Biology X:
Introduction to (evolutionary) game theory

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see Gintis, *Game theory evolving*, Chapters 2, 3, 10

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Overview

Evolutionary game theory: motivation and background

Classical game theory

Evolutionary game theory: Stable states formalized

Beginnings of evolutionary GT

- Why do competing animals usually not fight to death?
  - Idea: strategic behavior
- How can strategic behavior be explained?
  - Idea: (Simple) behaviors are determined genetically, evolution generates them
- What kinds of behaviors can this ultimately lead to?
  - Idea: Behaviors that are resistant to invasion by mutants

Hawk-Dove

- Consider a population of animals competing for food, where each (pairwise) conflict is solved by fighting ("Hawk")
- Contestants get severely injured, decreasing their fitness

- Assume a mutant occurs that withdraws before getting hurt, when defeat is evident ("Dove")
- When two Doves meet, they share; when a Dove meets a Hawk, she retreats
- Avoiding injury, Doves can overall be fitter
- So their genes can spread in the population

- What happens in a population consisting purely of Doves?

- EGT examines dynamics and stable states ("equilibria")

Alarm calls

- Vervet monkeys have a sophisticated system of alarm calls
- Why would a monkey put itself at risk by calling out?

- In repeated interactions, the mutual benefit may outweigh the risk
- So a small mutant population can spread in a non-signaling population

- Again, in a signaling population, some "cheaters" may profit from alarm calls without contributing themselves

Important features in these examples

- Population of individuals with (partial) conflict of interest
- Encounters take place among groups of individuals
- Behavior is controlled by genes and inherited
- Repeated interaction
- Random encounters, "anonymous", no history
- But there may be correlation of encounters:
  - Spatial structure/geometry
  - Kinship
  - ...
- Depending on the parameters, different dynamics and equilibria may occur

Evolutionary game theory (EGT)

- EGT puts these ideas into a mathematical framework and studies their properties
- Put differently, EGT studies dynamics and equilibria of individual behaviors in populations
- Most important initiator of EGT:
  - John Maynard Smith (1920–2004); *Evolution and the Theory of Games* (1982)
- Other people paved the way:
  - Ronald Fisher (1890–1962); his work on sex ratios (1930)
  - William D. Hamilton (1936–2000); his notion of an unbeatable strategy (1967)
  - George R. Price (1922–1975); JMS's coauthor on their seminal 1973 *Nature* paper

see also `http://en.wikipedia.org/wiki/Evolutionary_game_theory`

Based on game theory

- EGT is an application of game theory to evolutionary biology
- To properly understand it, we must therefore start with classical game theory

- (Non-cooperative) game theory is interactive decision theory
- The basic entity is the rational (self-interested) agent
- A rational agent acts so as to maximize his own well-being
- Agents may have conflicting interests
- What the best act is may depend on how other agents act

- Game theory studies the behavior of such agents
- Important people:
  - John von Neumann (1903–1957), Oskar Morgenstern (1902–1977); *Theory of games and economic behavior* (1944)
  - John Nash (1994 Nobel prize in Economics)

Outline

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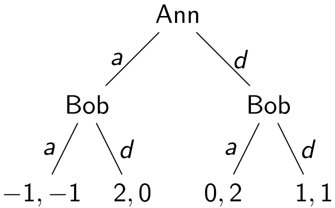
Basic ingredients of game theory

- Agents, or players: $N = \{1, \ldots, n\}$
- Actions, or strategies: $S_1, \ldots, S_n$
- Utilities, or payoffs: $\pi_1, \ldots, \pi_n : S \to \mathbb{R}$,
  where $S = S_1 \times \cdots \times S_n$

- The payoff to a particular agent can depend not only on his choice of action, but on that of all players.
- Payoffs reflect an agents' preferences over the possible outcomes of an interaction.
- Agents are assumed to be rational, i.e., they try to maximize their (expected) payoff and only care for their own payoff.

Basic concepts of game theory

Extensive form game:



Normal/strategic form game:

		Bob: *aa*	Bob: *dd*	Bob: *ad*	Bob: *da*
Ann	*a*	$-1, -1$	$2, 0$	$-1, -1$	$2, 0$
	d	$0, 2$	$1, 1$	$1, 1$	$0, 2$

Basic concepts of game theory

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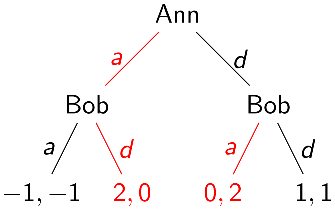

- Backward induction

Normal/strategic form game:

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Ann	*aa*	*dd*	*ad*	*da*
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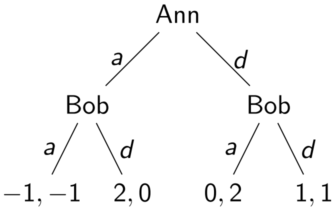

- Backward induction
- Equilibria

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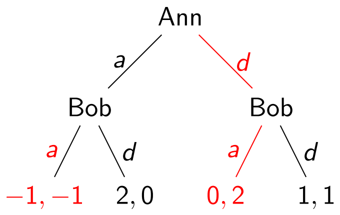

- Backward induction
- Equilibria
- Incredible threats

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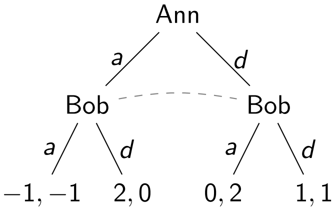

