Structure of lecture notes

- Part 1 of this lecture is available only in yellow-on-blue
- (Slides made by my colleague Peter Beerli)
- Here is a key formula from it for reference:
  - Altruism spreads when $C < B * r$
  - C is cost to donor
  - B is benefit to recipient
  - r is coefficient of relatedness (e.g. parent/child=1/2)

One-minute responses

- Q: How does migration change when there are multiple alleles (3+) with uneven distribution?
- A: It doesn't change much: you can still calculate new allele frequencies as a weighted average of donor and receipient populations
- Q: How is the breakpoint different for multiple alleles?
- A: It's still around $2N_em$

Interactions among individuals

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

- Cooperative (mutualistic) behavior benefits both individuals
- Selfish behavior benefits only the actor (predation)
- Spiteful behavior harms both parties, and is rare in nature
- Altruistic behavior hurts the actor but helps the recipient
  - Why doesn't natural selection eliminate it?

Inclusive fitness

William Hamilton developed a model showing that a gene that favors altruistic behavior could spread in a population or species.

$$Br - C > 0$$

B is the benefit to the recipient

C is the cost to the donor

r is the coefficient of relatedness

Altruism will spread if the benefits to the recipients are high, the cost is low, and the individuals are related.

Inclusive fitness

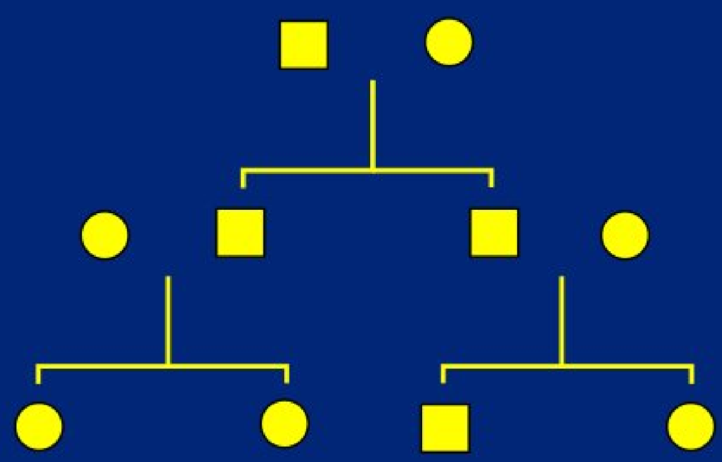
Inclusive fitness = direct fitness + indirect fitness

- Direct fitness is due to personal reproduction.
- Indirect fitness is due to reproduction by relatives.

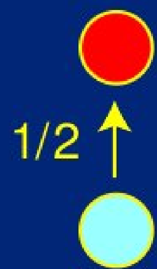
Natural selection that favors the spread of alleles that increase indirect fitness is called **KIN SELECTION**.

Relatedness r

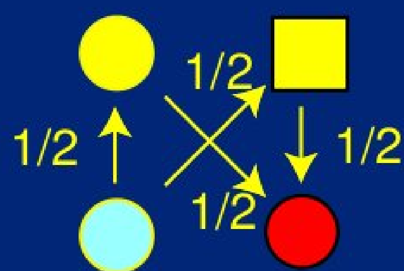
To calculate relatedness we need a pedigree and on this we calculate probabilities of sharing genes between Actor and Recipient. This is done by following all possible path of genes from the actor to the recipient taking into account the chance that a parent contributes genes with probability of 1/2 to its offspring.



