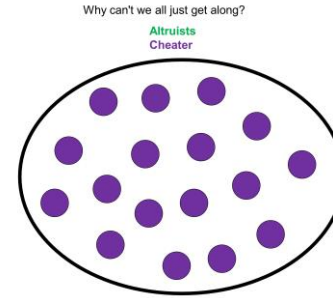
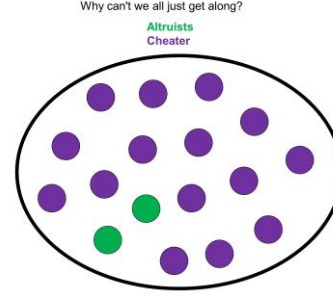
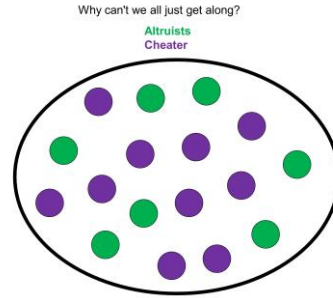
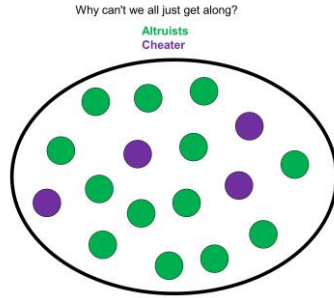
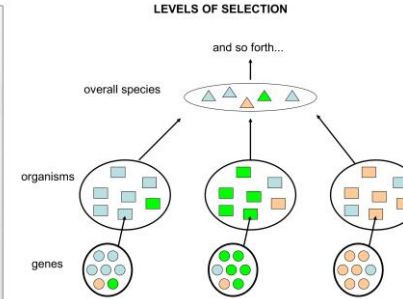


Higher ranking females have more offspring
 Fitness advantage to dominance in females
 Straightforward, right?



Spotted hyenas, *Crocuta crocuta*

<http://www.msu.edu/user/hobekamp/hyena.html>



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



Food and sex

Alpha female
 ↓
 Alpha female's kids
 ↓
 Other females
 ↓
 Senior male
 ↓
 Other males



Stripped hyena
 Brown hyena
 Spotted hyena

scavengers
 scavengers
 predators

"Within minutes, a 220 Kg wildebeest 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)

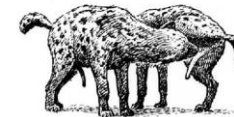


This is an animal called the YEEN, which is accustomed to live in the sepulchres of the dead and devour their bodies. Its nature is that at one moment it is masculine and at another moment feminine, and hence it is a dirty brute.

It is true that if an YEEN 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 bestiary)

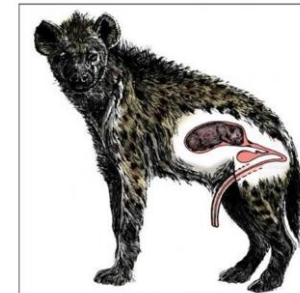


Female and male hyenas greet each other by sniffing penises/phalli. This behavior is similar to other hyena species.

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



Problem?



Frank, L. 1997. Trends in Eco. Evol. 12:58-62

The "t" locus in *Mus musculus*



BUT: population genetics calculations predict a frequency of $p=0.7$, observed is $p=0.4$.

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.



The "t" locus in *Mus musculus*



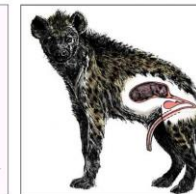
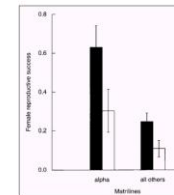
Many deleterious alleles segregate at this locus, causing sterility or death when homozygous

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 $p=0.4$.



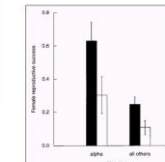
Individual level selection leads to a species that is poorly-designed and may be considered "less fit" (higher mortality rates during childbirth).

Individual > group

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

Frank, L. 1997. Trends in Eco. Evol. 12:58-62