- Backward induction
- Equilibria
- Incredible threats
- Alternating vs simultaneous moves

Normal/strategic form game:

		Bob			
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	d	$0, 2$	$1, 1$	$1, 1$	$0, 2$

	Bob	
	a	*d*
a	-1,-1	2,0
d	0,2	1,1

Prisoner's dilemma

	Cooperate	Defect
Cooperate	2,2	0,3
Defect	3,0	1,1

- Defection dominates
- (Can be fixed by repetition)

Stag hunt: Risky cooperation vs safe defection

	Stag	Hare
Stag	2,2	0,1
Hare	1,0	1,1

- (Stag, Stag) and (Hare, Hare) are both equilibria
- Outcome depends on mutual beliefs and risk attitude

Nash equilibrium

- Strategy profile $s = (s_1, \dots, s_n)$: one strategy for each player
- Strategies of players except i: $s_{-i} = (s_1, \dots, s_{i-1}, s_{i+1}, \dots, s_n)$

Definition

s_i is a best response to s_{-i} iff

$$\pi_i(s_i, s_{-i}) \geq \pi_i(s_i', s_{-i}) \text{ for all } s_i' \in S_i$$

Definition

A strategy profile s is a Nash equilibrium iff

for each player i, s_i is a best response to s_{-i}.

- No player "regrets" his choice, given the others' choices
- No player would benefit from unilaterally deviating.

Matching pennies: no pure strategy equilibrium

	H	T
H	1,-1	-1, 1
T	-1, 1	1,-1

- "Circular" preferences, zero sum
- No equilibrium in pure strategies

Mixed strategies

- Mixed strategy $\sigma_i \in \Delta S_i$: random choice among i's pure strategies S_i
- Assigns some probability $\sigma_i(s_i)$ to any pure strategy $s_i \in S_i$
- E.g., flipping the penny gives σ_i with $\sigma_i(H) = \sigma_i(T) = 0.5$

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- Mixed-strategy profile: $\sigma = (\sigma_1, \ldots, \sigma_n)$
- E.g., $\sigma = (\sigma_1, \sigma_2)$ with $\sigma_1 = \sigma_2 = \sigma_i$ above
- Since players are independent, for a joint strategy $s \in S$ we let

$$\sigma(s) = \sigma_1(s_1) \cdot \ldots \cdot \sigma_n(s_n)$$

- E.g., $\sigma(H, H) = \sigma_1(H) \cdot \sigma_2(H) = 0.5 \cdot 0.5 = 0.25$

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- E.g., $\sigma(H, H) = \sigma_1(H) \cdot \sigma_2(H) = 0.5 \cdot 0.5 = 0.25$
- Rational players maximize their expected payoff:

$$\pi_i(\sigma) = \sum_{s \in S} \sigma(s)\pi_i(s)$$

Nash equilibrium in mixed strategies

Definition

σ_i is a best response to σ_{-i} iff

$$\pi_i(\sigma_i, \sigma_{-i}) \geq \pi_i(\sigma_i', \sigma_{-i}) \text{ for all } \sigma_i' \in \Delta S_i$$

Definition

A mixed-strategy profile σ is a Nash equilibrium iff

for each player i, σ_i is a best response to σ_{-i}.

Theorem (Nash, 1950)

Every finite game has a Nash equilibrium in mixed strategies.

- E.g. (σ_1, σ_2) from before is a Nash equilibrium

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From rationality to evolution

- Strategy: genotypic variants
- Mixed strategy: different ratios of pure-strategy individuals in a population
- Game: repeated random encounters ("stage game")
- Payoff: fitness
- Rationality: evolution
- Equilibrium: fixation of (mix of) genetic traits

- How do we get to an equilibrium? (Dynamics, to be discussed later)
- What equilibrium concept reflects evolutionary stability?

Hawk-Dove: Aggressive vs defensive

	Hawk	Dove
Hawk	-1,-1	2,0
Dove	0,2	1,1

- Two pure-strategy Nash equilibria: (Hawk, Dove), (Dove, Hawk)
- But no pure strategy can stably be adopted by a population
- Not immune against small perturbations ("mutants")

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- Stage game is symmetric in strategies and payoffs

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- Refinement of Nash equilibrium

Hawk-Dove revisited

	Hawk	Dove
Hawk	-1,-1	2,0
Dove	0,2	1,1

- Assume a population of Doves: $\sigma(H) = 0$, $\sigma(D) = 1$
  and a mutant Hawk: $\tau(H) = 1$, $\tau(D) = 0$
- $\pi(\sigma, \sigma) = 1 < 2 = \pi(\tau, \sigma)$
- Hawks can invade

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- But $\pi(\sigma, \tau) = 0 > -1 = \pi(\tau, \tau)$, so Hawks have an advantage only while the population has still mostly Doves
- Hawks won't be able to take over completely

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- Mixed-strategy Nash equilibrium: $\sigma(H) = \frac{1}{2}$, $\sigma(D) = \frac{1}{2}$
- This is also the unique ESS

Summary

- Evolutionary Game Theory tries to explain observed stable states of populations as equilibria in an evolutionary process
- It is based on classical game theory ("interactive rational choice theory"), replacing rationality by evolution and choice by genotypic variants
- Members of a population are assumed to repeatedly participate in random encounters of a certain strategic form
- Payoffs represent fitness

- Nash equilibrium is a set of strategies such that no single player would benefit from deviating
- Evolutionary Stable Strategy is a refinement of Nash equilibrium for symmetric games
- Intuition: if played by a population, then no small mutant population can invade