{ and } E(I,M) > E(M,M)$$
Back to hawk and dove

Example 1: $G=2, C=1$

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<td>2</td>
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Which strategy would win in this game?
Back to hawk and dove

Example 1: \( G=2, \ C=1 \)

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Which strategy would win in this game?

\( E(D,H)=0 < E(H,H)=0.5 \)

Hawk is an ESS!

What are the conditions for that in terms of \( G \) and \( C \)?
Back to hawk and dove

Example 1: \(G=2, \ C=1\)

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Which strategy would win in this game?

\[E(D,H)=0 < E(H,H)=0.5\]

Hawk is an ESS  \(\text{Whenever } G-C>0\)
Back to hawk and dove

Example 2: $G=2$, $C=6$

If it meets a hawk | If it meets a dove
--- | ---
A hawk receives | -2 | 2
A dove receives | 0 | 1

-What is the best strategy when doves are common?
-What is the best strategy when hawks are common?
Back to hawk and dove

Example 2: $G=2$, $C=6$

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- When doves are common, it is good to be a hawk:
  $E(H,D)=2 > E(D,D)=1$
- When hawks are common, it is good to be a dove:
  $E(D,H)=0 > E(H,H)=-2$

No ESS?
Pure and mixed strategies

In the hawk-dove game with $C > G$, no pure strategy is an ESS.

However, in some cases we can consider mixed strategies: where more than one pure strategy is played with probability $> 0$.

Let $I$ be the strategy: play 'hawk' with probability $p$ and 'dove' with probability $1-p$.

Can we find a value of $p$ for which $I$ is an ESS?
Mixed strategies

Let $I$ be the following strategy: play ‘hawk’ with probability $p$ and ‘dove’ with probability $1-p$.

Can we find a value of $p$ for which $I$ is an ESS?

If $I$ is an ESS, then:

When most of the population plays $I$, the payoff of a rare individual playing $H$ must be equal to the payoff of a rare individual playing $D$.

Proof: Let us assume this is not the case, so the payoff of one pure strategy (say, $H$) is higher than that of the other. Then a mutant that always plays $H$ can invade an $I$ population $\rightarrow I$ is not an ESS!
Mixed strategies

More generally:

If I is a mixed ESS, in which strategies A, B, C... are played with non-zero probabilities, then in a population of I's the payoffs to A, B, C... must be equal.
Let I be the following strategy: play 'hawk' with probability p and 'dove' with probability 1-p.

If I is an ESS, then:

\[ E(H,I) = E(D,I) \]

\[-2p + 2(1-p) = 1-p \rightarrow p = \frac{1}{3} \]

Does this mean that the strategy: play H with probability 1/3 and D with probability 2/3 is an ESS?
Mixed strategy: hawk and dove

Remember, for I to be an ESS we need:

\[ E(I,I) > E(M,I) \] - not in this case, as \( E(I,I) = E(D,I) = E(H,I) \)

or

\[ E(I,I) = E(M,I) \text{ and } E(I,M) > E(M,M) \]

We need to show \( E(I,D) > E(D,D) \) and \( E(I,H) > E(H,H) \)

\[ E(I,D) = (1/3)(2) + (2/3)(1) = 4/3 > 1 = E(D,D) \]

\[ E(I,H) = (1/3)(-2) + (2/3)(0) = -2/3 > -2 = E(H,H) \]

\[ \rightarrow \text{ I is an ESS!} \]
Effect on average fitness

When $p=1/3$, then:

$$E(H,I) = E(D,I) = E(I,I) = 2/3$$

If everybody played 'dove', the average payoff would have been $E(D,D) = 1$

Thus, ESS not necessarily increases average fitness!
Is there always an ESS?

With two players, yes:
If there is no ESS with pure strategies, there is always a mixed ESS, with probability \( p \) playing strategy \( A \) and probability \( 1-p \) playing \( B \). To find it

\[
pE(A,A) + (1-p)E(A,B) = pE(B,A) + (1-p)E(B,B)
\]

\[
\]

\[
p=\frac{E(B,B)-E(A,B)}{[E(A,A)+E(B,B)-E(A,B)-E(B,A)]}
\]

With more players, not necessarily.
# Rock-paper-scissors

<table>
<thead>
<tr>
<th>Payoff of:</th>
<th>Rock</th>
<th>Paper</th>
<th>Scissors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paper</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Scissors</td>
<td></td>
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</table>

Against:

- Rock
- Paper
- Scissors
# Rock-paper-scissors

## Payoff Table

<table>
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<tr>
<th></th>
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<th>Scissors</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rock</strong></td>
<td>0</td>
<td>-1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Paper</strong></td>
<td>1</td>
<td>0</td>
<td>-1</td>
</tr>
<tr>
<td><strong>Scissors</strong></td>
<td>-1</td>
<td>1</td>
<td>0</td>
</tr>
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</table>

ESS?
Exmaples of Rock-Paper-Scissors in Nature?

