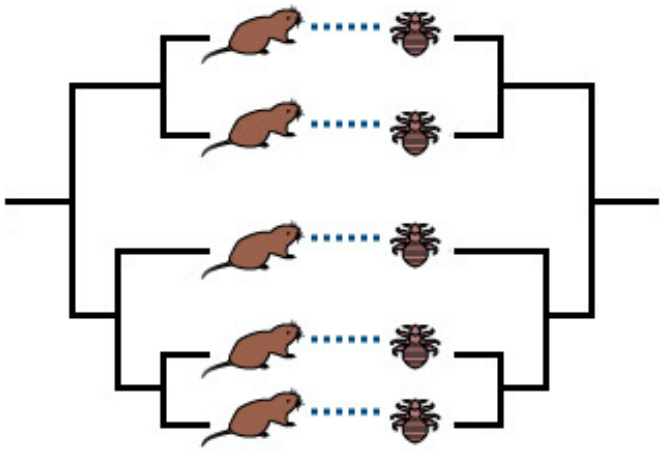
Roadmap

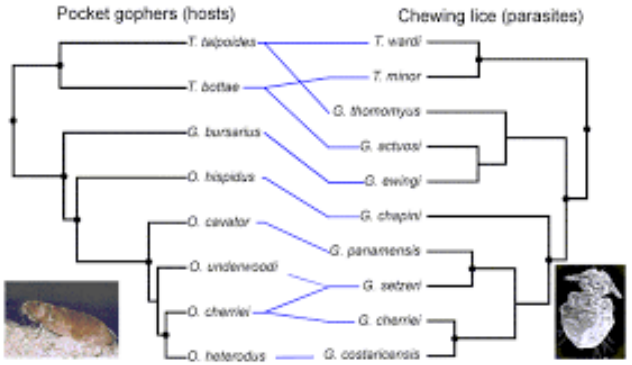
- Co-speciation
- Indirect fitness:
  - Kin selection
  - Group selection
  - Species selection?
- Some slides in this lecture don't work in black and white: sorry!

Cospeciation

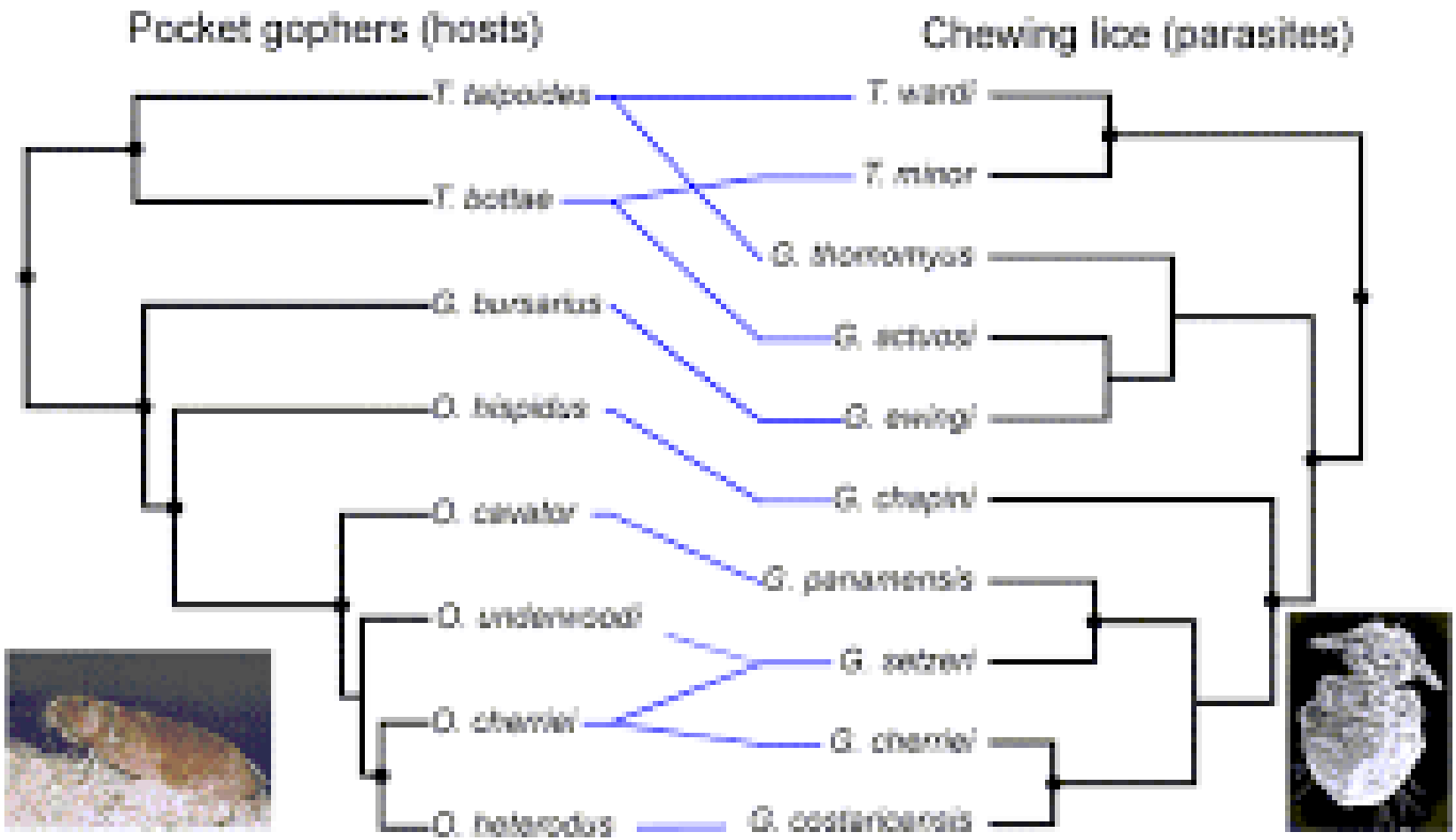
- Host species and parasite species often speciate together
- Species trees of the two groups will look very similar
- Example: gophers and gopher lice
- Reproductive isolation of hosts may isolate parasites
- Adaptation of hosts may spur adaptation of parasites (or vice versa)



