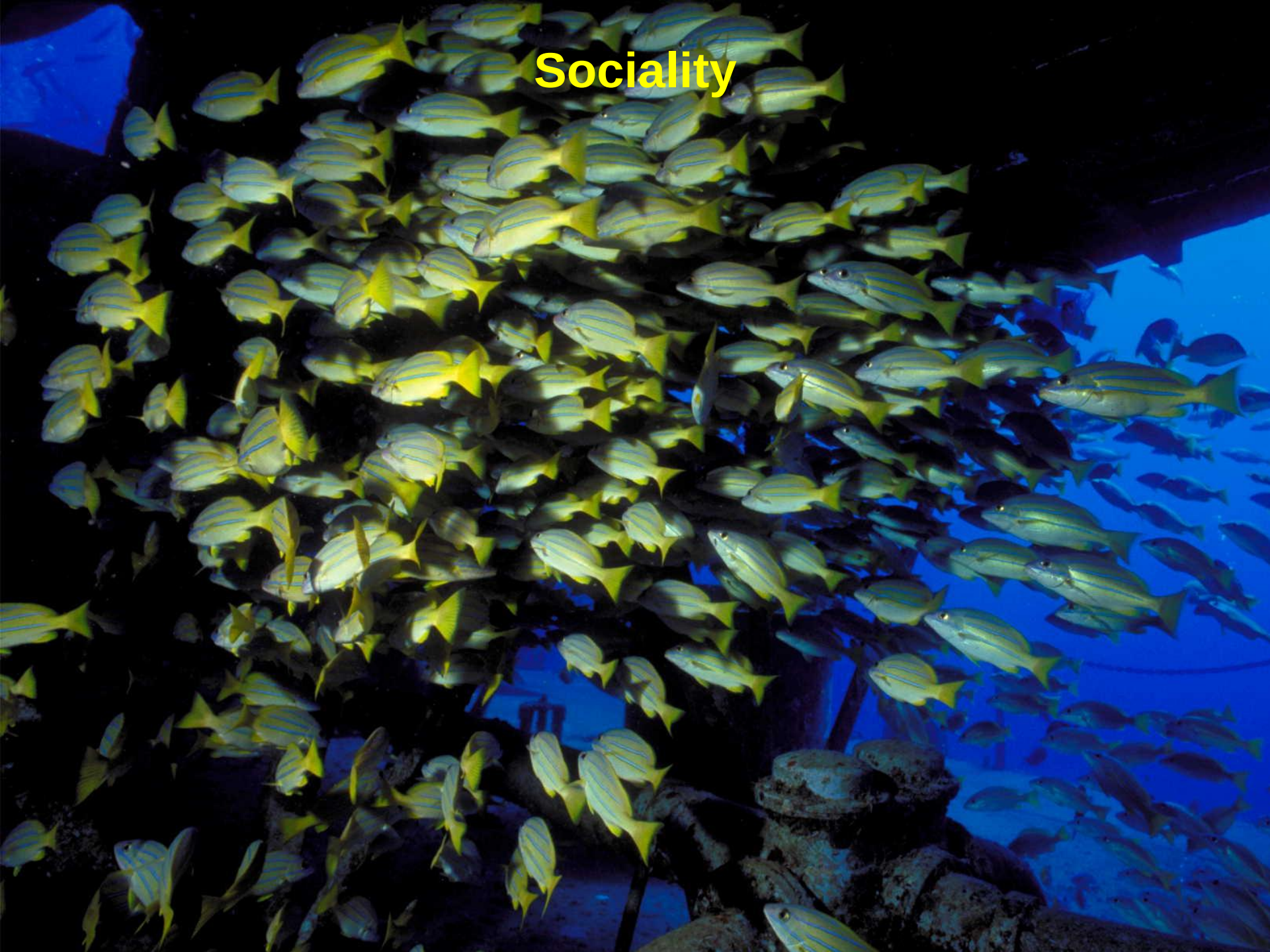

Sociality

Costs and benefits of social groups

Benefits

- Predation
  - Collective detection
  - Predator dilution
- Food
  - Information sharing
  - Cooperative hunting

Costs

- Predation
  - Predator attraction
- Resource competition
- Disease transmission

Social interactions

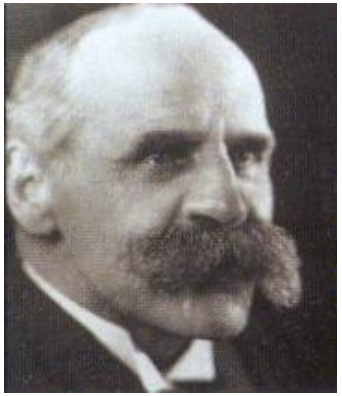
Behavior towards others depends on costs and benefits to actor and recipient *and genetic relatedness between the two*

Fitness of recipient	Fitness of actor: -	Fitness of actor: +
+	Altruism	Cooperation
-	Spitefulness	Selfishness

Genetic relatedness

- Sharing copies of gene from same relative (identical by descent)
- Coefficient of relatedness (*r*) = average proportion of genes identical by descent

0.50 = Parent, full sibling
0.25 = Grandparent, half sibling,
aunt/uncle, nephew/niece
0.125 = First cousin



"*Would I lay down my life*
to save my brother?
No, but I would to save
two brothers or eight cousins."

Approximate quote by J.B.S. Haldane

Types of fitness

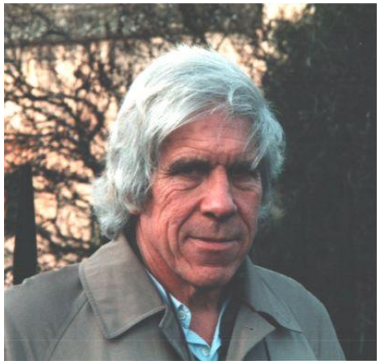
- Own offspring = direct fitness
- Related offspring = indirect fitness
- Direct + indirect = inclusive fitness
- Kin selection = process of maximizing inclusive fitness

Hamilton's rule

- In order for altruistic behavior to occur

$$C < r\,B$$

- *r* is coefficient of relatedness
- Cost to actor (C)
- Benefit to recipient (B)



W.D. Hamilton

Hamilton's rule

- Another way to think about it...

$$C < rB$$

- C is direct fitness lost due to altruistic behavior
- B is indirect fitness gained due to altruistic behavior

Hamilton's rule

- Also predicts spiteful behavior

$$C < rB$$

- C is direct fitness lost due to spiteful act
- B is negative benefit (= cost) to recipient
- *r* is negative relatedness

Negative *r* ?

- *r* = relative relatedness compared to population
- 0 = average relatedness
- According to Hamilton's rule, spite can only occur between individuals with negative *r*

Social interactions

Selfishness, cooperation easy to explain because both maximize individual fitness

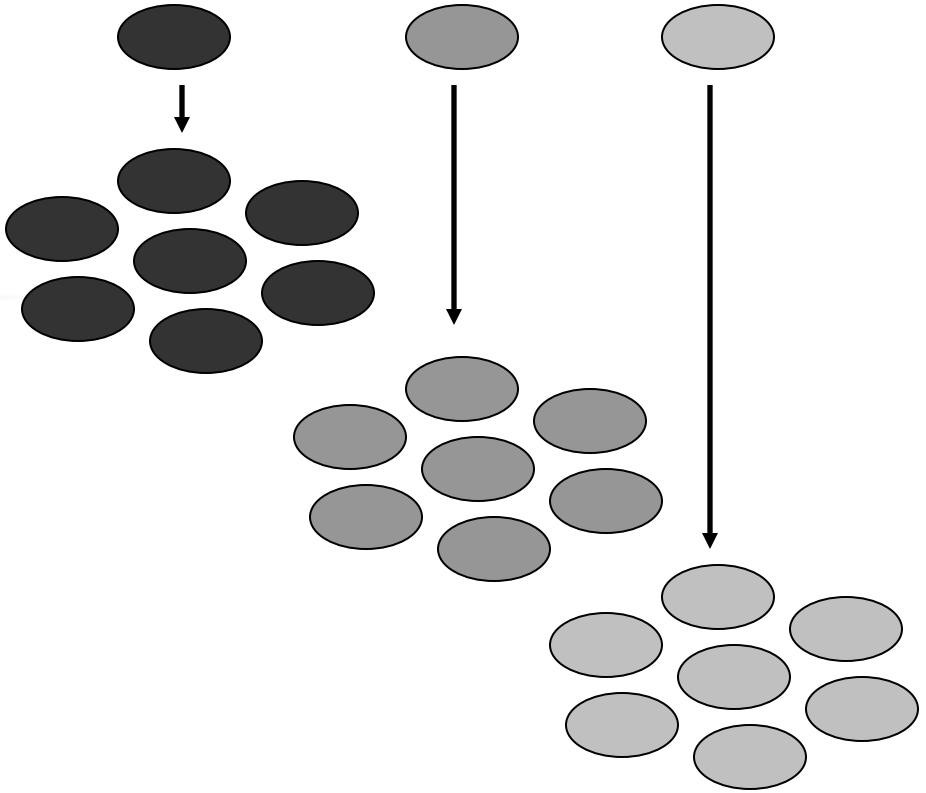
Does spitefulness occur in nature?

