Game theory

Population genetics

- Genes produce phenotypes
- Selection acts on phenotypes, and hence on genes
- Model this evolution with mutation, selection, recombination
  - deterministic replicator equations
  - stochastic Wright-Fisher or Moran model including random genetic drift
- Problem: genotype -> phenotype not easy
- Selection doesn't really act on genes

Game theory

- Simplify still further: forget about genes, have selection act directly on phenotype
- Individuals have "strategies" not genes
- Offspring inherit strategy
- No diploidy, no recombination
- Successful strategies get arbitrary points (economic game theory) or reproductive fitness (evolutionary game theory)
- Much of evolution, unlike economics, is a zero-sum game, at least in the long run: relative fitness

Prisoner's dilemma

	Cooperate	Defect
Cooperate	3,3	0,5
Defect	5,0	1,1

Defection is a dominant strategy
whatever your partner does, defecting does best

Nash equilibrium is all-defection:
each player's strategy is the best possible response to equilibrium frequency of encounters

Axelrod's tournament

- Repeated interactions
- Cooperation this round may encourage your partner to cooperate next round: reciprocity
- Simulate evolution between strategies

Axelrod's tournament

- A very simple strategy won: tit-for-tat
- Cooperate first: then do whatever your opponent just did
- Tit-for-tat is
  - nice: cooperates first
  - forgiving: one cooperation is enough for it to forgive past defections
  - retaliatory: one defection is enough

After a misunderstanding, 2 TFT players will defect forever

- With "noise" or "mistakes", good to be a little
  - generous: occasionally cooperate
- One such strategy is Pavlov:
  - do what you just did if it went well
  - do the opposite if it went badly

Can we predict winning strategies?

- Normal pop gen solution: fitness
- Problem?
- Fitness depends on frequencies of strategies in population

Evolutionary stable strategy

- ESS, *once adopted*, cannot be invaded by any other strategy
- Invasion = increase frequency (~ fitness) when rare
- Looking only when rare avoids frequency-dependence

- Defection is the only Nash equilibrium for the Prisoner's dilemma
- Both defection and tit-for-tat are ESSs

Can an ESS *never* be invaded?

- Real populations are finite, and stochasticity may allow invasion
- Tit-for-tat cannot invade an all-defect population, since there is nobody to cooperate with
- Once tit-for-tat rises above a threshold frequency, it will increase from there
- This is easier in a spatial model: more likely to interact with relatives

Sometimes there are multiple ESSs. Which one will win?

- Occasional stochastic transitions in time between ESSs
- Different groups in space might evolve different ESSs
- Selection at the group level determines winner
- A bit like Wright's shifting balance theory, without the genetic complications

1 player vs. environment

- After g good rounds and b bad ones, fitness $\propto w_{good}^{g} w_{bad}^{b}$
- Strategy that has highest geometric mean fitness will do best

	Strategy 1	Strategy 2	50-50 strategy
Good env. (50% likely)	2	1	1.5
Bad env (50% likely)	0.25	0.5	0.375
Geometric mean fitness	0.707	0.707	0.75 bet-hedging

Hawk-dove game

- Two players want the same resource
- Hawk escalates a fight until injured or until opponent retreats
- Dove displays, but immediately retreats if fight escalates

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

- Doves can be invaded by rare hawk mutation
- Hawks can be invaded by dove mutation if $C>V$
- The ESS is a probabilistic mixed strategy rather than a pure strategy

Mixed strategy vs. polymorphism

- Say the evolutionary stable strategy is to be a hawk 70% of the time
- An evolutionary stable state can also be polymorphic population with 70% individuals having a pure hawk strategy and 30% having a pure dove strategy
- Not clear to what extent evolution generates ESS mixed strategies vs. polymorphisms

Asymmetric games

- Asymmetry can be real (one player is bigger and stronger) or an arbitrary convention
- Bourgeois strategy: "play hawk when owner and dove when intruder"
- Bourgeois can defeat mixed hawk/dove
- Anti-bourgeois is also ESS, but may be a small cost to frequent changes in ownership
- Bourgeois convention makes V higher, which changes things again…
- Not a problem for speckled wood butterfly, which defends territorial patches of sunlight, and resident always wins: sunlight is transient

Parental care

Should mother and/or father care for offspring?

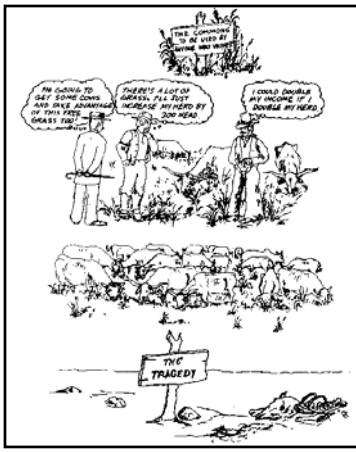
V_i offspring survive when i parents care for them

Male who deserts has probability p of finding a second female

Female who deserts has probability q of finding a second male

		Female: Care	Female: Desert
Male	Care	V_2,V_2	V_1,V_1+qV_2
	Desert	V_1+pV_2,V_1	$0,0$

Different if male gets to choose first



Tragedy of the commons

Like the Prisoner's dilemma with n players

Public good game

- Have assets x
- Devote c to public good, keep the rest
- All contributions are multiplied by some factor and distributed evenly, including to non-contributors

Limited war

- Many animal fights are ritualized eg snakes that wrestle each other without using fangs
- Strategies (Maynard Smith and Price 1973):
  - mouse (never escalate, retreat if opponent does)
  - hawk (always escalate)
  - bully (start by escalating, do opposite of opponent, retreat if opponent escalates twice)
  - retaliator (like tit-for-tat)
  - prober-retaliator (sometimes escalate first)

Paper-scissors-rock

- Male side-blotched lizard can be
  - orange-throated, big, fight for females
  - blue-throated, bond strongly with females
  - yellow-throated, small, mimic females
- Yellow is a "sneaker", steals mates from orange
- Blue doesn't let yellow steal
- Orange beats up blue

Paper-scissors-rock

- Same thing with bacteria
  - produce costly antibiotic
  - just be resistant to antibiotic
  - ditch resistance and grow faster

- Producers beat fast-growers
- Resisters beat producers
- Fast-growers beat resisters