Idealized schematic



Real data



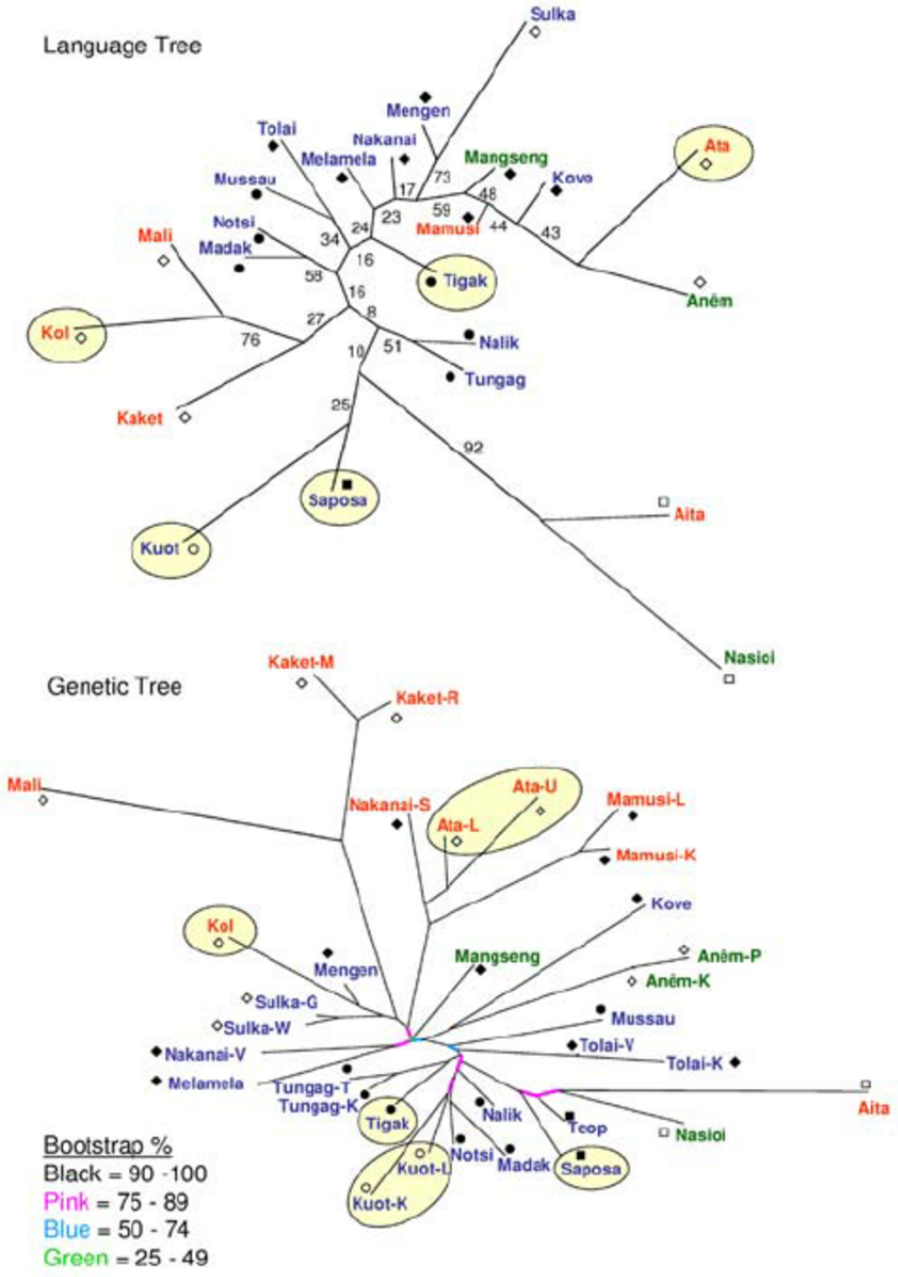
I'm not actually sure these trees agree more than chance....

