Why can't we all just get along?

Altruists
Cheater
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Altruists

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Individual selection eliminates altruism
(unless memory and long term relationships are important)

Groups that are altruistic would be more fit, but selection prevents it

**group selection**: selection that acts to raise the
overall fitness of the group

Individual selection > group selection in general
LEVELS OF SELECTION

and so forth...

overall species

organisms

genesis
“We’re scavengers, we’re ugly and we smell bad. If we didn’t laugh, we’d crack.”
Spotted hyenas, *Crocuta crocuta*  

http://www.msu.edu/user/holekamp/hyena.html
Stripped hyena scavengers
Brown hyena scavengers
**Spotted hyena** predators

"Within minutes, a 220 Kg wildebeast is reduced to bloody stains on the grass by the mass of squabbling hyenas, each eating as fast as possible."

Eating determined by social rank within the group (50-60 adults + 20 juveniles)
Food and sex

Alpha female
  ↓
Alpha female’s kids
  ↓
Other females
  ↓
Senior male
  ↓
Other males
Higher ranking females have more offspring
Fitness advantage to dominance in females
Straightforward, right?
This is an animal called the YENA, which is accustomed to live in the sepulchres of the dead and devour their bodies. Its nature is that at one moment it is masculine and at another moment feminine, and hence it is a dirty brute.

It is true that if an YENA walks around any animal three time, the animal cannot move.

Since they are neither male or female, they are obviously the people concerning whom Solomon said: "A man of double mind is inconstant in all his ways". About whom also the lord said: "Thou canst serve God and Mammon"

- T. H. White (Translation of 12th century beastiary)
Female and male hyenas greet each other by sniffing penises/phalli. This behavior is similar to other hyena species.

Males and females appear identical from a distance, only minor differences exist in external genitalia.

Problem?
9-18% of females die during first child birth

Over 60% of first born offspring die

Later births easier due to changes in birth canal structure, no apparent increase in mortality for these births

Dominant females have ~2.5 times more offspring than subordinates.

Favors bigger and tougher females (enhanced since rank is partially hereditary).

Androgens during development increase body size at birth (for baby duels) and later throughout life.

Side-effect = masculinized genitalia

Individual level selection leads to a species that is poorly-designed and may be considered "less fit" (higher mortality rates during childbirth).

Individual > group
The "t" locus in *Mus musculus*

Many deleterious alleles segregate at this locus, causing sterility or death when homozygous.

Alleles are seen in up to 90% of all sperm of +/t heterozygotes (instead of normal 50%).

The deleterious "t" alleles have **meiotic drive**, distortion of representation during meiosis (destroy the alternative chromosome with wildtype allele).

Gene selection > individual selection:
reduces the fitness of the individuals with 't' alleles.

BUT: population genetics calculations predict a frequency of $p=0.7$, observed is $p=0.4$. 
The "t" locus in *Mus musculus*

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Why are "t" alleles rarer than predicted?

Mice live in small groups, if the "t" allele is too common the population goes extinct - reducing the overall number of "t" alleles.

Group selection (via extinction of groups) against the "t" allele keeps the frequency lower than gene level selection would make it.
2 fold cost of sex

Mother

Offspring 1

Why not?

Much better to just make clones (r=1)

Father

Offspring 2
Easy to evolve: asexual repro in rotifers, lizards, sharks, dandelions, etc.

Selection at levels of both gene and individual would favor asexual reproduction

Why do most organisms use sexual reproduction?
Disadvantages of sex:
- Hard to find mate
- 2-fold cost of sexual reproduction

Advantages of sex:
- Increases variation of offspring
- Speeds rate of evolution by allowing independent beneficial alleles to combine
- Allows removal of deleterious alleles from population

Note: Disadvantages are to individuals
Advantages are to populations
1. Increases variation of offspring (good and bad)
   - Bad for the **best** and best for the **worst**
   - May be important in variable environments

Ex:
**AA** is best genotype
**Aa** is intermediate
**aa** is inferior

Sex causes AA to have Aa kids :(
Sex causes aa to have Aa kids :)

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**Advantage of sex**
2. Speeds the rate of evolution, allowing independent beneficial alleles to combine in individuals.
3. Allows the removal of deleterious alleles  
- Prevents Muller's ratchet

**FIGURE 21.6** Muller's ratchet. The frequency of individuals with different numbers of deleterious mutations (0–10) is shown for an asexual population at three successive times. The least loaded class (0 in top graph, 1 in middle graph) is lost over time, both by genetic drift and by its acquisition of new mutations. In a sexual population, class 0 can be reconstituted, since recombination between genomes in class 1 that bear different mutations can generate progeny with none. (After Maynard Smith 1988.)
These are arguments showing that sex is good for the group, not for individuals.

Support: asexual species are generally very young
(Note: except rotifers with huge pops)

This is essentially the only widely accepted case in which group selection > individual selection.

Adaptations are almost always explainable by gene or individual level selection (parsimony removes need to invoke group selection)
Species

Group

Individual

Gene

Specious clades (insects, etc. ?)

Evolution of sex

Levels at which selection mainly acts