Relatedness r

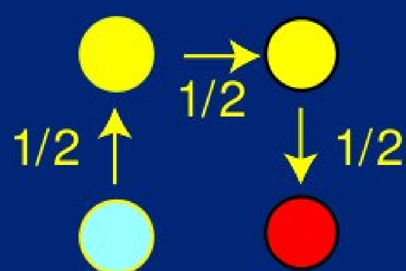


Offspring $r = \frac{1}{2}$



Full siblings

(through mother) $\frac{1}{2} \times \frac{1}{2}$
(through father) $\frac{1}{2} \times \frac{1}{2}$
$r = \frac{1}{2} \times \frac{1}{2} + \frac{1}{2} \times \frac{1}{2} = \frac{1}{2}$



Cousins

(actor→parent[here the mother])
(parent→aunt or uncle [here the aunt])
(aunt/uncle → cousin)
$r = \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1}{8}$

Relatedness r

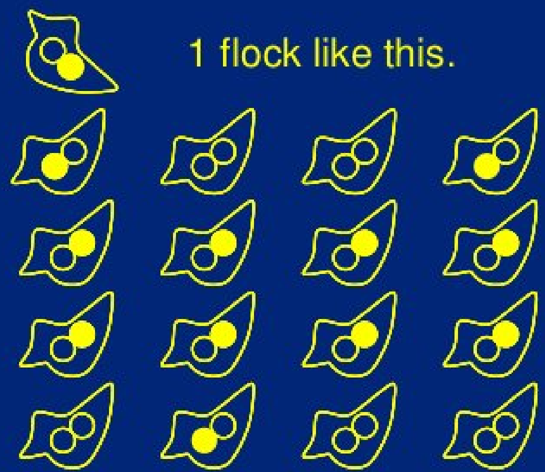
Relationship	r
Parent to offspring	$\frac{1}{2}$
Grandparent to grandchild	$\frac{1}{4}$
Aunt or uncle to niece or nephew	$\frac{1}{4}$
First cousins	$\frac{1}{8}$

Kin selection –– the case of an alarm call

Before

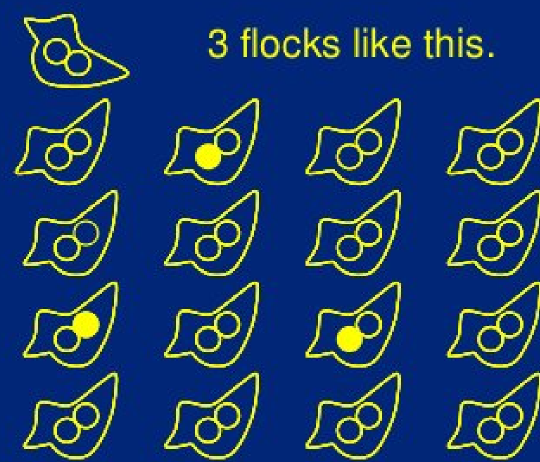
p = 18/136 = 0.132353

1 flock like this.



gives alarm call, is eaten
but flock is saved

3 flocks like this.



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

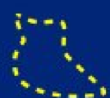
(Note that in the example the other flock members are relatives of the bird that gives the alarm call, so they tend to have the alleles that it has)

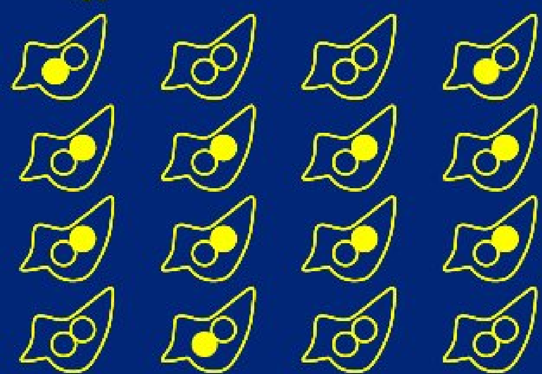
Note –– the numbers shown here are approximately correct at these gene frequencies. Infrequent occurrences such as homozygotes for the alarm call allele are omitted.

Kin selection –– the case of an alarm call

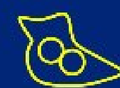
After

p = 14/86 = 0.16279


1 flock like this.



gives alarm call, is eaten
but flock is saved


3 flocks like this.