Linguistic trees?

- A relationship tree among languages might mirror relationships among populations

- Problems:
  - Population "tree" not necessarily a tree
  - Language "tree" not necessarily a tree either
  - Establishing homology in words is difficult and subjective: may be biased by preconceptions of the tree

- Next slide from Hunley et al. 2008, "Genetic and linguistic coevolution in Northern Island Melanesia"



Blue=coastal
Green=intermediate
Red=inland

Interactions among individuals

	Actor benefits	Actor harmed
Recipient benefits	Cooperative	Altruistic
Recipient harmed	Selfish	Spiteful

- Why doesn't natural selection eliminate behavior harmful to the individual?

- Two hypotheses:
  - Kin selection: altruistic behavior benefits kin
  - Group selection: altruistic behavior benefits group

- These are confounded in nature because most groups are kin groups

Hamilton formula for kin selection

- Altruism is selected when $Br - C > 0$
  - B is benefit to the recipient
  - C is cost to the altruist
  - r is coefficient of relatedness between them

- Complications:
  - Multiple individuals helped? Sum the Br and C terms
  - Hidden benefits to the altruist (reciprocity)
  - B and C are hard to measure
  - A gene copy next generation is worth more than a gene copy in this generation

Expanding the concept of fitness

- Total fitness = direct fitness + indirect fitness
  - Direct fitness – you transmit your alleles to the next generation
  - Indirect fitness – someone else transmits them
- Indirect fitness is as "real" as direct fitness
  - Eusocial workers have zero direct fitness (unless they cheat)
  - Terminally differentiated cells have zero direct fitness

Relationship coefficient

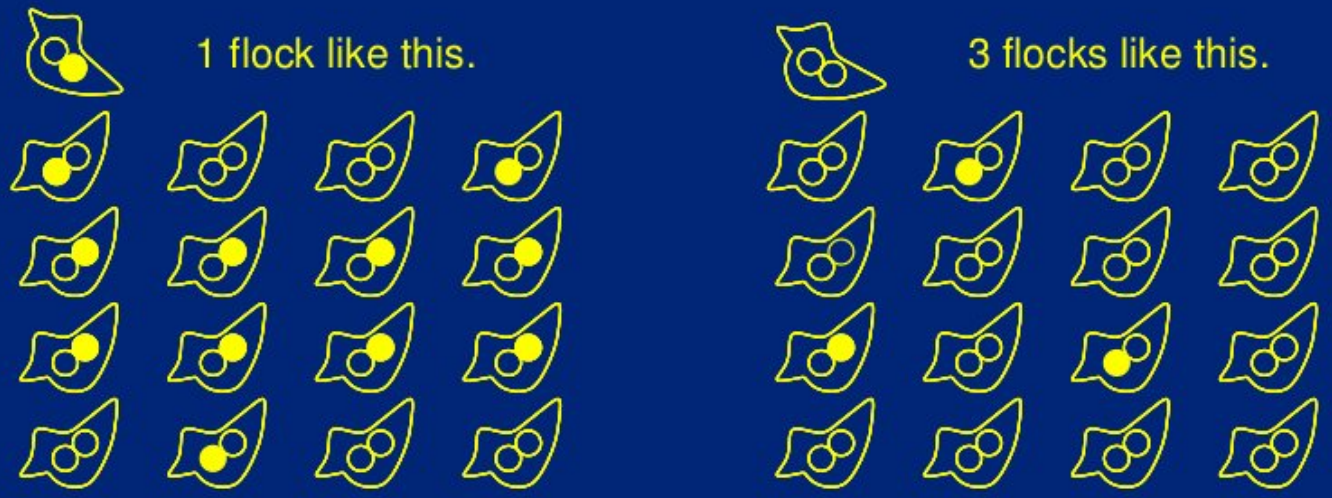
A reminder (for diploid organisms):

Relationship	r
Parent/child, full siblings	1/2
Grantparent/grandchild	1/4
Aunt or uncle/niece or nephew	1/4
First cousins	1/8