Spiteful behavior

- Unlikely to occur because requires restrictive conditions
  - Extreme competition for resources
  - Negative relatedness among participants
  - Ability to recognize close relatives

Spiteful behavior in parasitoid wasps

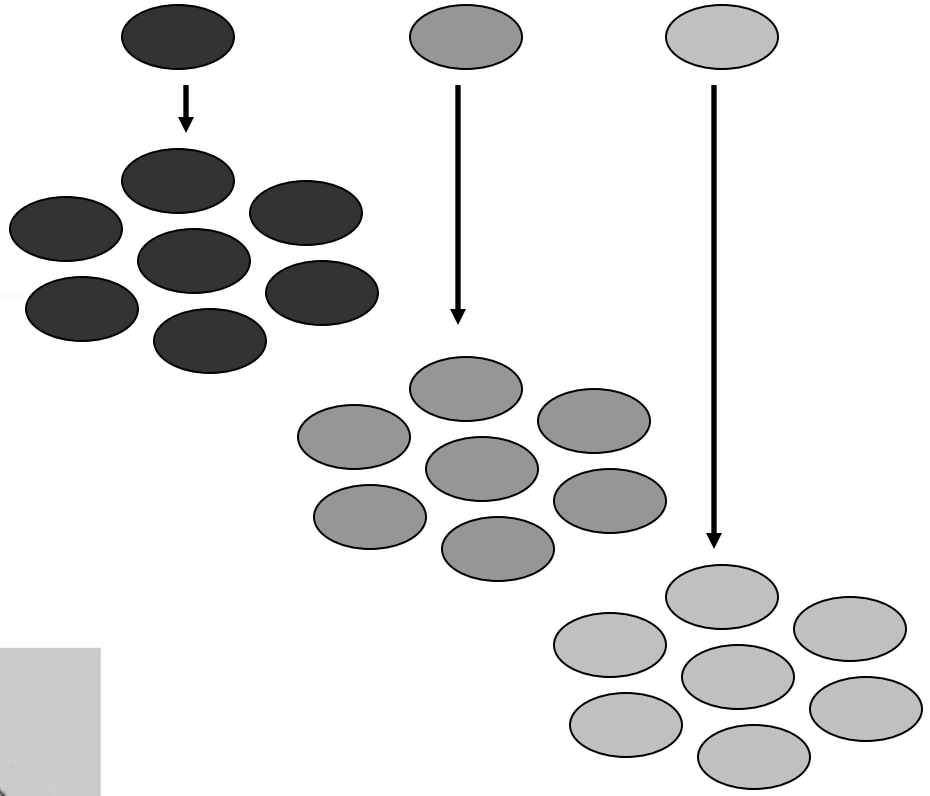
Polyembryonic *Copidosoma floridanum* reproduces clonally

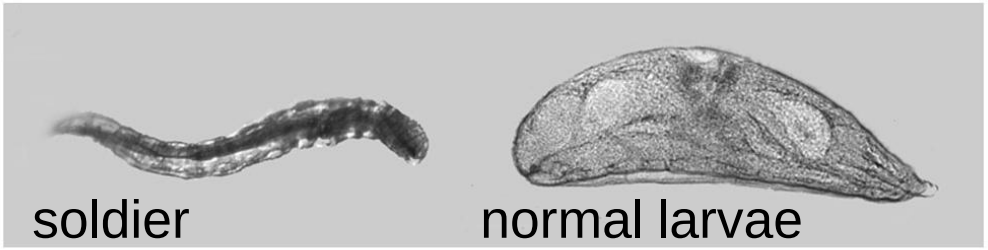


Some “siblings” are more related than others

Spiteful behavior in parasitoid wasps

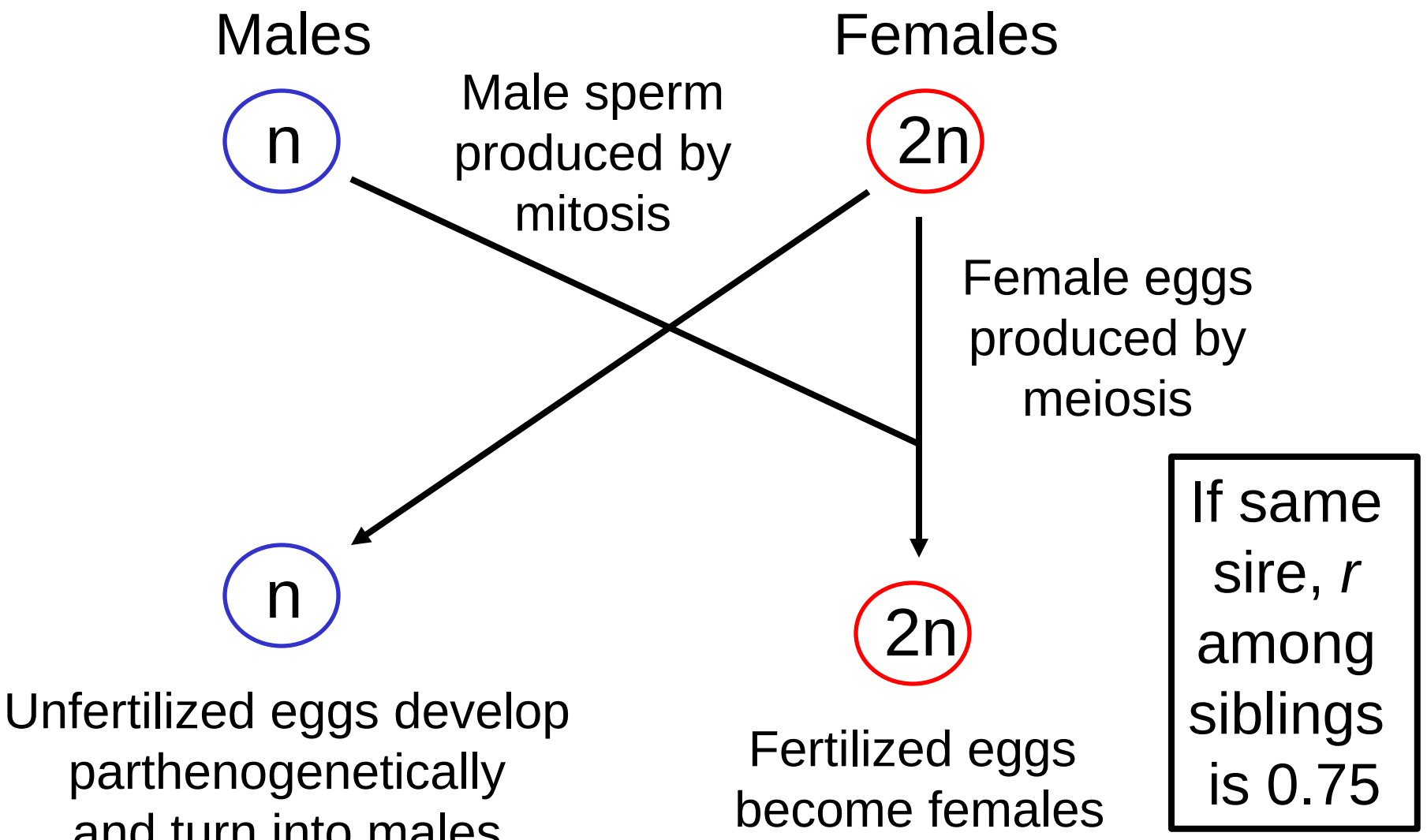
Polyembryonic *Copidosoma floridanum* reproduces clonally



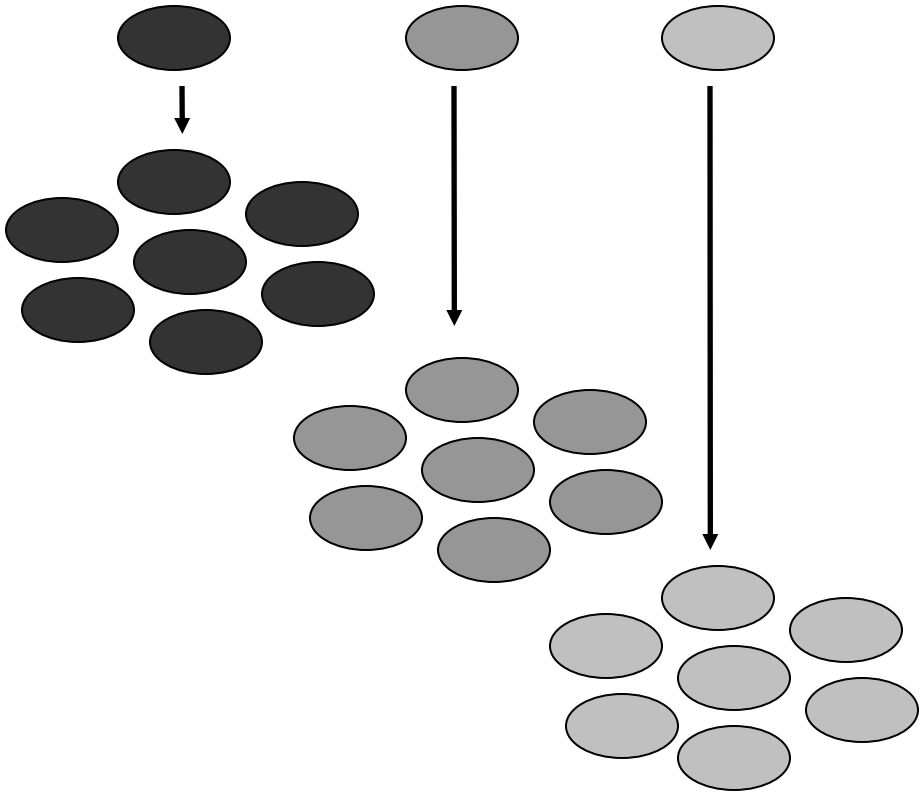


Some become soldiers, do not reproduce

Sex determination in wasps



Negative *r* ?