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

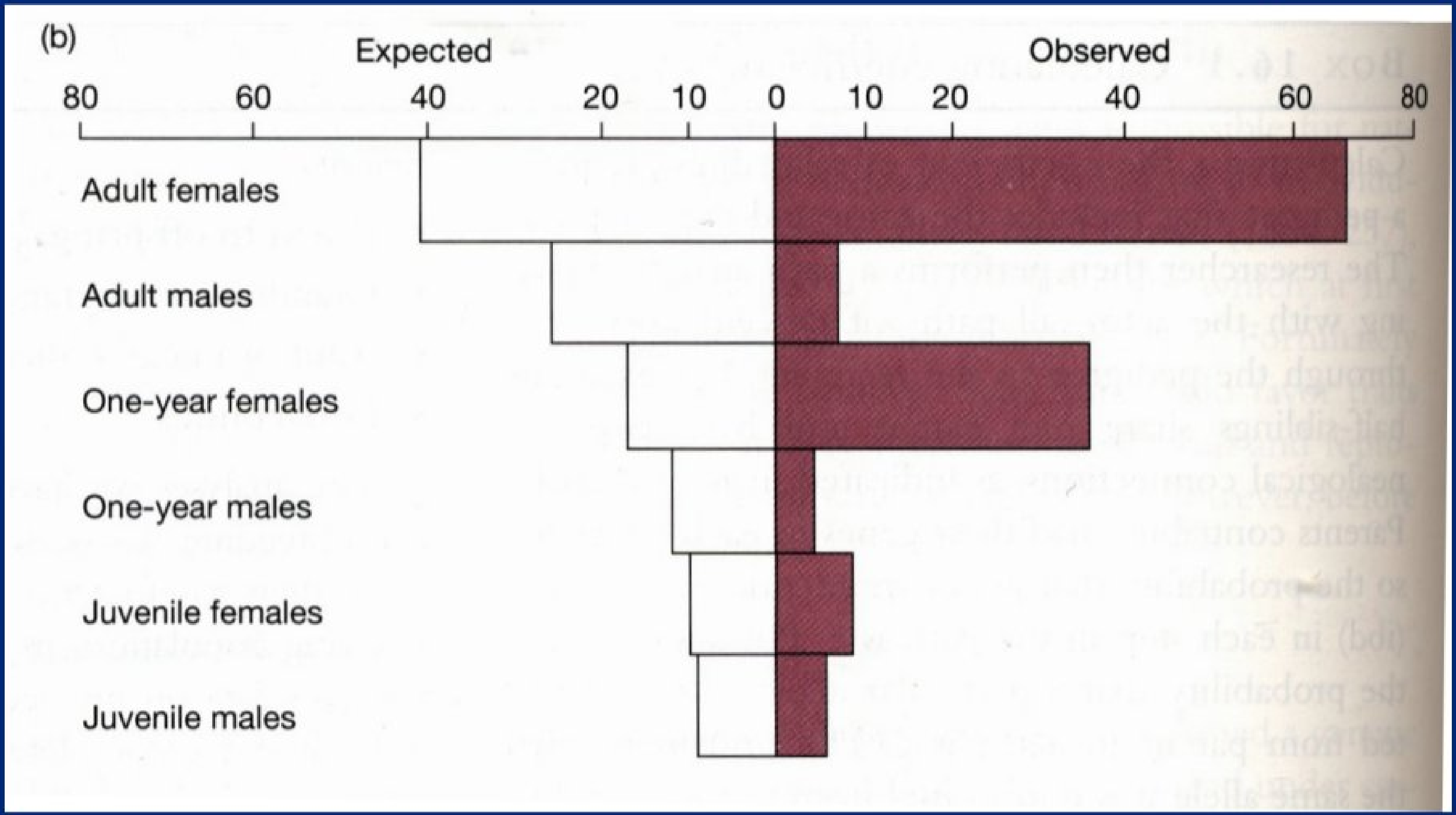
cost = 1

benefit = 8