Kin selection –– the case of an alarm call

Before

p = 18/136 = 0.132353



gives alarm call, is eaten
but flock is saved

doesn't give alarm call, saves self
half of others eaten

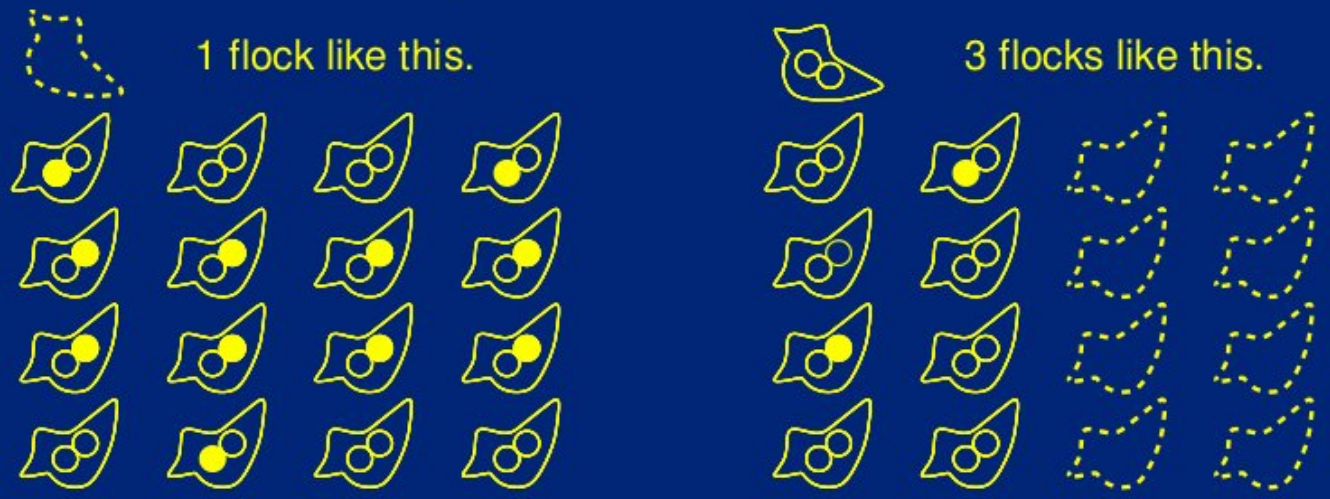
(Note that in the example the other flock members are relatives of the bird that gives the alarm call, so they tend to have the alleles that it has)

Note –– the numbers shown here are approximately correct at these gene frequencies. Infrequent occurrences such as homozygotes for the alarm call allele are omitted.