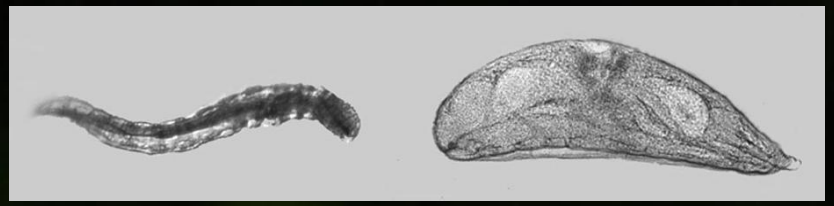


related to by *r* = 1.0 clonal siblings

related to by *r* = 0.75 full siblings

related to by *r* = 0.25 half siblings

Soldiers attack and kill less-related clones



Spiteful behavior in parasitoid wasps

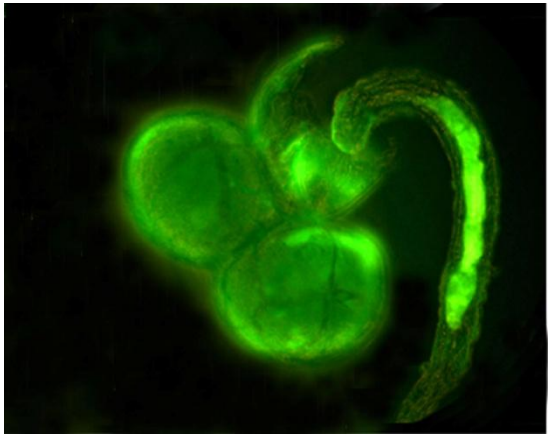
Spite vs. “indirect altruism” depends on

- Number of parasitoids laying per host
- Precision of kin recognition

Social interactions

Selfishness, cooperation easy to explain
because both maximize individual fitness

Spite constrained by unique circumstances



What about altruism?

Altruism

Toward relatives

Toward non-relatives

Reproductive helpers

Some altruism explained by inclusive fitness

Juveniles may postpone breeding,
assist rearing younger siblings

Reproductive helpers

Juvenile males can become

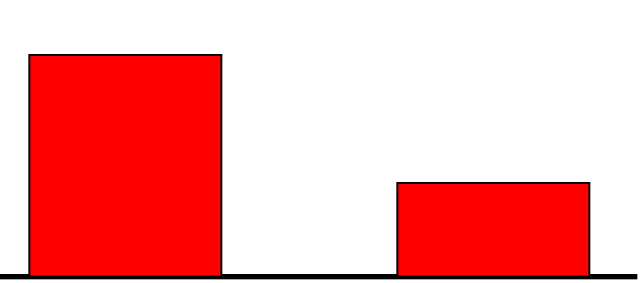
primary helper

secondary helper

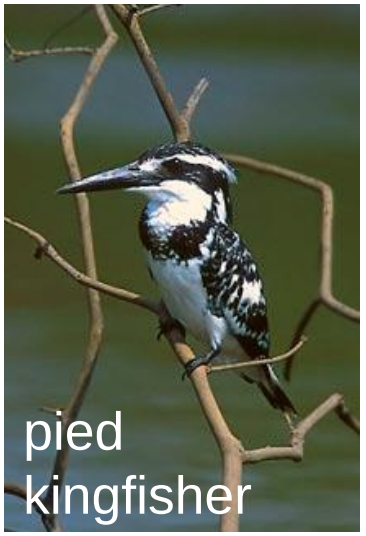
delayer

Second year (Direct)

First year (Indirect)



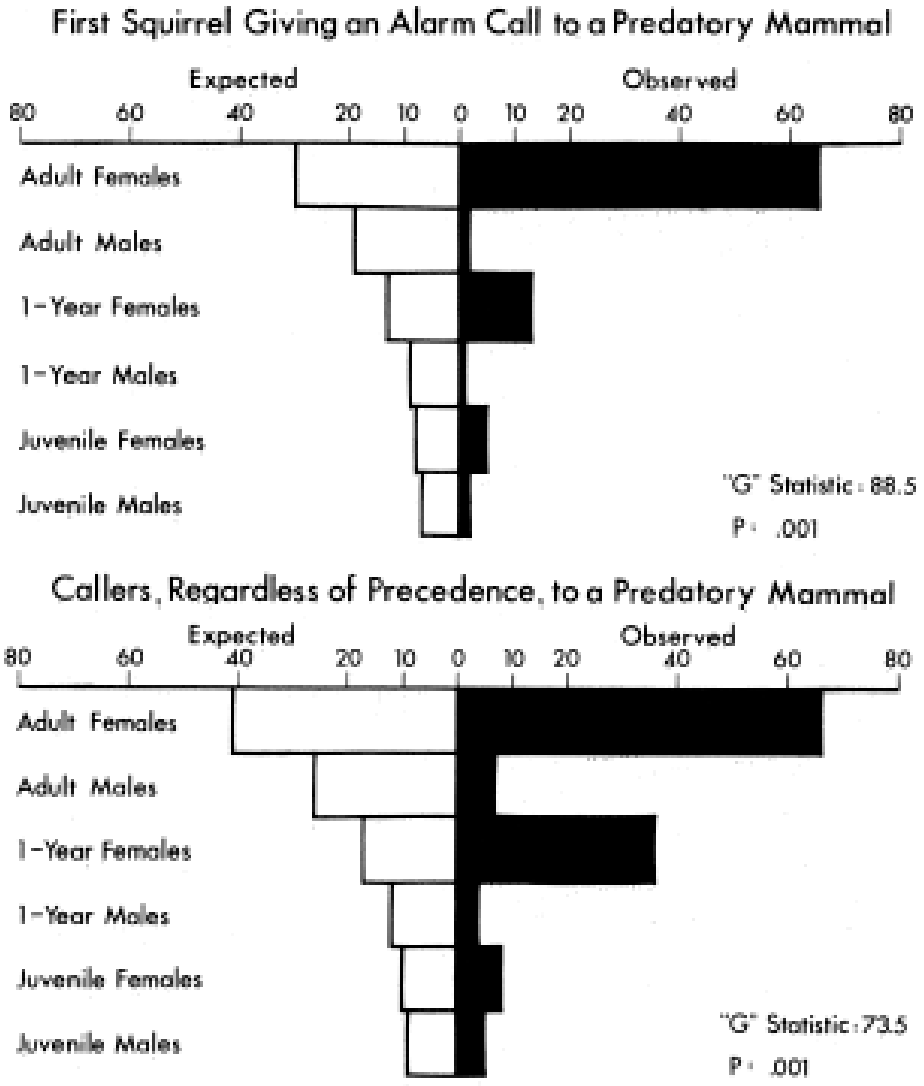
Fitness



Altruistic alarm calling

- Callers at greater risk (C)
- Call when relatives near (B)
- Given matrilineal social system, who should do the alarm calling?