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

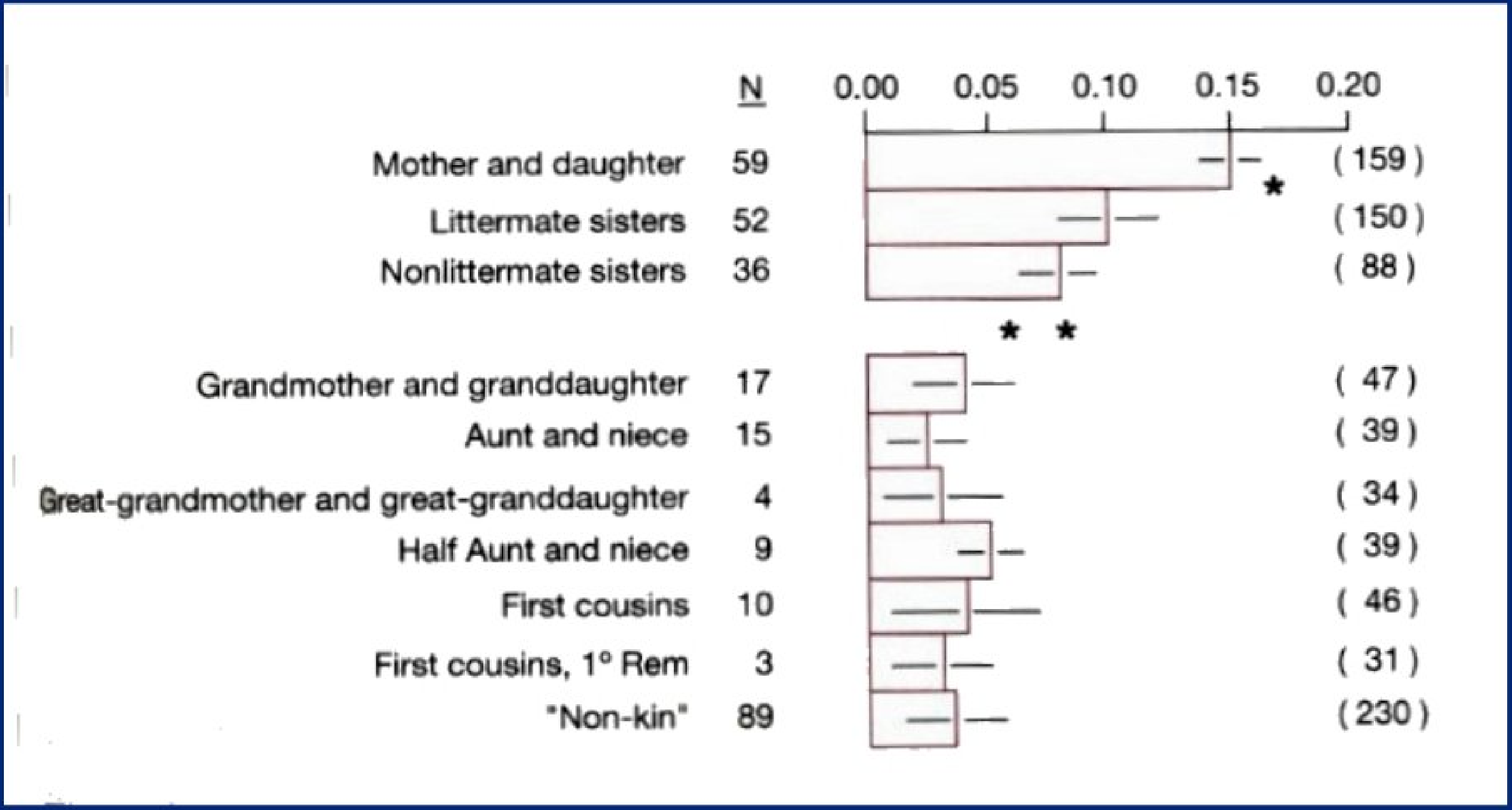
Belding's ground squirrels

Alarm calling "duty"