Kin selection –– the case of an alarm call

After

p = 14/86 = 0.16279



gives alarm call, is eaten
but flock is saved

doesn't give alarm call, saves self
half of others eaten

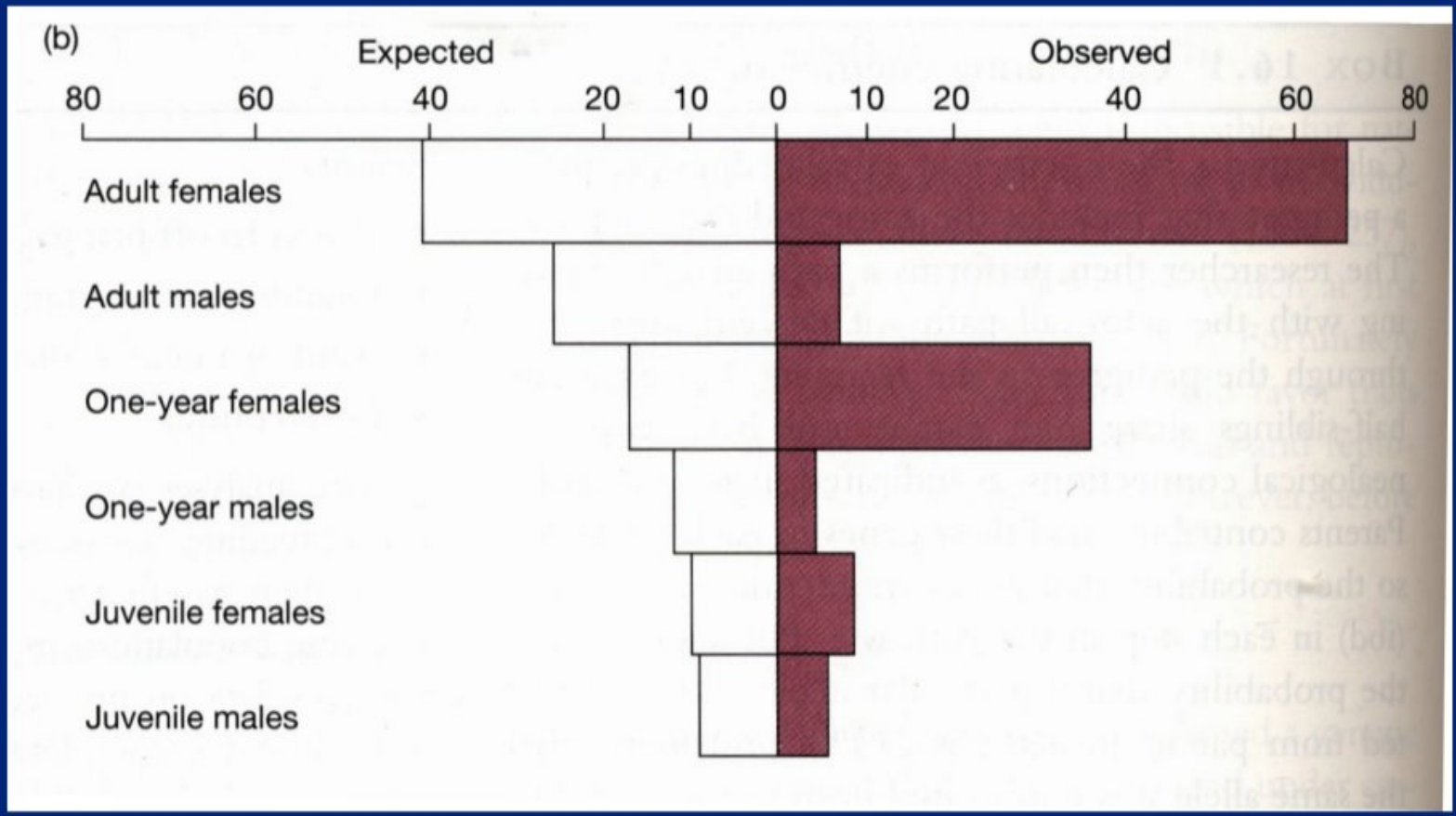
cost = 1

benefit = 8

Alarm call allele will increase with any coefficient of relationship > 1/8

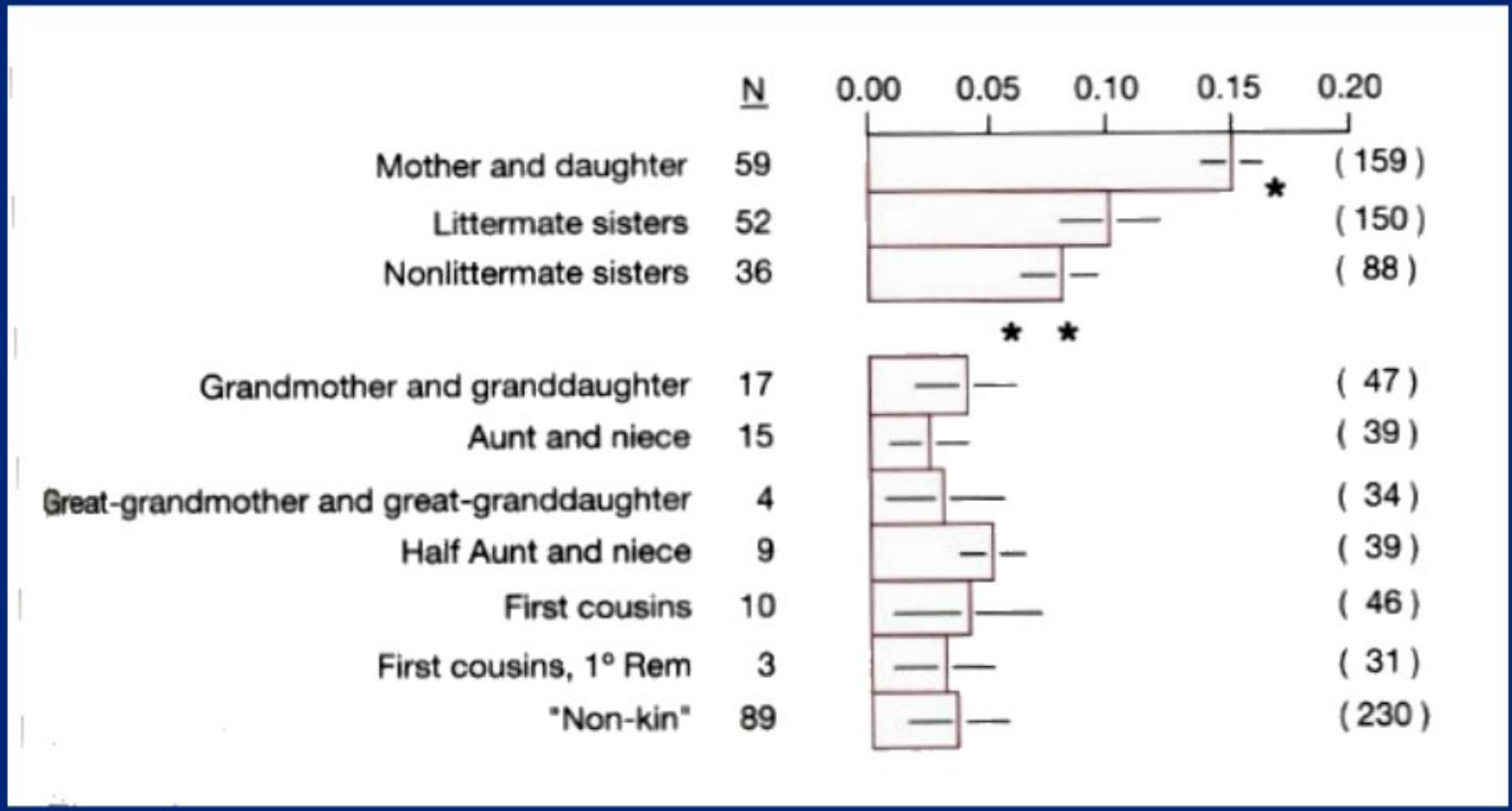
Belding's ground squirrels

Alarm calling "duty"



Belding's ground squirrels

Cooperation in chasing away trespassers



Does kin selection imply kin recognition?