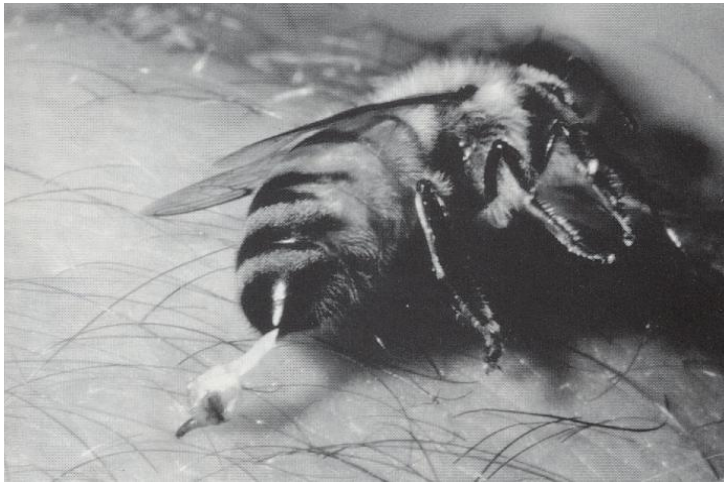
Altruistic alarm calling



Altruism in social Hymenoptera

Reproduction limited
to one or few queens

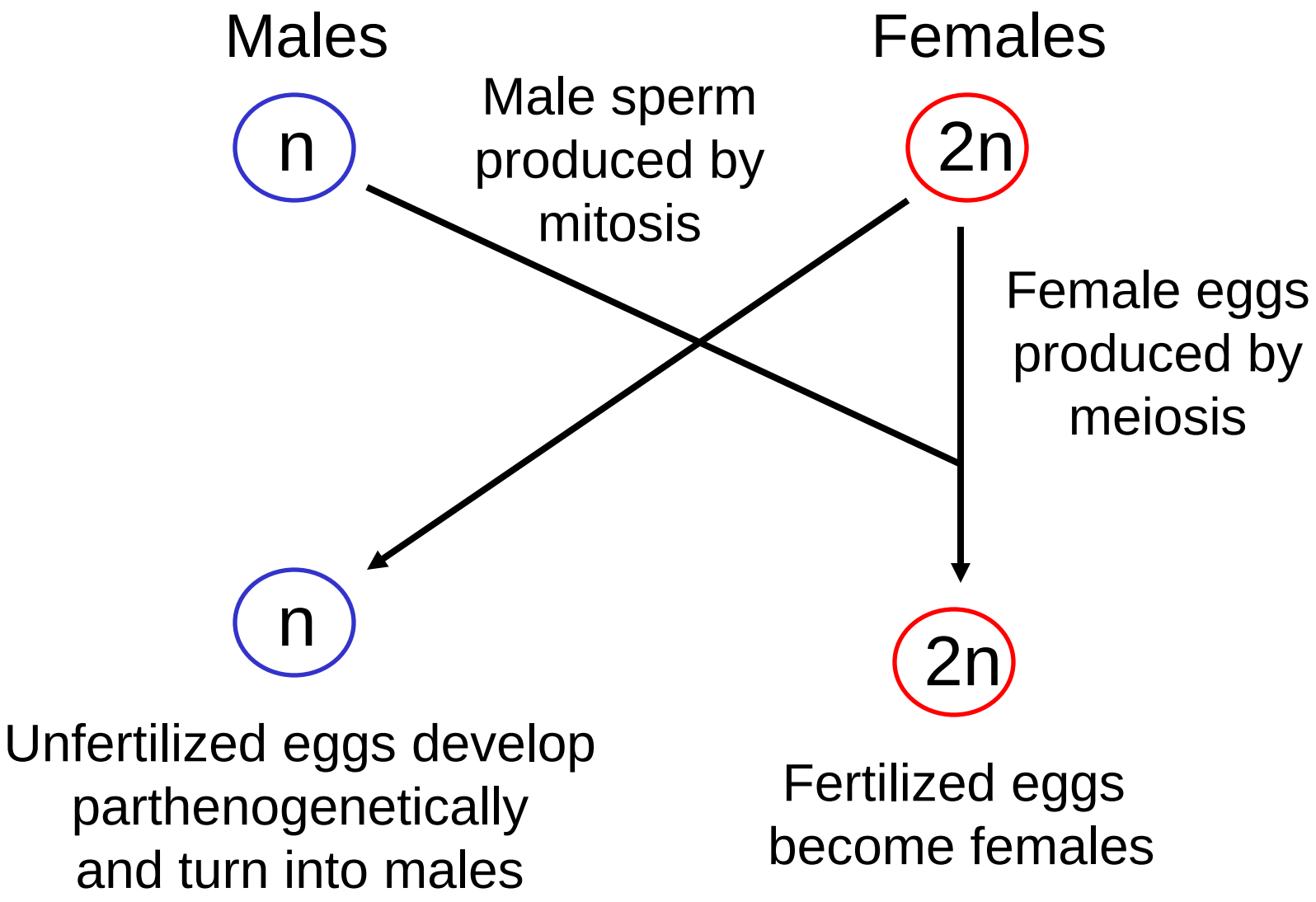
Cooperative care of young

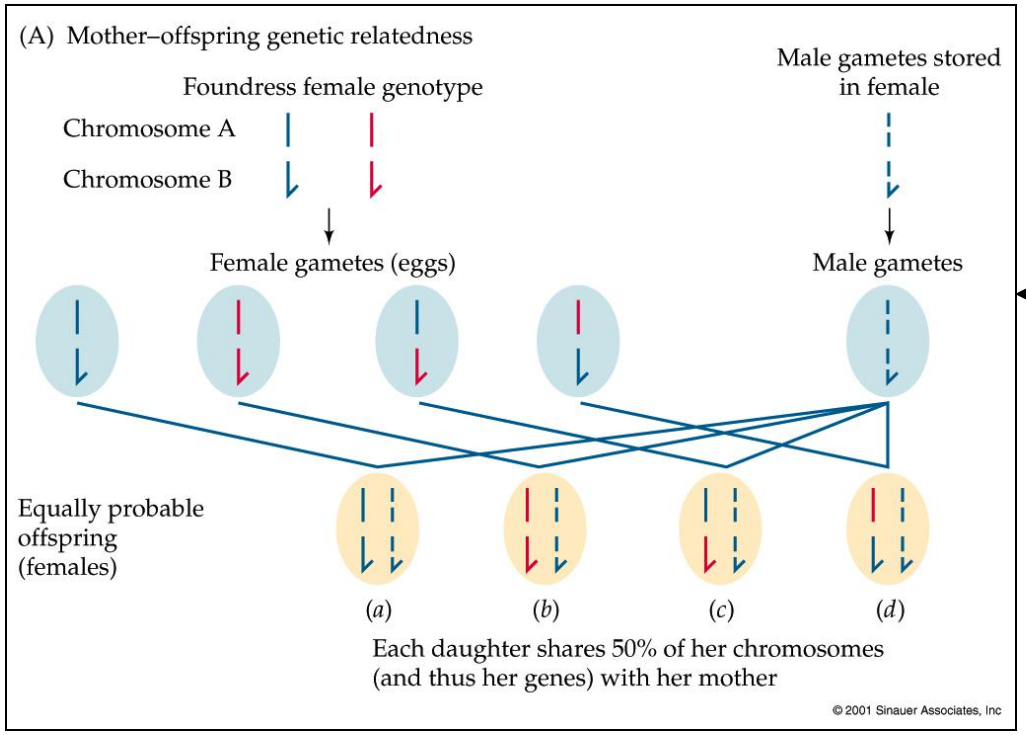


Workers may die
defending colony

Altruism due in part to unusual
sex determination system

Haplodiploidy in social Hymenoptera

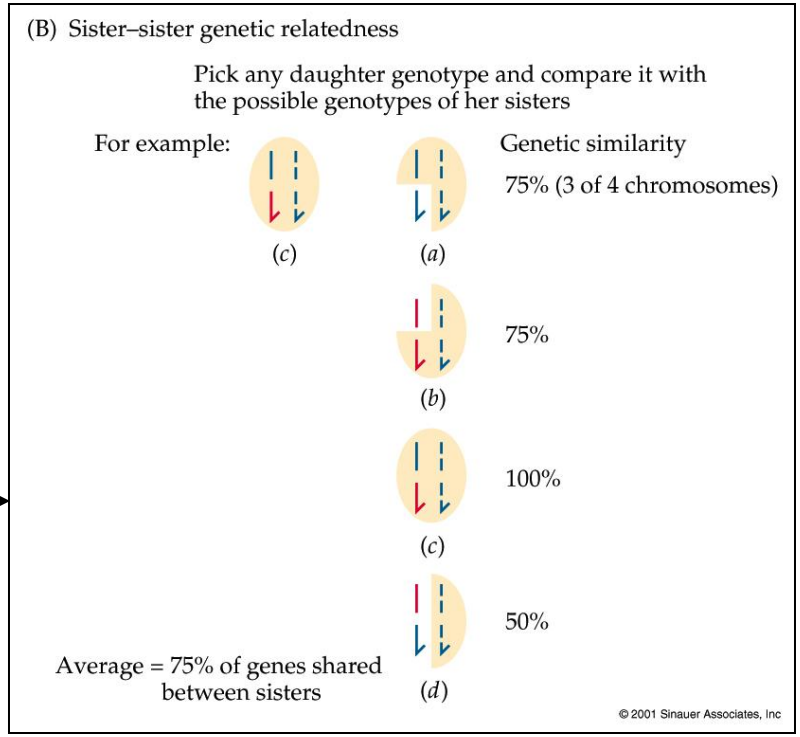




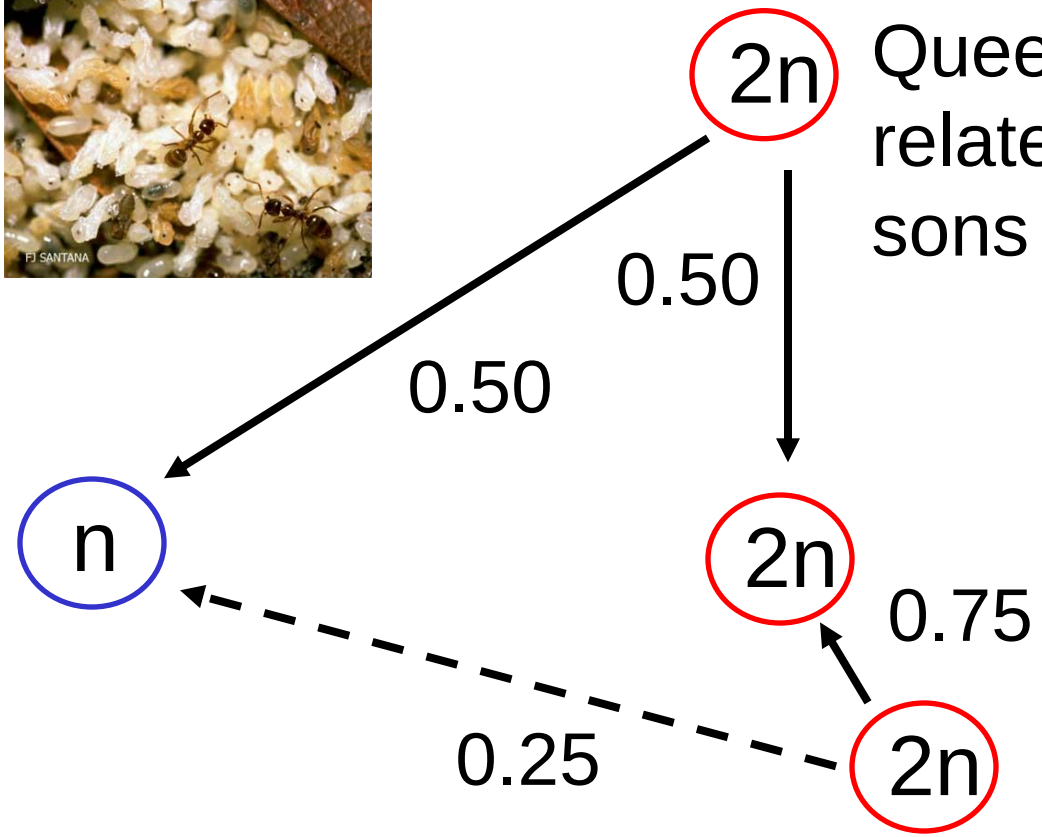
r = 0.50 between queen and female offspring

r = 0.75 between sisters

Assumes one male sire!



Haplodiploidy affects kin selection



How does this affect their behavior?

