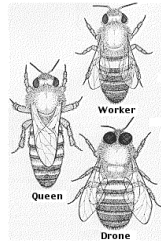


Lect. 17: Social behavior

- Altruism & cooperation
- Inclusive fitness, kin selection
 - Hamilton's rule
 - Relatedness
- Eusociality and Hymenoptera
 - Sex ratio bias
- Eusociality in diploids



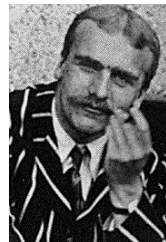
- Exam II: 1 Nov. Study guide Tuesday, 24 Oct
- Seminar, 4:10, Today, 306 Abelson
 - Bethany Marshall: "Forensic entomology"

Altruism: Cooperative male display, alarm calling



A solution?

JBS: "If I had a one in 10 chance of drowning but saved the life of my child, I would save 5 copies of genes for this behaviour...."



JBS Haldane, 1953

Kin selection

Favors traits that increase indirect fitness



Hamilton's rule

$$rB - C > 0$$

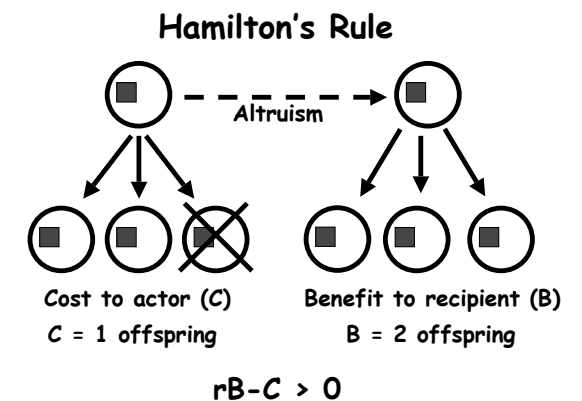
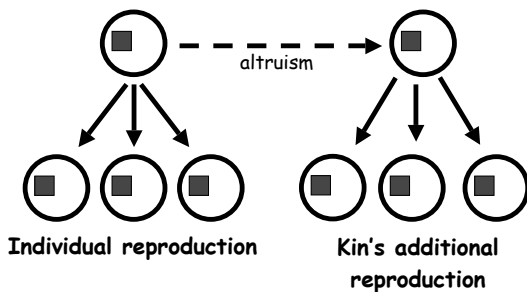


WD Hamilton 1964

Natural Selection favors altruistic acts when indirect fitness benefits to the receiver, reduced by the coefficient of relatedness, exceeds costs to the altruist

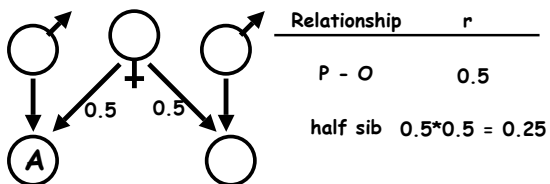
Who is the altruist?

- *r*, coefficient of relatedness
 - Probability that homologous alleles in two individuals are IBD

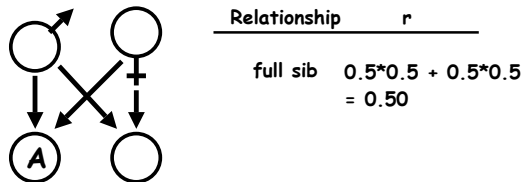


r = coefficient of relatedness

= probability that an allele found in one individual will be found also in another due to inheritance from common ancestor (IBD).



r = coefficient of relatedness



r = coefficient of relatedness

Relationship	r
Parent - offspring	0.5
Full siblings	0.5
Half siblings	0.25
Cousins	0.125



Belding's Ground Squirrel

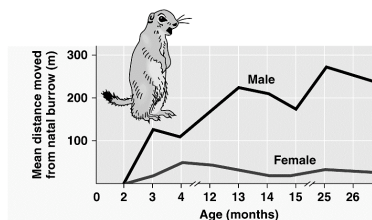
BGS: "I will alarm call and risk my life for 2 siblings, 4 half-sibs, or 8 cousins"



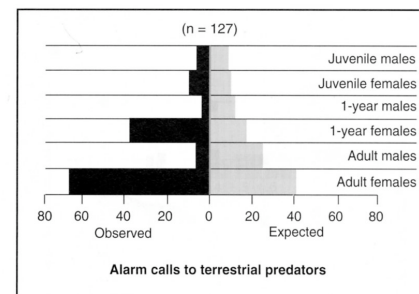
Who alarm calls?



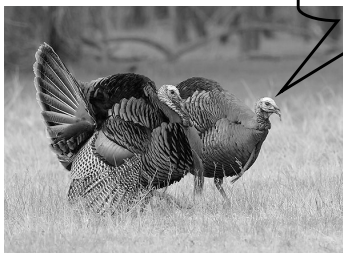
- BGS dispersal: Male > female



Females call for terrestrial predators



rB - C > 0?



rB - C > 0?



Male	Avg. RS
Solo	0.9 young
Dom.	7.0 young
Subord.	0.0 young

Cost = reduced # of offspring to subord.
= 0.9 - 0.0 = 0.9 young



Male	Avg. RS
Solo	0.9 young
Dom.	7.0 young
Subord.	0.0 young

Benefit = # extra offspring to dominant
= 7.0 - 0.9 = 6.1 young

Solve for relatedness?