- Not necessarily:
  - Being generally helpful can pay off if your neighbors are kin
  - No kin recognition in alarm call example
  - See bacterial example later in lecture
- Can promote kin selection:
  - Littermate ground squirrel sisters more helpful than non-littermates
    - More likely to be full siblings rather than half?
    - More able to recognize each other?
- Vervet monkeys cooperate with maternal kin, not (unknown) paternal kin

Group selection

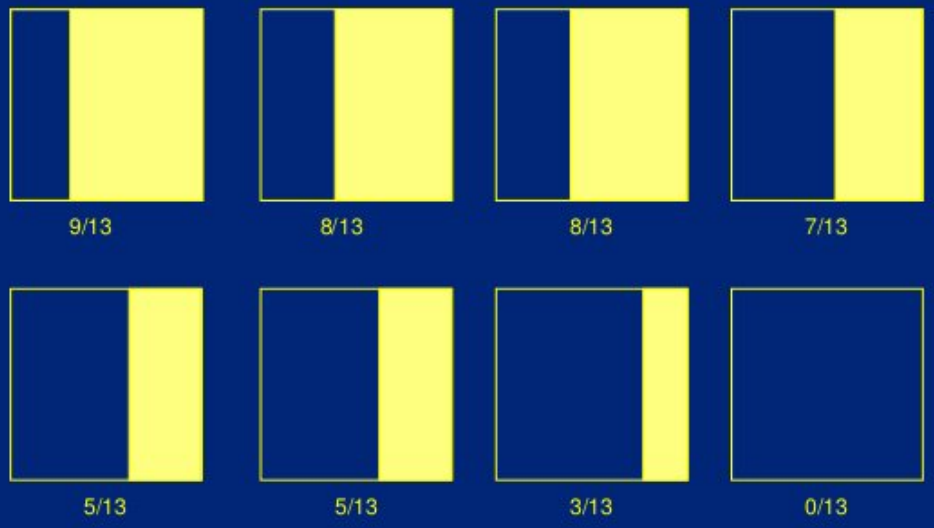
- Can selection favor a trait that is good for the group but bad for the individual?
- Clearly yes if group is related (kin selection)
- What if group is random (group selection)?
  - Possible to create scenarios where this works
  - Not clear if they are common or important in nature
- Strict-sense group selection requires:
  - Groups that differ in frequency of a key allele ...
  - ...that didn't get that way by being kin (otherwise it's kin selection)

Group selection

Whole local populations survive or go extinct, in a way that depends on their frequency of the altruistic allele

Before $p = 45/104 = 0.4327$

local populations, which differ in gene frequency

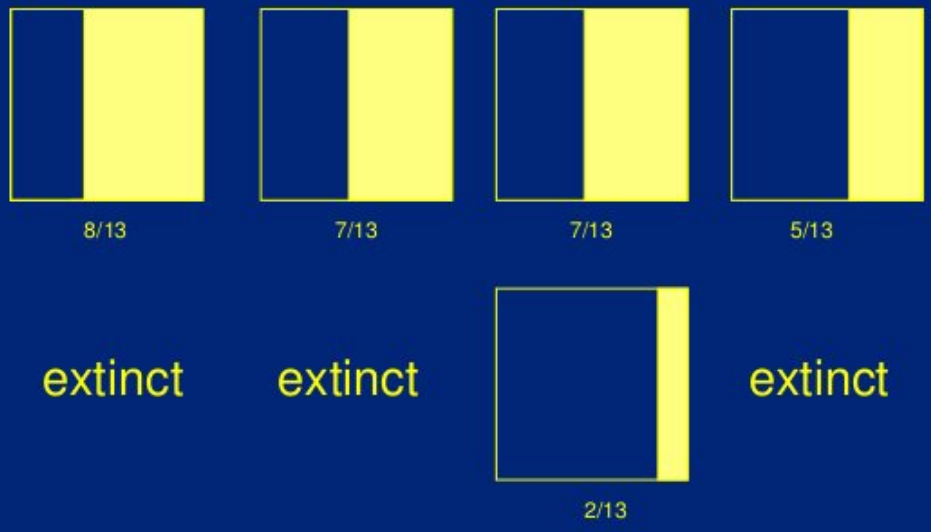


Group selection

Whole local populations survive or go extinct, in a way that depends on their frequency of the altruistic allele

After $p = 29/65 = 0.446$

Within each population, individual selection against altruists reduces the frequency of the allele



Kin selection vs. group selection–an example

- Luria-Delbruck experiment
- Does phage resistance exist before phage are added, or is it induced by the presence of phage?