Reciprocal altruism

- Repaying an altruistic act
- Cost of altruistic act is usually low

Robert Trivers

Reciprocal altruism

Vampire bats need to eat 50-100% of their body weight in blood per night

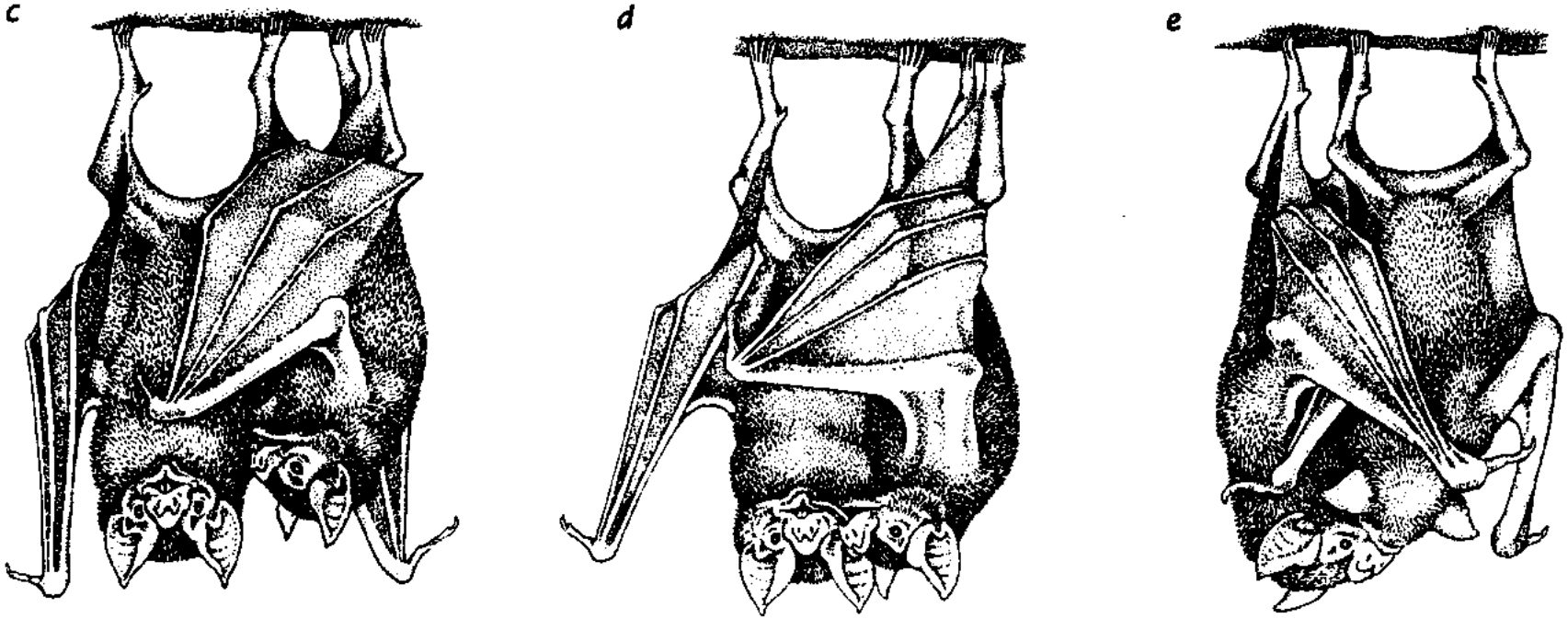
33% of juvenile and 7% of adult bats find no food each night

Energy budget allows for 48-72 hours before they starve

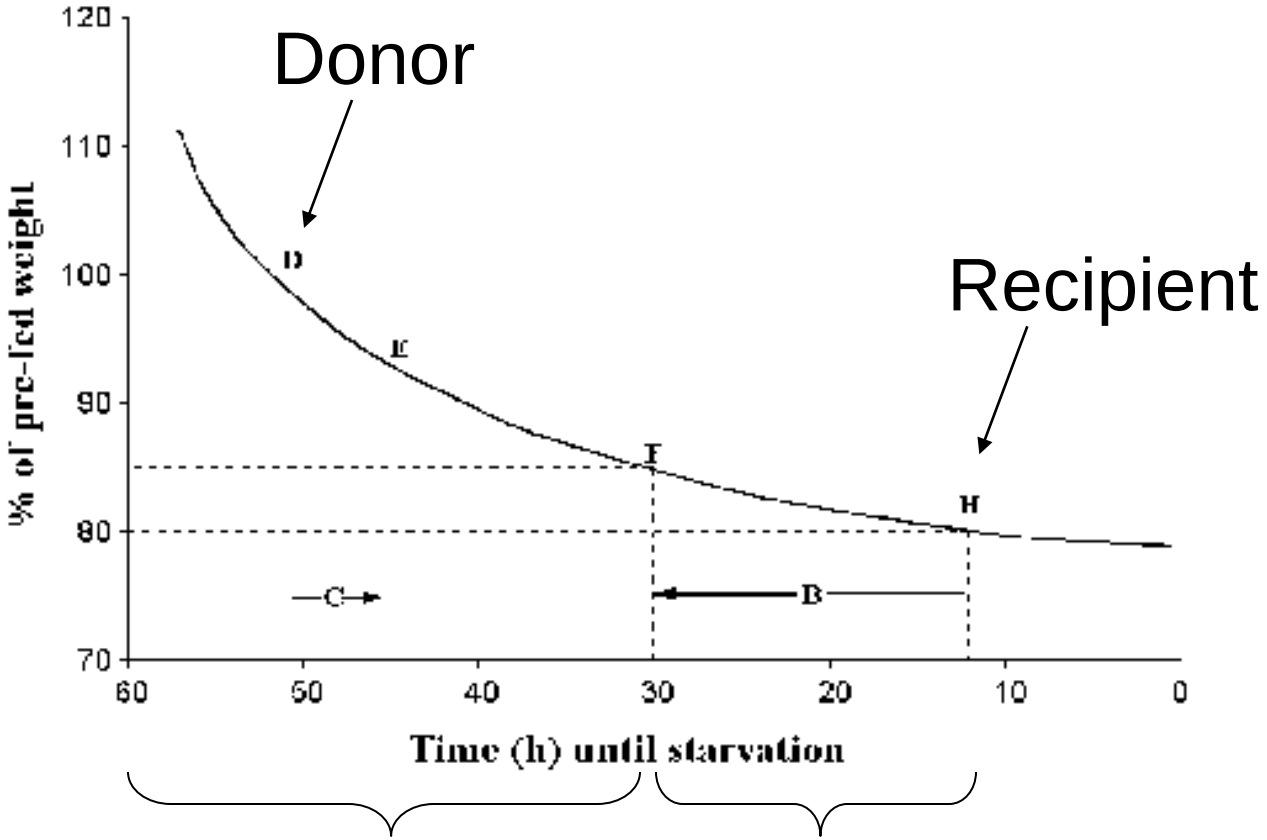
Based on these parameters, annual adult mortality should be 82% but is only 24%

Reciprocal altruism

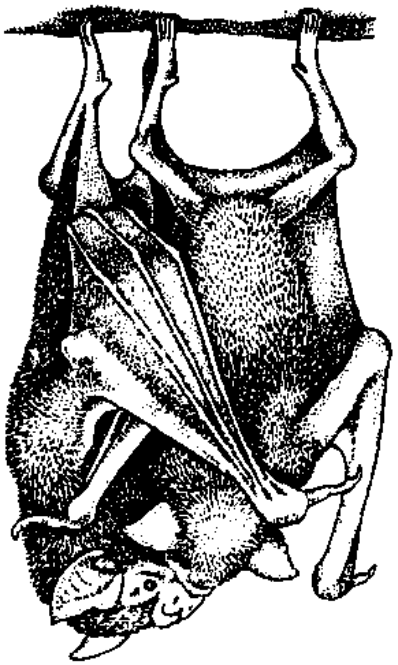
Successful foragers share blood meals with unsuccessful foragers

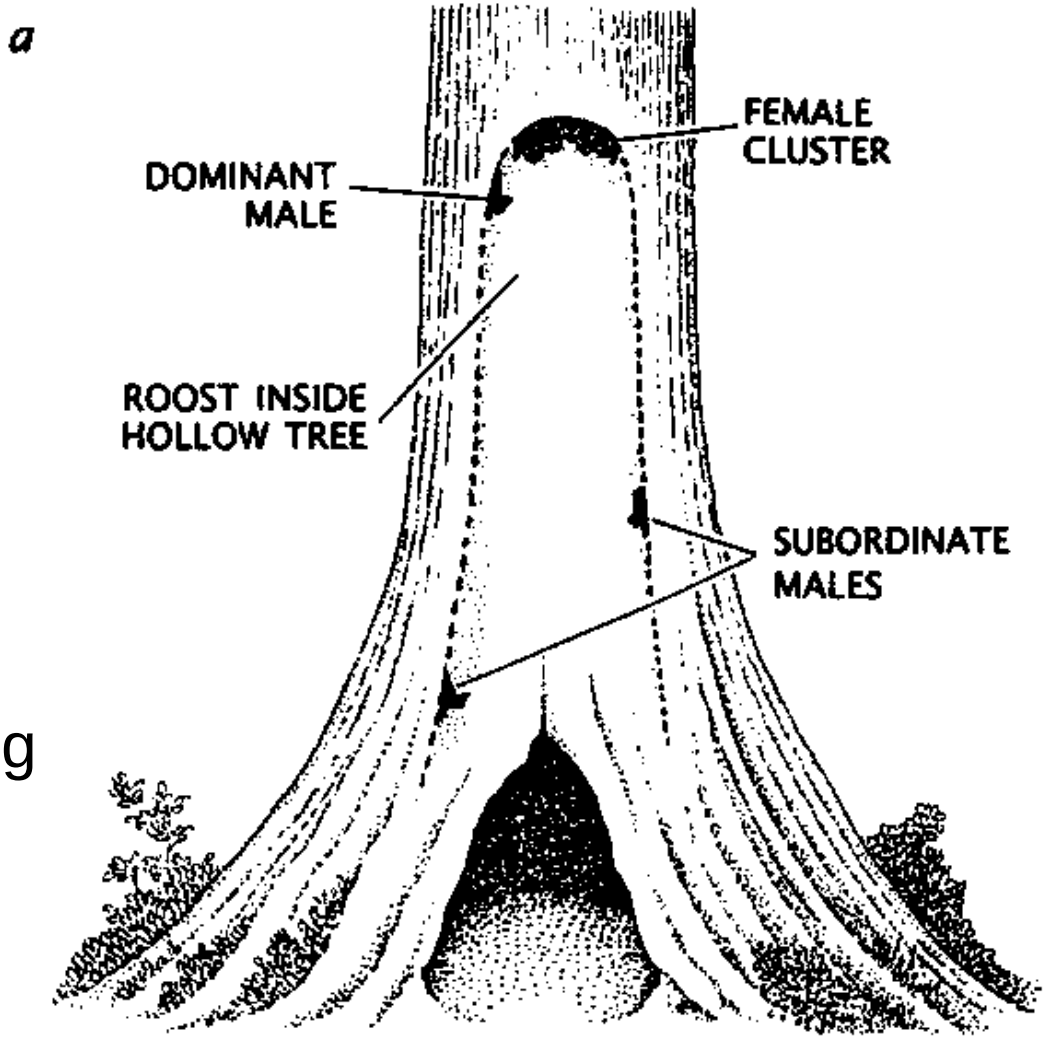


Reciprocal altruism



Reciprocal altruism





Excluding parent-offspring sharing, females most likely to share with regular roostmates

Why is reciprocity rare?