Sinervo and Lively (Nature, 1996)
Male Side-blotched Lizards (Uta stansburiana):

ORANGE  “Offense”
BLUE    “Defense”
YELLOW  “Deception”
Rock-paper-scissors in lizards

ORANGE: “Offense”
Aggressive, hold large territories
(+): Dominate BLUE males
(-): YELLOW males can infiltrate territory

BLUE: “Defense”
Smaller territories, guarded well
(+): Catch and attack YELLOW
(-): Lose fights to ORANGE

YELLOW: “Deception”
Mimic female color/behavior
(+): Unnoticed by ORANGE
(-): Noticed by BLUE
Field Data

• No difference in juvenile survival
• Adult morph survival (L) varies:
  \[ Ly = 0.167 \]
  \[ Lb = 0.136 \]
  \[ Lo = 0.048 \]
• Morph is heritable
The fitness function was calculated from the empirical data, and a simplified model

\[ p_{i,t+1} = p_{i,t} \left( \frac{W_{i,t}}{W} \right) \]

Where

\[ W_{i,t} = p_{1,t} W_{i,1} + p_{2,t} W_{i,2} + p_{3,t} W_{i,3} \]

\[ \bar{W} = \sum_i p_{i,t} W_{i,t} \]

was run numerically

Sinervo and Lively (Nature, 1996)
Games with more than one ESS?
Games with more than one ESS?

- Driving

<table>
<thead>
<tr>
<th></th>
<th>Right</th>
<th>Left</th>
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<tbody>
<tr>
<td>Right</td>
<td>1</td>
<td>-100</td>
</tr>
<tr>
<td>Left</td>
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</table>

[Image of snails]
Symmetric and asymmetric games

Until here we considered only symmetric games, where both players have the same set of strategies and the same payoffs.

However, this is not always the case.

In asymmetric games different players have different strategies available, and different payoffs. (Also called Bi-matrix games because there are two different payoff matrices).
Possible asymmetries

Value of resource may differ between rivals, affecting motivation

Fighting ability:
Size, strength, condition

Ownership - why is it important?
• ownership may be correlated with resource value - the owner knows its resource better and may have more to lose.
• ownership may be correlated with fighting ability
Bourgeois

Respect for ownership - behaves like Hawk if owner, like Dove if intruder

Assumptions:
- Individuals find themselves in the role of owner half the time and in the role of intruder half the time
- competitors still equal
New strategy, B: play Hawk when owner, Dove when intruder

<table>
<thead>
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<tr>
<td><strong>H</strong></td>
<td>(G-C)/2</td>
<td>G</td>
<td></td>
</tr>
<tr>
<td><strong>D</strong></td>
<td>0</td>
<td>G/2</td>
<td></td>
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**Owner and intruder**
**Owner and intruder**

New strategy, B: play Hawk when owner, Dove when intruder

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<tr>
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</tr>
<tr>
<td>B</td>
<td>(G-C)/4</td>
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</table>
**Owner and intruder**