Belding's ground squirrels

Cooperation in chasing away trespassers

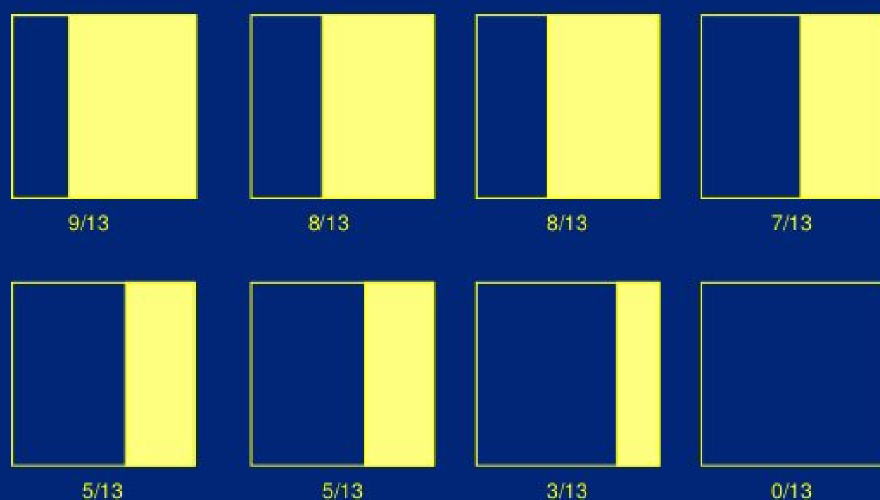


Group selection

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

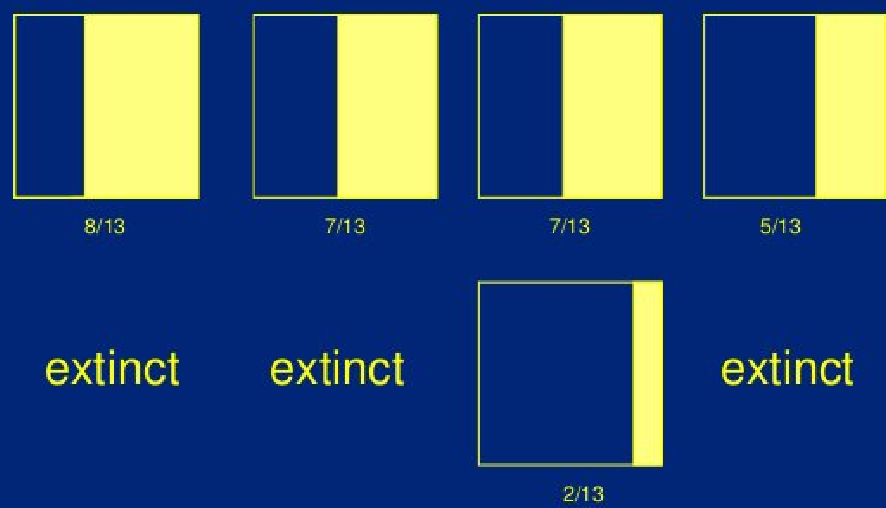


Group selection

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

After $\quad p = 29/65 = 0.446$

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

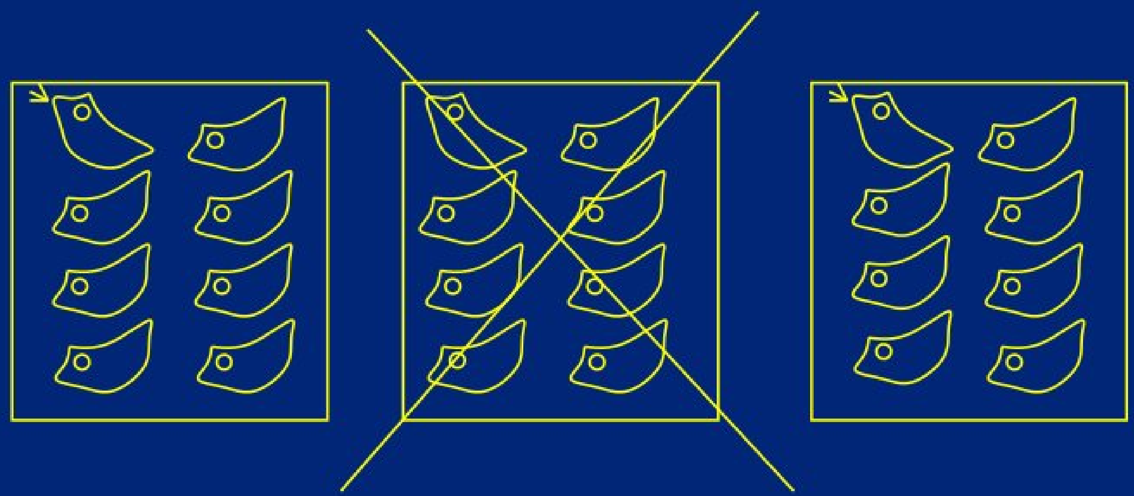


Group selection

Actually, group selection is a kind of kin selection!

Because ...

1. Groups must vary in gene frequency to have group selection work
   (usually, the gene frequencies differ because, the members of a group are related to each other)
2. Having an altruistic behavior reduces the fitness of the individual
   (just as it does in the case of kin selection).
3. Being in a group with altruists means you are related to them and you benefit from their presence
   (by having a lower chance of group extinction).



Eusociality

Eusociality is characterized by

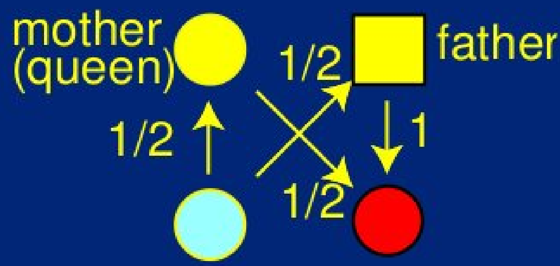
1. Overlap in generations between parents and offspring
2. Cooperative brood-care
3. Specialized castes of non-reproductive individuals

Examples:Hymenoptera

Examples: Hymenoptera

Hymenoptera have an unusual form of sex determination called a **haplodiploid system**: females are diploid and males are haploid, they develop from unfertilized eggs.

As a result of this system female ants, bees, and wasps are more closely related to their siblings than to their own offspring.



Relatedness between sisters is $(1 \times \frac{1}{2}) + (\frac{1}{2} \times \frac{1}{2}) = \frac{3}{4}$

Example: Snapping Shrimp

Duffy, J.E. (1996) Eusociality in a coral-reef shrimp. Nature 381: 512-414.

Example: naked mole rates

Naked mole rats

- A mole rate "hive" contains around 80-90 individuals, the queen mates with about 2-3 reproductive males.
- Queen can have up to 900 offspring (record for a mammal).
- It is believed that Eusociality is maintained in mole rats because of their high inbreeding, often queens mate with siblings or male offpsring. $r=0.81$, one of the highest values found.

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

Practice problem–altruism

- Suppose, hypothetically, that the cost of nursing in a primate is 10%
- This would mainly represent inability to conceive while nursing
- What benefit to the infant would be needed to evolve nursing of one's own offspring?
- What benefit would be needed for nursing one's nieces and nephews (full sibling's children)?
- Is this behavior necessarily altruistic?