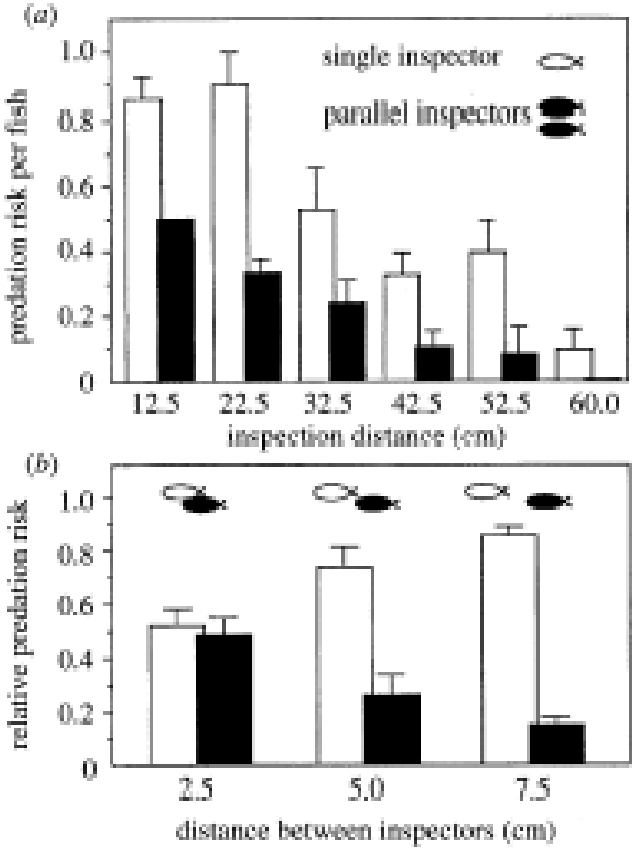
Consider the prisoner's dilemma:

Player A \ Player B	Cooperate	Defect
Cooperate	A, B rewarded for cooperation	A gets maximum punishment
Defect	A gets maximum reward	A, B punished for mutual defection

Good strategy is always to defect first!

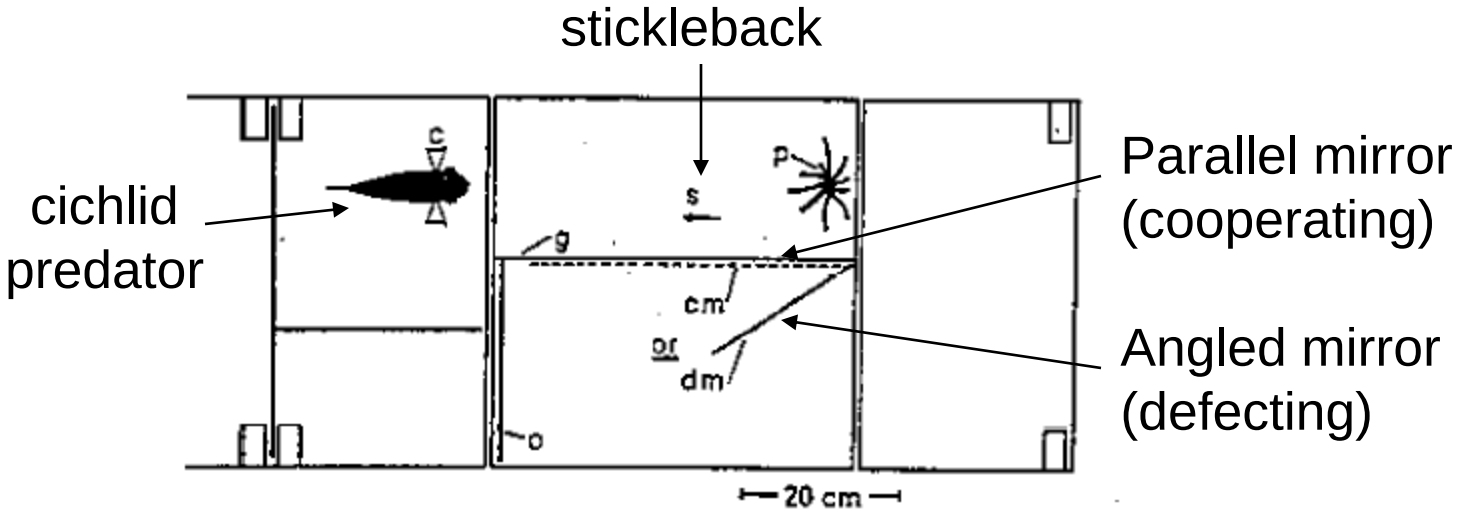
The problem of defection

Many fish (e.g. sticklebacks) approach and inspect potential predators

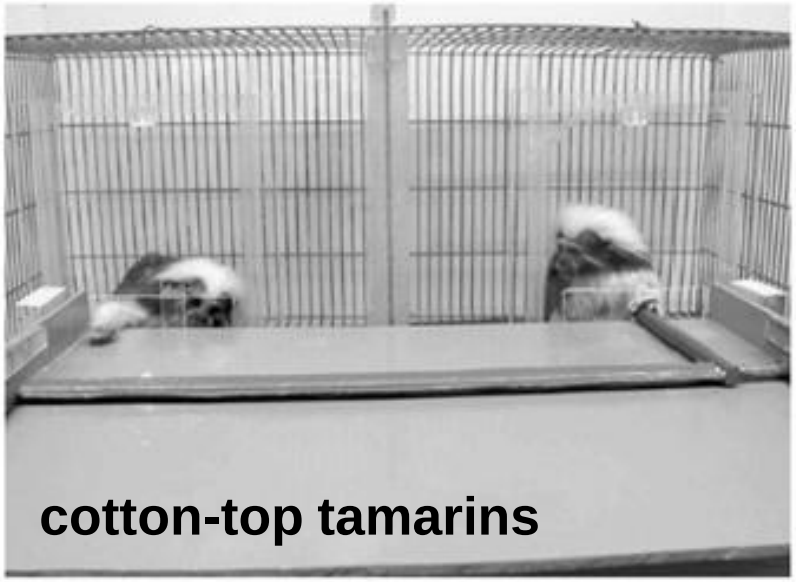


The problem of defection

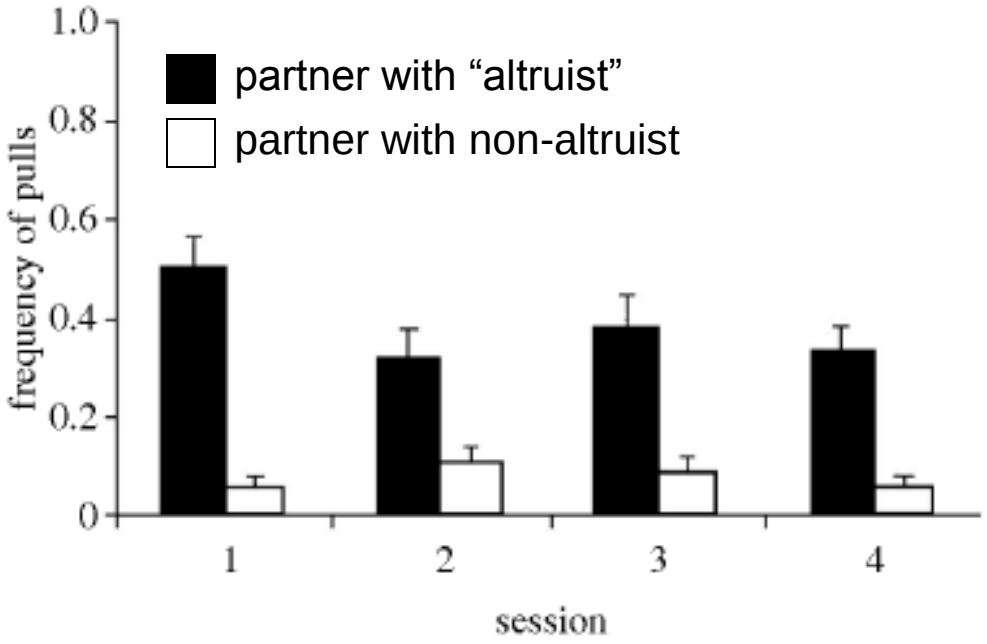
Willingness to approach predator can be experimentally manipulated



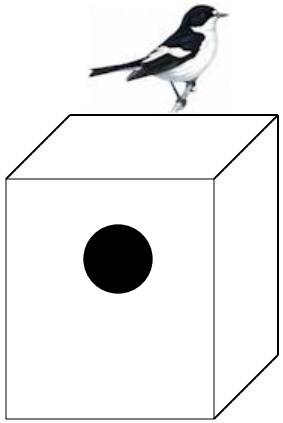
Does reciprocity exist?