Kin selection vs. group selection–an example

- Divide bacteria into ten tubes
- Grow them up to high density
- Test a drop from each tube for percentage of resistant bacteria
- Throw away all tested bacteria
- Keep highest-scoring tube, discard others
- Split high-scoring tube into ten more tubes and repeat

Kin selection vs. group selection–an example

- Eventually tubes with very high rates of resistance were produced
- None of the bacteria in the tube had been exposed to phage
- This shows that phage resistance does not require the presence of phage

Kin selection vs. group selection–an example

- This experiment shows kin selection, as bacteria within the tube are more related than bacteria in different tubes

- Group selection variant:
  - Instead of dividing winning tube into ten new tubes, pour it into a flask
  - Just before testing, stir flask and divide into ten tubes
  - Only random sampling gives different frequencies of resistance in different tubes–there is no kin relationship

- To my knowledge the group selection experiment has not been done

- I suspect it would fail as the group advantage is too small to overcome the cost of phage resistance

Eusocial *Hymenoptera*

- If the queen mated only once:
  - r between:
    - worker and full-sister reproductive female $= 3/4$
    - worker and reproductive male $= 1/4$
  - Workers therefore prefer the queen to produce daughters
  - Queen prefers 50/50 ratio (for the usual reason)
  - In honeybees, more female reproductives than males–do the workers get a say in this?


Example: naked mole rates

Naked mole rats

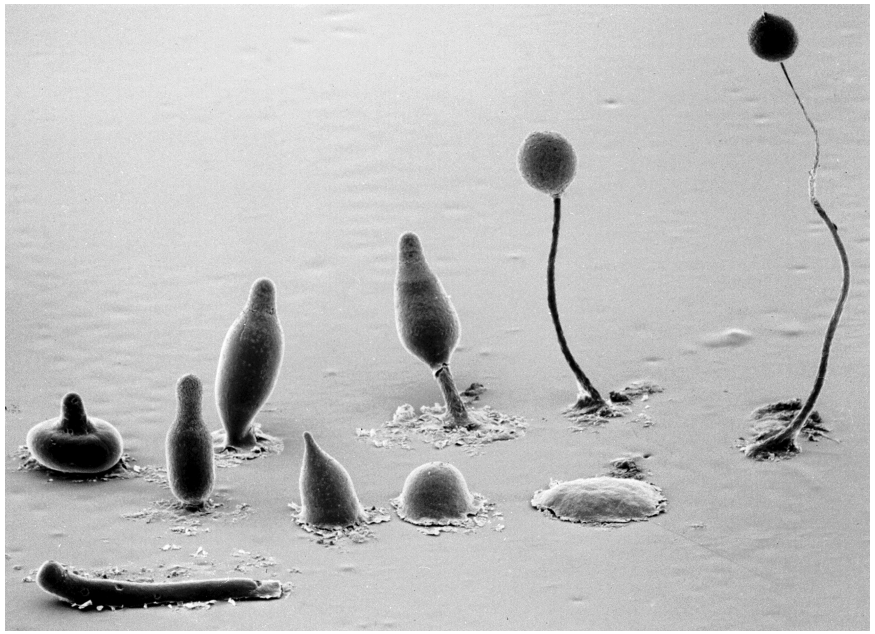
- Only known eusocial mammal
- Diploid!
- 1 reproductive female and 2-3 reproductive males per colony of 80-90
- Queen has up to 900 offspring (mammal record!)
- High inbreeding, measured as $r = 0.81$

Vampire bats

- Vampire bats have difficulty finding food every night
- Successful bats often feed unsuccessful ones
- Alternative hypotheses:
  - Kin selection for altruism
  - Reciprocity
- How could we distinguish these?

Group selection without kin selection

- *Dictyostelium discoides* may be an example
- Free-living amoeba band together to form fruiting bodies
- There is no apparent preference to band with kin



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The "greenbeard" effect

- Richard Dawkins coined the name "greenbeard" for a gene that can:
  - Produce a distinctive phenotype
  - Allow its possessor to recognize that phenotype
  - Cause its possessor to behave altruistically toward those who share the phenotype

