

# Ontology of Evolution: Units and Levels

---

---

---

---

---

---

---

---

## Units and Levels

- What are the units/entities that figure in evolution
  - Population genetics tells the story in terms of alleles in the gene pool
  - Are there any units larger (at a higher level) than genes that need to be considered?
    - Linkage groups?
    - Chromosomes?
    - Genomes?
    - Organisms?
    - Groups?
    - Species?

---

---

---

---

---

---

---

---

## Can Units Higher than Genes be Units of Selection?

- What does selection operate on
  - Genes, chromosomes, gametes, organisms (individuals), kin-groups, groups, species
- Traditional accounts of group selection: group traits can be selected because of the benefit they confer on the group
  - Wynne-Edwards: groups keep the number of offspring low because the whole group will benefit
  - George Williams: groups do not exhibit traits that are the products of natural on the group selection (adaptations)
    - No mechanism for group selection
    - Group selection ineffectual

---

---

---

---

---

---

---

---

## House Mouse and t-allele



- Evolutionary processes on the t-mutant at three levels
  - ↑ – 80% of the sperm of heterozygotes for the t-allele carry it (normal = 50%)
  - ↓ – Males homozygotic for the t-allele are sterile
  - ↓ – Groups with all sterile males go extinct
- Overall fitness of the t-allele is affected by what individual it is in and what kind of group it is in
- Recognized by most as a legitimate case of group selection

---

---

---

---

---

---

---

---

## Waters and Pluralism



- Many equally adequate representations of the evolutionary process
  - Tell the story at any point in the hierarchy of genes, genomes, organisms, etc.
- Strategy for telling the whole story at the genic level
  - Build in all the higher-level factors into the environment of individual genes
  - “What appears as a multiple level selection process (e.g., selection of the t-allele) to those who draw the conceptual divide [between environments] at the traditional level, appears to genic selectionists of Williams’s style as several selection processes being carried out at the same level within different genetic environments” (Waters, 1991, p. 571)

---

---

---

---

---

---

---

---

## Bookkeeping vs. Causality



- One might do all the bookkeeping for evolution in terms of gene frequencies in the gene pool
- The causal processes, however, might lie at multiple levels
  - Lloyd: the genic level causal story is derived from accounts characterizing higher-level causes
    - “despite the pluralists’ repeated claims, we can see *from their own calculations and examples* that theirs are *derivative* models, and thus, that their “genic” level causes are derivative from and dependent on higher level causes.”
- Strategy for identifying causes—screening off

---

---

---

---

---

---

---

---

## The Gene as *the* Unit of Evolution



- Richard Dawkins:
  - Replicators: That which is directly copied
  - Vehicle: That which houses replicators and serves to protect and propagate them—organisms
    - Vehicles are selected
    - But the gene is the fundamental unit of evolution
- David Hull
  - Replicator: “an entity that passes on its structure directly in replication” (Hull 1980, p.318)
  - Interactor: The which interacts with the environment such that replication is differential
  - Natural selection: “a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them” (Hull 1980, p. 318)

---

---

---

---

---

---

---

---

## What Replicates?

- Organisms do not—their traits are broken up in reproduction
- Chromosomes do not—the genes on them can recombine
- Only genes! They are the “indivisible fragments”
  - They are the ultimate beneficiary of evolution
- Dawkins: Analyze evolution solely at the genic level
  - Focus on interactors is mistaken
  - An organism is just a gene’s way of making copies of itself
- But
  - Do genes replicate on their own?
  - Is the focus on replication alone appropriate?

---

---

---

---

---

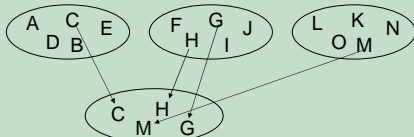
---

---

---

## A Common Strategy for Modeling Group Selection

- Start with several groups of individuals and let them selectively contribute to the pool from which new groups are formed



- Equivalent to blending inheritance
  - The model destroys all the variance on which selection could work

---

---

---

---

---

---

---

---

## Michael Wade and Tribolium

- Offspring groups (propagules) originate within a single group
- Select between groups for those with low fecundity
  - Within groups greater fecundity wins
  - But overall fecundity goes down
- Why?
  - Within a given group, fecundity more likely to rise
  - But there is variability between groups, and those groups with lower fecundity leave more offspring




---

---

---

---

---

---

---

---

## The Problem of Altruism

- Altruism characterized in terms of evolutionary consequences—any trait (esp. a behavioral one) that increases the fitness of others and reduces one's own fitness
- Puzzle—given that altruism apparently exists, how could it arise?
  - Wouldn't altruists tend to lose out to those who advance only their own evolutionary ends (selfish)?
- In any *quid pro quo* arrangement, a cheater (one who takes benefits but doesn't give back) should gain an advantage