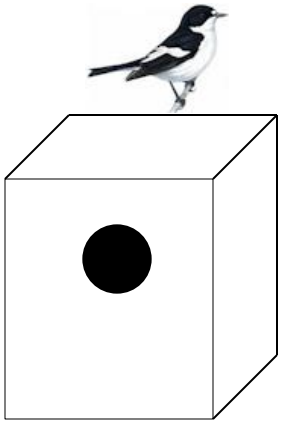
Researchers trained one tamarin to be an “altruist”



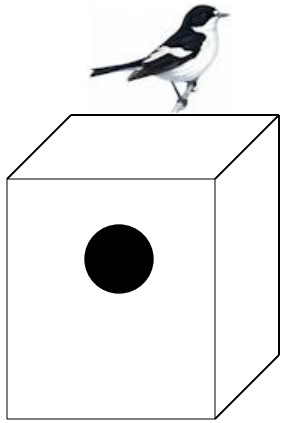
Does reciprocity exist?



A



B

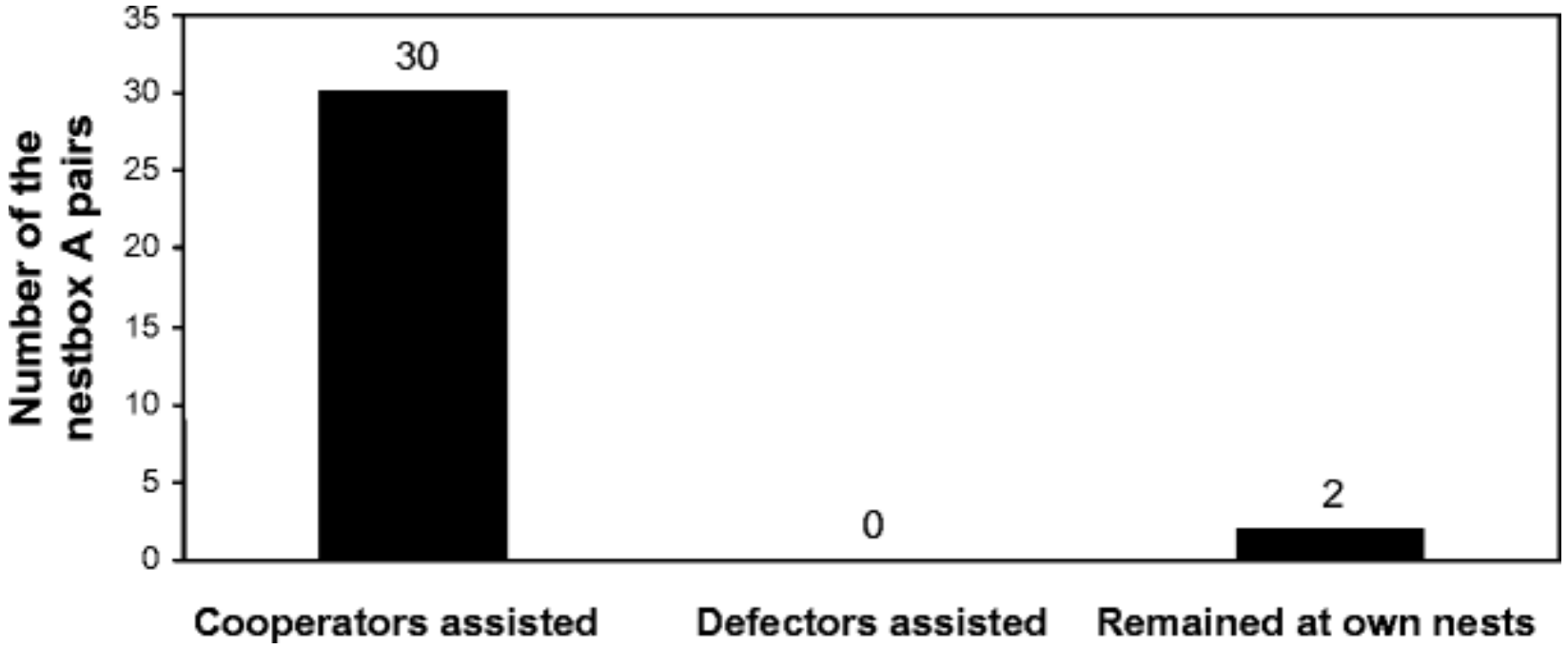


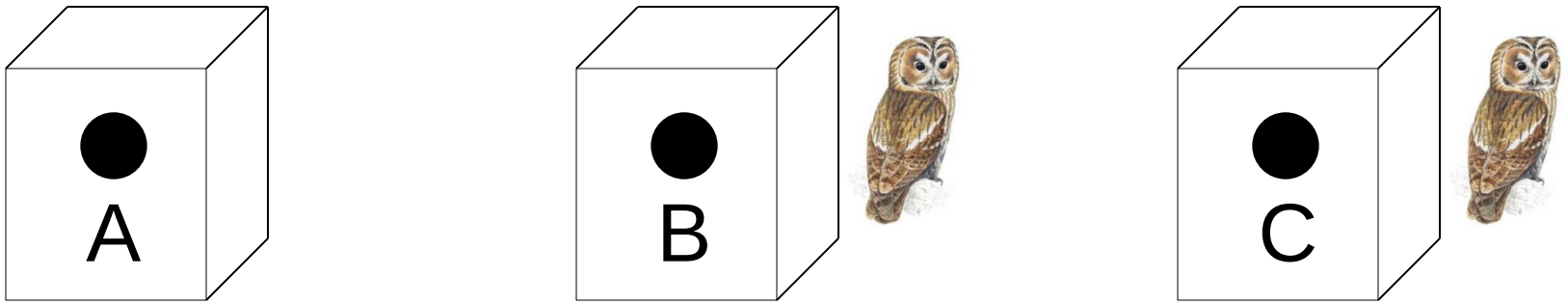
C

When owl model placed near box A

- pied flycatchers from box C cooperated
- pied flycatchers from box B defected

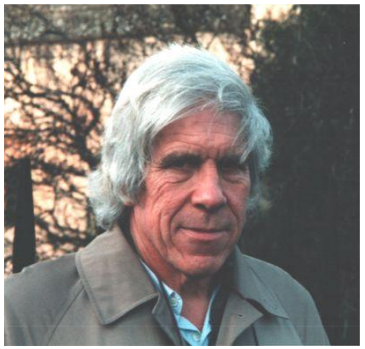
Does reciprocity exist?



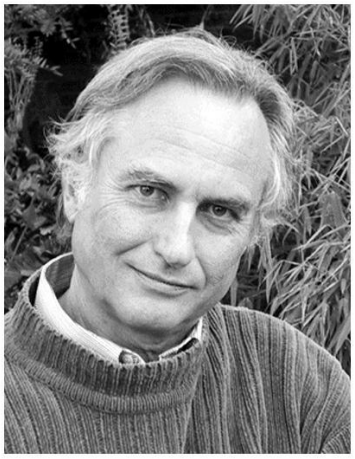


Greenbeard altruism

- Hamilton's rule predicts altruistic behavior based on average *r*



W.D. Hamilton



Richard Dawkins

Greenbeard allele(s):

- Produce trait
- Recognize trait
- Treat those with trait preferentially

Greenbeard altruism

Solenopsis invicta

Fire ants are polygynous (multiple queens)

BB and *Bb* genotypes for *Gp-9* locus (*bb* inviable)