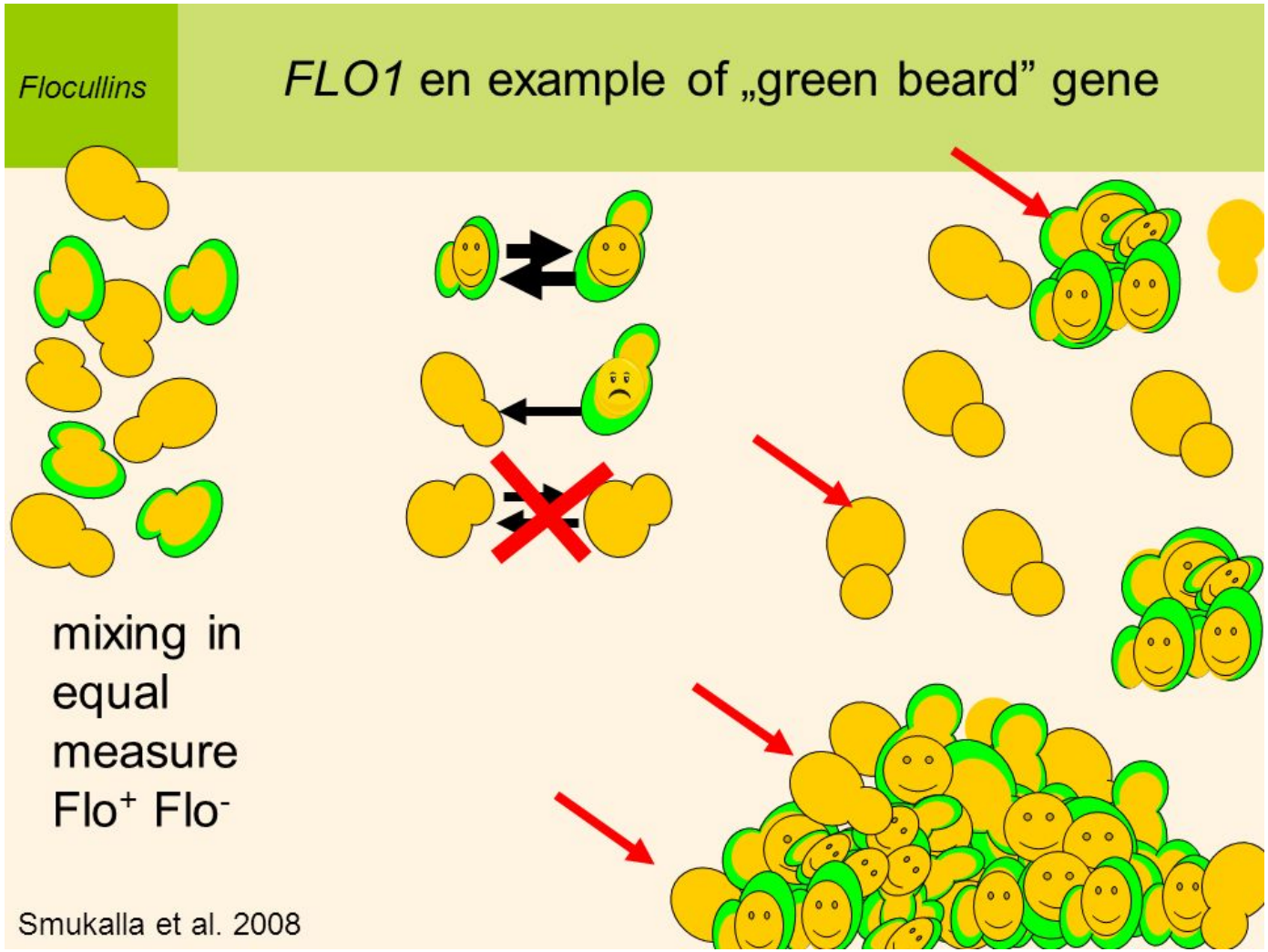
- Such a gene could spread in a population

csA greenbeard gene in *Dictyostelium*

- $csA+$ individuals adhere better
- They tend to altruistically end up in the stem, not the fruiting body
- However, they recognize each other and drag each other into the slug!
- A slug from a 50/50 mix of $csA+$ and $csA-$ will produce spores that are 82% $csA+$
- The $csA-$ cells preferentially end up in the fruiting body, but only if they can get into the slug in the first place

Queller, DC, Ponte E, Bozzaro S, Strassmann SE. Science 299(5603):105-106.

Another greenbeard gene, in yeast



Species selection

- Can a species be selected because of a trait which makes it produce many new species, even if that trait is harmful for individuals?
- A species advantage might be too slow to overcome an individual disadvantage
- One possible example: generalist species versus specialist species

Generalists versus specialists

- Specialists:
  - have more niches available
  - may speciate more rapidly
- Generalists:
  - may have longer "species lifespans"
  - may survive mass extinctions better
- Long term, most life on Earth may be descended from generalists
  - Does that affect the frequency of the generalist "phenotype"?
  - Species may switch from generalist to specialist over time

Friday

- Competition among levels of organization:
  - *Wolbachia* vs. arthropods
  - Mitochondria vs. eukaryotes
  - Cancer cells vs. organism