Practice problem–altruism

- Suppose, hypothetically, that the cost of nursing in a primate is 10%
- This would mainly represent inability to conceive while nursing
- What benefit to the infant would be needed to evolve nursing of one's own offspring? $C = B * r$ is tipping point. C=0.1, r=0.5, so altruism is advantageous if benefit $>$ 0.2
- What benefit would be needed for nursing one's nieces and nephews (full sibling's children)? Nephews are related at r=0.25 (factor of 1/2 for you to sibling, factor of 1/2 for sibling to nephew). Benefit $>$ 0.4
- Is this behavior necessarily altruistic?

Practice problem–altruism

Alternative explanations are possible:

- Reciprocity–you feed my baby, I'll feed yours
- Hidden advantage–mother's survival increased by delaying next pregnancy
- Lack of discrimination–too hard to tell kin from non-kin (not likely in this case)

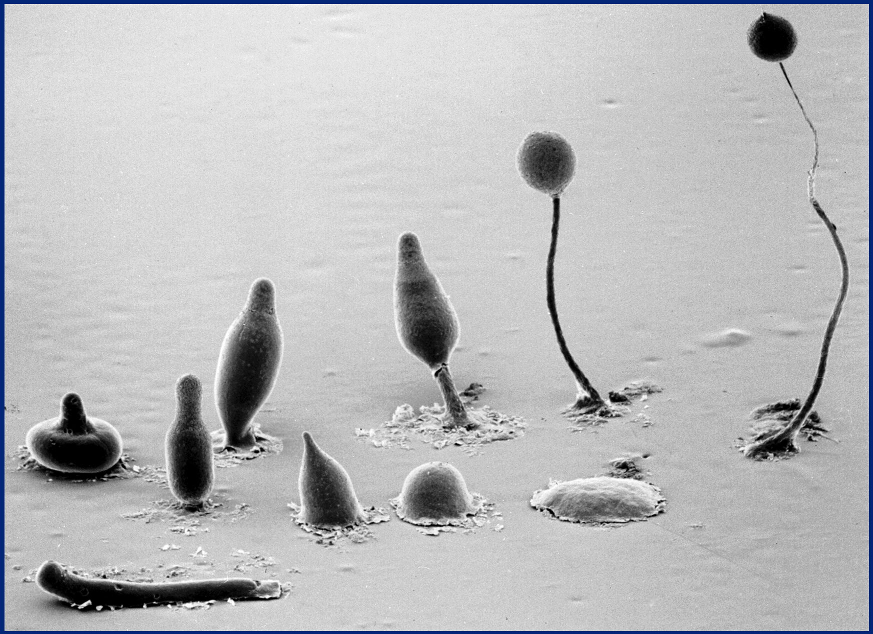
Testing these alternatives is a challenge, especially in social animals

Vampire bats

- Vampire bats have difficulty finding food every night
- Successful bats often feed unsuccessful ones
- Alternative hypotheses:
  - Kin selection for altruism
  - Reciprocity
- A partial test to differentiate:
  - Altruism should be directed mainly at kin
  - Reciprocity can be with known non-kin (but perhaps not strangers)
  - If a bat knows its kin best, the two are confounded
  - We would also want to know if bats are capable of recognizing kin in the first place
  - Both could be true