Ownbyphotography.com

$$B = 6.1$$

$$C = 0.9$$

$$rB - C > 0$$

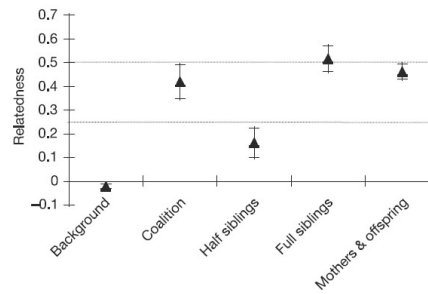
Altruism pays:

$$r > C/B$$

$$> 0.9/6.1$$

$$> 0.15$$

Cooperative mating: are male coalitions related?



Krakauer (2005) Nature 434:69-72

Inclusive fitness?



$$B = 6.1 \text{ young}$$

$$C = 0.9 \text{ young}$$

$$r = 0.42$$

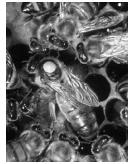
Net gain:

$$rB - C > 0$$

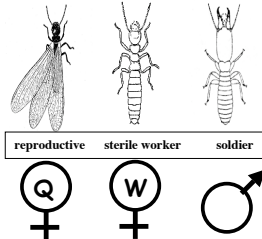
$$1.7 > 0$$

Krakauer (2005) Nature 434:69-72

Eusociality: reproductive altruism



- Specialized reproductive caste (Queen)
- Non-reproductive castes (e.g. workers, drones, soldiers)
- Common in the Hymenoptera: bees, wasps, ants

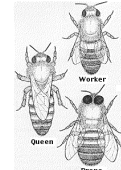
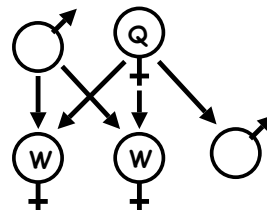


How does eusociality evolve?

- In Hymenoptera?
 - Haplodiploid sex determination:
 - fertilized eggs (diploid) -> females
 - unfertilized eggs (haploid) -> males.

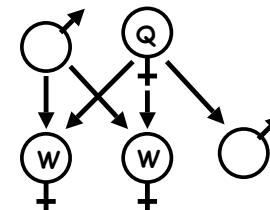


WD Hamilton 1972



Eusociality & hymenoptera

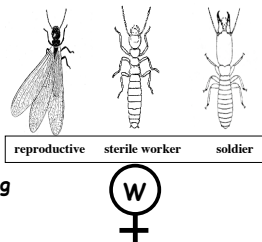
Sisters share 100% the genes they inherit from their father, which is 50% of their genome



Relationship	r
fem - mom	0.5
sis - bro	$0.5 \times 0.5 = 0.25$
sis - sis	$0.5 \times 0.5 + 0.5 \times 1 = 0.75$

Kin selection & Hymenoptera?

- Favors altruistic female worker caste in haplodiploids
 - Helping to raise their sisters ($r = 0.75$)
- Favors biased sex ratio

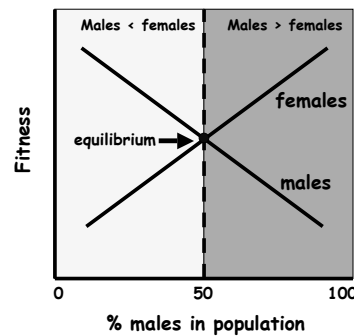


Workers raise offspring

Fisher's sex ratio theory



- Frequency-dependent fitness
- Predicts a 50:50 sex ratio



Kin selection & Hymenoptera?

- Favors biased sex ratio

Worker-Worker $r = 0.75$
 Worker-Brother $r = 0.25$
 Predicted sex ratio 75:25

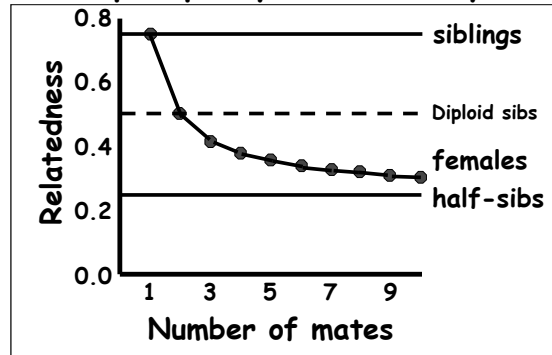


Haplodiploidy & Eusociality?

- Multiple mating by queen erodes relatedness among sisters

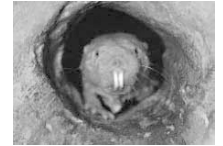
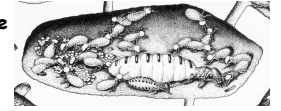


Haplodiploidy & Eusociality?



How does eusociality evolve?

- Haplodiploidy?
 - Not all haplodiploids are eusocial
 - Eusocial Diploids
 - Termites
 - A shrimp
 - Naked mole rats



Genetic & Ecological factors favor eusociality

Kin selection & Social behavior

- Mechanisms to explain altruism
- Hamilton's rule: $rB - C > 0$
- Benefits of altruistic act discounted by r
- Relatedness in haplodiploid systems helps explain eusociality and biased sex ratios
- Reproductive altruism favored by
 - Genetic factors: Haplodiploidy, inbreeding
 - Ecological factors