Assume $G=2$, $C=6$. Which strategy is ESS?

```
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<td>H</td>
<td>-2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>B</td>
<td>-1</td>
<td>1.5</td>
<td>1</td>
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```

Payoff of: Against:
**Owner and intruder**

Can there be more than one ESS in this game?

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Owner and intruder

Consider I: play H with probability 1/3, play D with probability 2/3. \( E(I,I) = E(D,I) = E(H,I) = 2/3 \)
\( E(B,I) = (1/3)(-1) + (2/3)1.5 = 2/3 \)

Remember: For I to be an ESS we need:

\( E(I,I) > E(M,I) \) - not satisfied!

or

\( E(I,I) = E(M,I) \) and \( E(I,M) > E(M,M) \)

I is not ESS any more!

Is it a Nash equilibrium?
Effect on average fitness

When Bourgois is common, then:

\[ E(B,B) = 1 \]

Average fitness increases because fighting never occurs!

Note: at the moment there is no real difference between owner and intruder in fighting ability!
Example: the speckled wood butterfly

Davies, 1978:
The resident always wins!

But things are more complicated.... later:

Stutt and Willmer, 1998:
The hottest wins

Kemp and Wiklund, 2003:
The more aggressive wins
Asymmetric games

Let us assume asymmetry: if fighting occurs, the owner is more likely to win with $p(\text{owner winning})=d$

<table>
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<tr>
<th>Owner:</th>
<th>a hawk</th>
<th>a dove</th>
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<td>A hawk receives</td>
<td>$Gd-C(1-d)$</td>
<td>$G$</td>
</tr>
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<td>0</td>
<td>$G/2$</td>
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| Intruder:                      |               |                |
| A hawk receives                | $G(1-d)-Cd$   | $G$            |
| A dove receives                | 0             | $G/2$          |
**Owner and intruder**

New strategy, B: play Hawk when owner, Dove when intruder

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<td>[G(1-d)-Cd +G]/2</td>
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<td>G/4</td>
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<td>[(Gd-C(1-d))/2+0</td>
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## Owner and Intruder

B: play Hawk when owner, Dove when intruder
X: play Hawk when intruder, Dove when owner

### Payoff of:

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<tr>
<td>H</td>
<td>( \frac{[(Gd-C(1-d)) + G(1-d) - Cd]}{2} )</td>
<td>( G )</td>
<td>( \frac{[G(1-d) - Cd + G]}{2} )</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>( \frac{G}{2} )</td>
<td>( \frac{G}{4} )</td>
<td></td>
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<tr>
<td>B</td>
<td>( \frac{[Gd-C(1-d) + O]}{2} )</td>
<td>( \frac{3}{4}G )</td>
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Owner and intruder

Can X be an ESS?

\[
\frac{Gd-C(1-d)}{2} + \frac{G}{4} < \frac{G}{2}
\]

Or

\[
\frac{Gd-C(1-d)}{2} + \frac{G}{4} = \frac{G}{2}, \text{ and}
\]

\[
\frac{G(1-d)-Cd}{2} + \frac{G}{4} > \frac{G}{2}
\]
Owner and intruder

Can X be an ESS?

\[ \frac{[Gd-C(1-d)]}{2} + \frac{G}{4} < \frac{G}{2} \]

Or

\[ \frac{[Gd-C(1-d)]}{2} + \frac{G}{4} = \frac{G}{2}, \text{ and} \]

\[ \frac{[G(1-d)-Cd]}{2} + \frac{G}{4} > \frac{G}{2} \]

\[ [Gd-C(1-d)] > [G(1-d)-Cd] \]
Owner and intruder

Can X be an ESS?

\[ \frac{Gd-C(1-d)}{2}+G/4 < G/2 \]

\[ G/C < \frac{(1-d)}{(d-0.5)} \]
Multi-level selection
The prisoner's dilemma

Consider two prisoners...
The prisoner’s dilemma

A possible solution - multiple interactions with the same partner.

Axelrod and Hamilton (1981)
A tournament of strategies, each playing 200 games against each other. The winner...

TIT For TAT: a strategy starting with C, and then follows its opponents - answers C for C and D for D.

A second tournament. More strategies, and more complicated ones. The winner now is...
The prisoner’s dilemma

A possible solution - multiple interactions with the same partner.

Axelrod and Hamilton (1981)
A tournament of strategies, each playing 200 games against each other. The winner...

TIT For TAT: a strategy starting with C, and then follows its opponents - answers C for C and D for D.

A second tournament. More strategies, and more complicated ones. The winner now is… TIT For TAT again
TIT for TAT

What properties of TFT make it advantageous in this tournament?

'nice' - starts with cooperation
'provokable' - defects in response to defection
'forgiving' - returns to cooperation if opponent does
Multi-player prisoner’s dilemma

“The tragedy of the commons”: Each member of a group of neighboring farmers prefers to allow his cow to graze on the commons, rather than keeping it on his own inadequate land, but the commons will be rendered unsuitable for grazing if more than some threshold number $n$ use it. More generally, there is some social benefit $G$ that each member can achieve if sufficiently many pay a cost $C$. We might represent the payoff matrix as follows:

$$
\begin{array}{c|c|c}
\text{less than } n & \text{\geq } n \\
\text{others choose } C & \text{others choose } C \\
\hline
C & -C & G - C \\
D & 0 & G \\
\end{array}
$$
The tragedy of the commons

Implications: Marine conservation
  - overfishing
  - pollution
The tragedy of the commons

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The tragedy of the commons

Example: Pseudomonas fluorescens
Pseudomonas cells can survive only at the surface (obligate aerobe). Cells with the gene ‘wrinkly spreader’ (green) secrete a polymer that forms a buoyant mat (left). Producing the polymer has a metabolic cost for the cell.
Non-secreting mutants (yellow) can live as freeloaders, benefiting from their neighbors’ exertions. The freeloader cells reproduce faster; when they become too numerous, however, the entire mat disintegrates and sinks (right)
The volunteer dilemma

A group of penguins is standing on the ice. They are hungry. There are fish in the water, but there might also be a predator.

In terms of 'the tragedy of the commons'?
Game theory refs

Some introduction to game theory can be found in:
Maynard Smith "Evolution and the theory of games",
Maynard Smith "Evolutionary genetics",
Sean Rice “Evolutionary theory”, chapter 9, or
http://www.holycross.edu/departments/biology/kpres
twi/behavior/ESS/ESS_index_frmset.html