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



The "greenbeard" effect

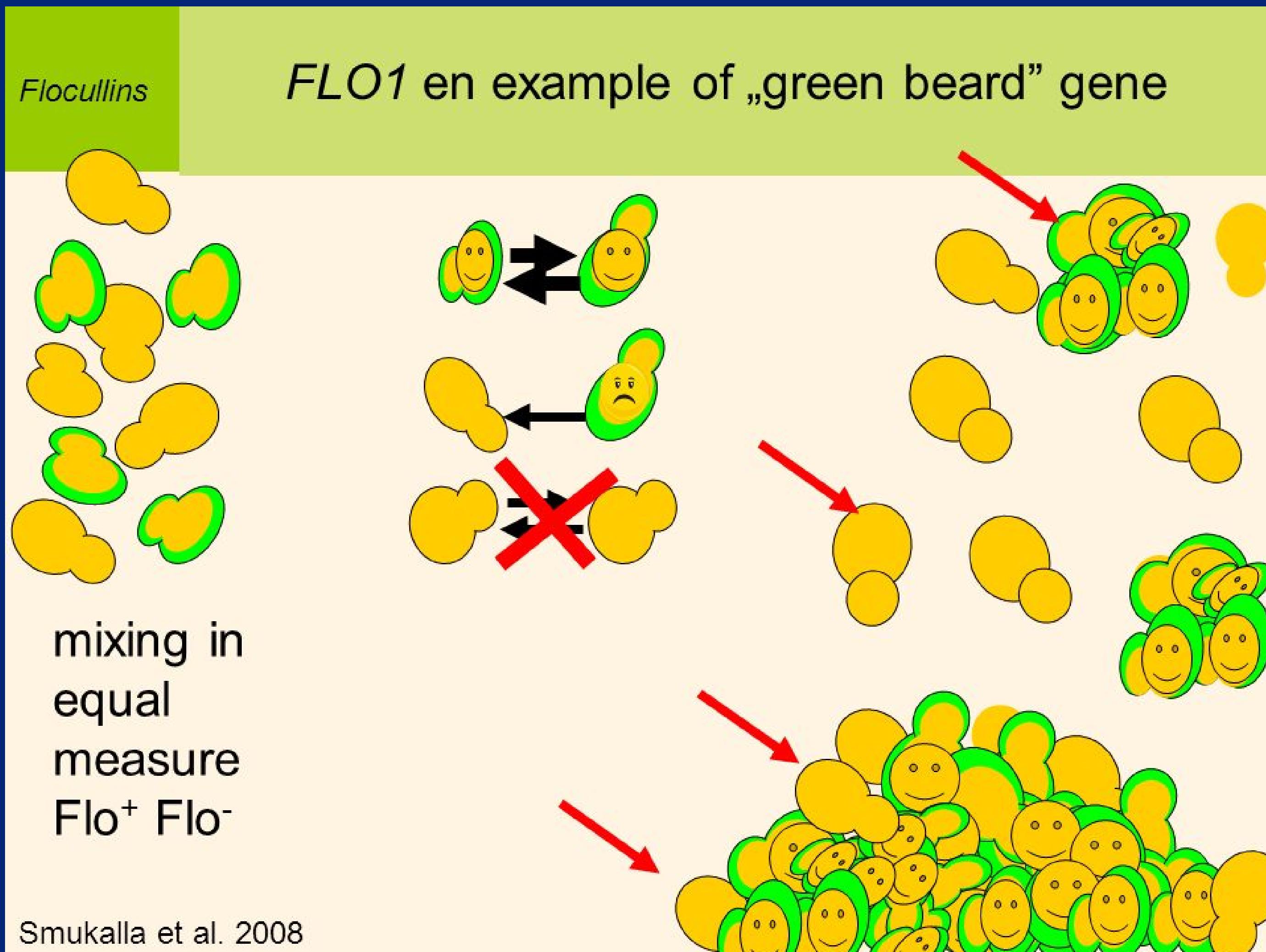
- Richard Dawkins coined the name "greenbeard" for a gene that can:
  - Produce a distinctive phenotype
  - Allow its possessor to recognize that phenotype
  - Cause its possessor to behave altruistically toward those who share the phenotype
- Such a gene could spread in a population

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

- Generalist species inhabit a broad ecological niche
  - Tent caterpillars eat rose, cherry, plum, apple, hawthorn
  - Brown bears eat fish, rodents, large game, fruits, berries
- Specialist species inhabit a narrow ecological niche
  - Monarch caterpillars eat milkweed
  - Pandas eat bamboo

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

One-minute responses

- Tear off a half-sheet of paper
- Write one line about the lecture:
  - Was anything unclear?
  - Did anything work particularly well?
  - What could be better?
- Leave at the back on your way out