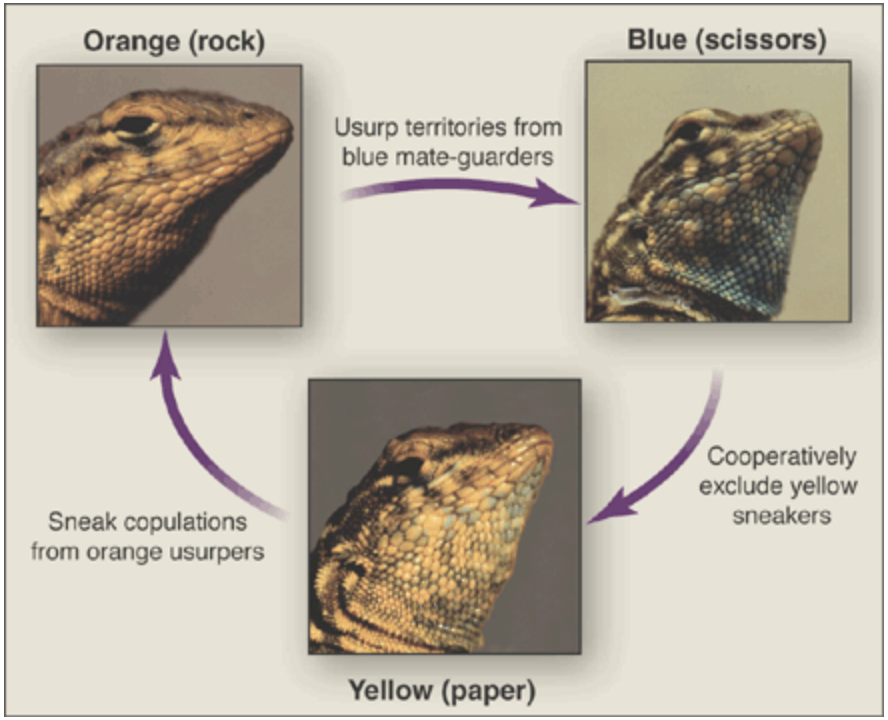
queens	~~BB~~	Bb
workers	BB	Bb

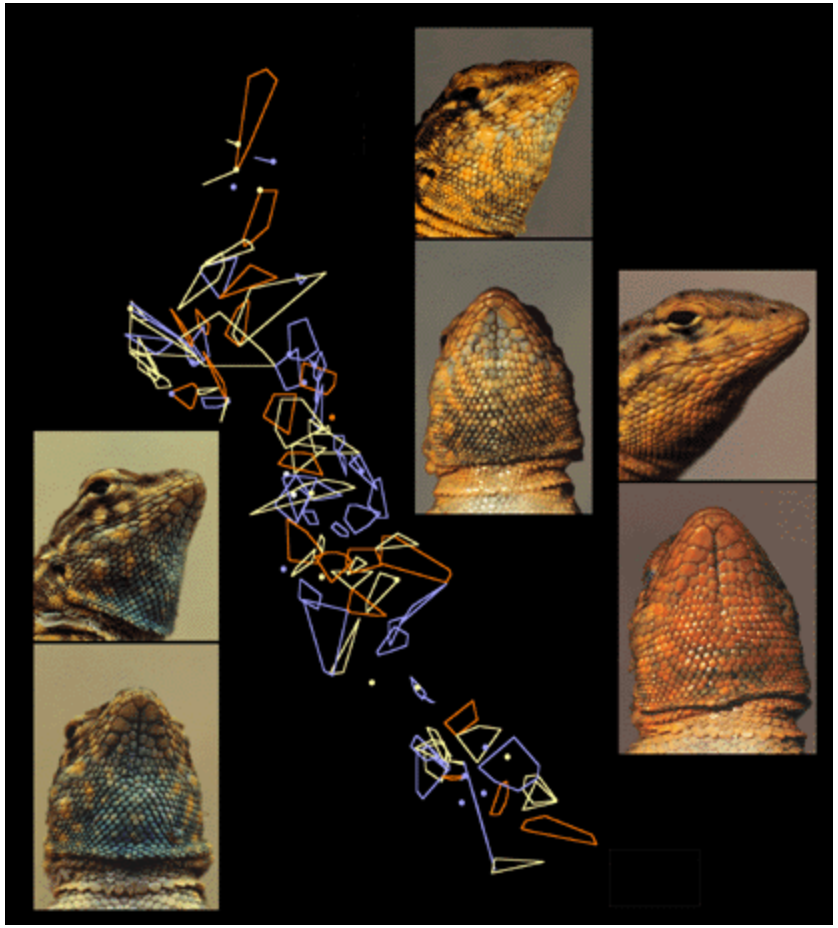
BB queens killed by *Bb* workers

- when develop from *BB* workers
- when introduced into colony

Role of transferrable odor cue?

Greenbeard altruism





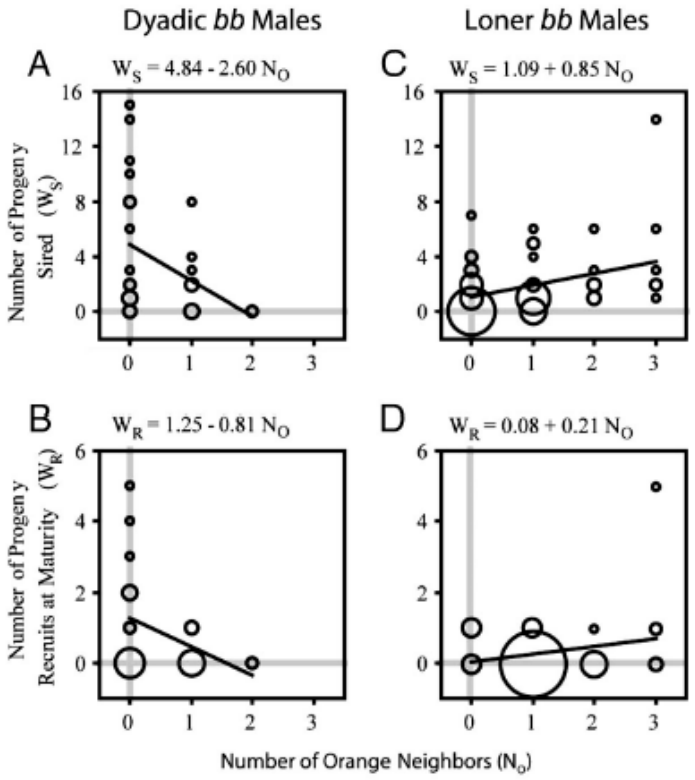
side-blotched lizard
Uta stansburiana

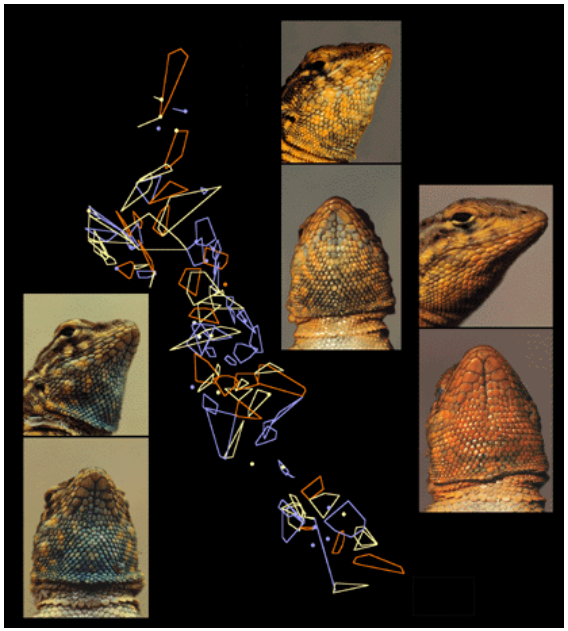
Three color morphs represent three strategies
Genetically determined, evolutionarily stable

Blue males (*bb*) more likely to settle near unrelated blue males

bb dyads more similar at 9 microsatellite loci than other males in population

Orange (O) males attracted to *bb* dyads

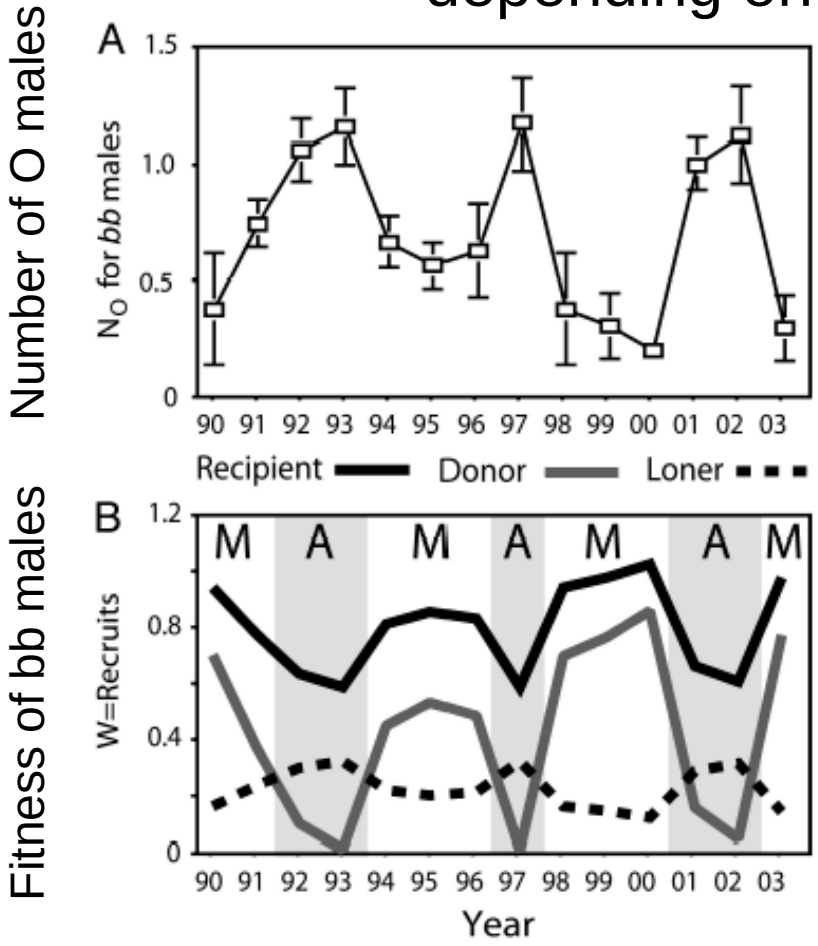


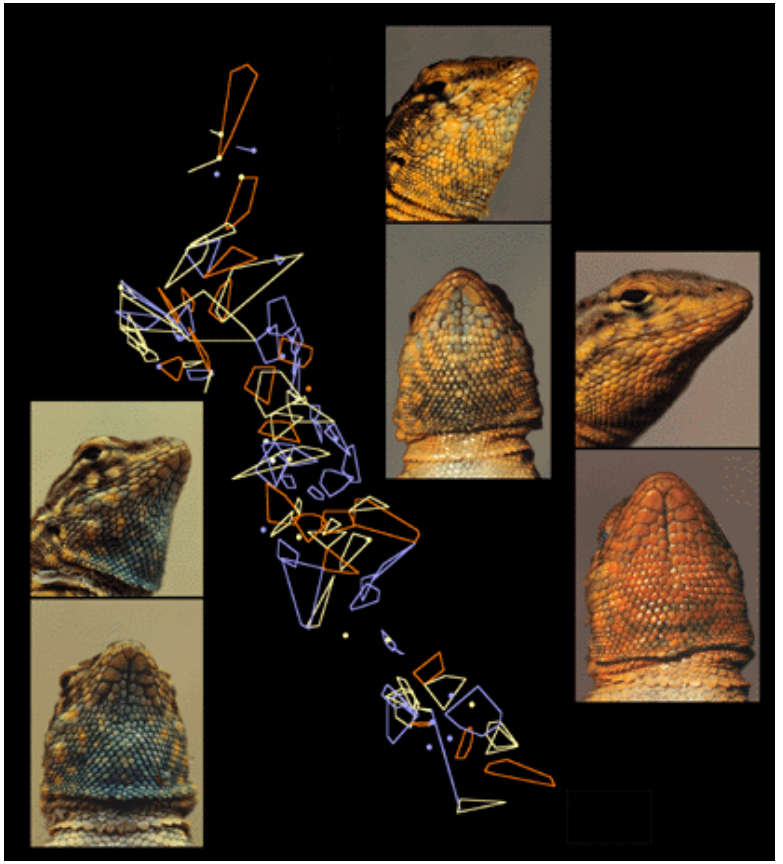


Usurping O males reduce fitness of *bb* dyads relative to loner *bb*; cost usually borne by one male

Greenbeard altruism

Alternates between altruism and mutualism depending on number of O males





Lifespan suggests no reciprocity