---

---

---

---

---

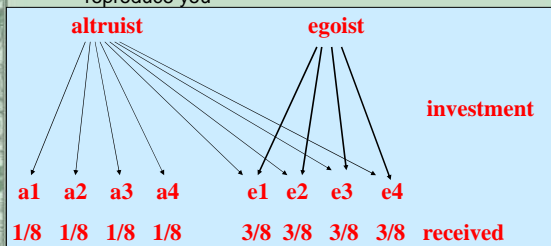
---

---

---

## Altruism

- Altruism *ought* to destroy itself
  - Benefits go to the genes of others, who then out reproduce you



- So, why does altruism persist?

---

---

---

---

---

---

---

---

## Kin Selection and Inclusive Fitness



- Hamilton's Rule: perform altruistic act when
  - $rb > c$
  - relatedness  $\times$  benefits  $>$  costs of altruistic act
- You can gain direct fitness benefits through producing and raising your own offspring
- You can gain indirect fitness benefits through helping to raise offspring of related individuals (kin selection)
- Direct fitness + indirect fitness = total fitness

---

---

---

---

---

---

---

---

## The social insects



- Worker castes do not reproduce—the benefits of their labor go to those who are fertile
- Why does selection not eliminate the sterile classes?
- Distinctive genetics of social insects:
  - Haplody-diploidy
    - Females are diploid—have both a mother and a father
    - Males are haploid—only have a mother
    - Result: sisters are more closely related to each other than to their daughters
    - Raising their sister's children very likely to produce copies of their own genes



---

---

---

---

---

---

---

---

## Simpson's Paradox

- Partitioning a population into two parts can result in a reversal in the direction of relation between two variables
  - The death rate from tuberculosis for African Americans was **lower** in Richmond than in New York.
  - The death rate from tuberculosis for Caucasians was **lower** in Richmond than in New York.
  - The death rate for the total combined population of African Americans and Caucasians from tuberculosis was **higher** in Richmond than in New York.

---

---

---

---

---

---

---

---

## Simpson's Paradox

Population	New York	Richmond
White	4,675,174	80,895
Black	91,709	46,733
Combined	4,766,883	127,628
Deaths	New York	Richmond
White	8,365	131
Black	513	155
Combined	8,878	286
Mortality rate	New York	Richmond
White	.179%	.162%
Black	.560%	.332%
Combined	.186%	.224%

---

---

---

---

---

---

---

---

---

---

## Group Selection for Altruism

Selfish Group	Selfish Individuals	Altruistic Individuals
Before	40	5
After	20	0
Altruistic Group	Selfish Individuals	Altruistic Individuals
Before	5	40
After	8	40
Combined	Selfish Individuals	Altruistic Individuals
Before	45	45
After	28	40

---

---

---

---

---

---

---

---

---

---

## Two Group Selection Questions

- Are there group level traits that are adaptations (products of natural selection)?
  - For Williams, this was important
- Are groups the relevant interactors in the evolutionary scenario?
  - Adaptations may all be at the individual level but groups may be what gets selected
  - Wright, Wade, etc. treat this as the critical question in their defense of group selection

---

---

---

---

---

---

---

---

---

---

## Maynard Smith: Resolving Semantic Confusions

"There has been some semantic confusion about the phrase "group selection," for which I may be partly responsible. For me, the debate about levels of selection was initiated by Wynne-Edwards' book.

He argued that there are group-level adaptations...which inform individuals of the size of the population so that they can adjust their breeding for the good of the population. He was clear that such adaptations could evolve *only* if populations were units of selection.... Perhaps unfortunately, he referred to the process as "group selection." As a consequence, for me and for many others who engaged in this debate, the phrase came to imply that groups were sufficiently isolated from one another reproductively to act as units of evolution, and not merely that selection acted on groups. . . .



---

---

---

---

---

---

---

---

## Maynard Smith: Resolving Semantic Confusions

"The importance of this debate lay in the fact that group-adaptationist thinking was at that time widespread among biologists. It was therefore important to establish that there is no reason to expect groups to evolve traits ensuring their own survival unless they are sufficiently isolated for like to beget like.... When Wilson (1975) introduced his trait-group model, I was for a long time bewildered by his wish to treat it as a case of group selection and doubly so by the fact that his original model...had interesting results only when the members of the group were genetically related, a process I had been calling kin selection for ten years. I think that these semantic difficulties are now largely over. (Maynard-Smith 1987 p. 123)

---

---

---

---

---

---

---

---