Cooperation

Why is it surprising and
how does it evolve

Main points for today

- Sociality, cooperation, mutualism, altruism - definitions
- Kin selection – Hamilton's rule, how to calculate r
- Group selection – the price equation, green beards, and assortment
- Classic examples – alarm calls, helpers at the nest, social insects, predator inspection, food sharing

Cooperation:

Displaying a behavior that benefits another individual. (If both benefit that's mutualism.)

Altruism:

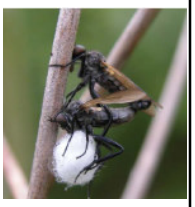
Displaying a behavior that benefits another individual at a cost to oneself.

Sociality/social behavior:

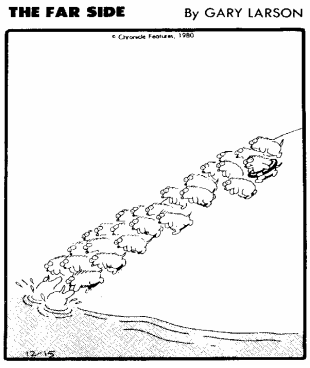
Living in a group/behavior in interactions with conspecifics

Group living vs. cooperation

Sociality-no-cooperation and cooperation-no-sociality



I define 'sociality' as living with other individuals of the same species at least semi-permanently.



How can altruism evolve?

- If the recipient of the cooperative/altruistic act benefits, it is going to leave more offspring.
- The actor however is not going to leave more offspring, or even fewer offspring – **fewer altruists in the next generation**.

If such behavior is heritable, and it goes on over many generations, it will ultimately die out.

The evolutionary mystery

Altruism: 5 possible explanations

- Group selection
- Kin-selection
- Reciprocal altruism, coalitions
- Status
- Sexual selection (handicap)

Evolution of altruism

Group selection

The Price equation: shows how variance partitioned among individuals and groups leads to selection effects at these levels

Generally selection at the individual level is faster and stronger than at the group level because:
- groups reproduce more slowly
- individuals migrate between groups
- cheaters (mutants) can arise in groups

Evolution of altruism

Kin-selection

Helping relatives increases your 'indirect fitness':

Indirect fitness: your own offspring ('fitness') plus your genes reproduced in relatives.

(This could also be seen as selection on the level of genes.)

Kin selection and relatedness

Kin-selection

Helping relatives increases your 'inclusive fitness' therefore means:

The more of your genes are in a relative, the more interest you have in helping them.

This is measured by r ('relatedness')

Kin selection and relatedness

Hamilton's rule

An individual can be altruistic if

c < b * r

The cost should be smaller than the benefit multiplied by relatedness.

E.g. an individual may not reproduce (c=1) to help its sibling (r=0.5) if this helps the sibling raise at least two additional offspring (b=2).

Kin selection and relatedness

Relatedness 'r'

(also called coefficient of relationship)

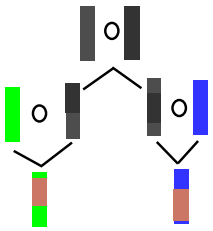
Usually defined as:

The average proportion of alleles of an individual A that are identical by descent to those in individual B.

Or, the probability that A and B carry the same allele, derived from the same ancestor, at a particular locus.

Kin selection and relatedness

Computing relatedness



you – cousin:
0.125

parent	0.5
sibling	0.5
uncle/aunt	0.25
cousin	0.125
grandparent	0.25

$0.5^4 = 0.0625$
0.0625 + 0.0625 = 0.125

Kin selection and relatedness

Relatedness 'r'

However, the definition that really reflects the 'r' in Hamilton's rule is:

r is a measure stating how genetically similar the two individuals are relative to two random members of the population.

This is on average the same as r calcutated by pedigree only in a large, randomly mating, outbred population. (Essentially, when inbreeding=0)

Kin selection and relatedness

Relatedness as measure of genetic similarity

Essentially 'r' is similar to measures of population structure (such as the inbreeding coefficient F).

r = (expected – observed)/expected

number of differing alleles between two individuals

r = 1 if no differing alleles are observed
r = 0 if all alleles that are expected to differ actually do

Evolution of altruism

Kin-selection examples

Alarm calls:
mostly when relatives are present

Helpers at nest of parents

Evolution of altruism

Eusociality

- Reproductive skew: sterile workers
- Cooperative brood care
- Overlap of generations

Sterile workers are helping kin

Mechanisms of kin selection

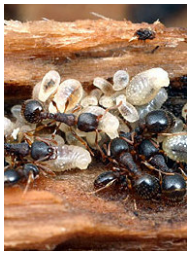
Kin-recognition

- By smell (rodents, humans, insects)
- By song (some birds)
- By learning/familiarity (mice, humans)
- By visual similarity (chimpanzees, humans)

Mechanisms of kin selection

Is kin-recognition necessary?

NO – kin selection can operate, and cause the evolution of altruism, as long as altruists are more likely to help kin than non-kin - for whatever reason.



Evolution of altruism

Inclusive fitness theory vs. kin selection

In fact, that's why some argue that it should be called 'inclusive fitness theory' rather than 'kin selection' –

Altruism can evolve as long as altruists are more likely than chance to dispense help to other altruists.

Evolution of altruism

Sorting altruists from cheaters

Maybe there are ways to associate preferentially with altruists?

- John's model: assortment

Evolution of altruism

Green beards

- If all altruists had a green beard, individuals could choose to cooperate only with green beard individuals… but why don't cheaters with green beards evolve?

Fire ants: BB queens are killed, and the b allele is kept in the population although bb ants die early. Thus workers only help queens with a similar allele.

Evolution of altruism

Reciprocity

Help if you get help back later – studied by game theory (prisoner's dilemma)

Frequent also between species: mutualisms

Evolution of altruism

Reciprocal altruism

Help if you get help back later – risky...

More likely if

- you will interact with the same individual later many times, in which you can reward or retaliate
- you can recognize individuals

Vampire bats: give blood

Summary

Evolution of altruism

- Natural selection acts on replicators
- That means mostly genes and individuals (*never* 'for the good of the species')
- But for the good of your genes can mean being altruistic to relatives
- Or helping/sharing etc. to get status or mates
- Or if helping is likely to be reciprocated

Evolution of altruism

Selfish altruism?

If altruism was ultimately costly to reproduction, it would disappear in evolution.

- Altruism can occur at the level of individuals, but if we see it today, we have to assume that it benefits reproduction at some level in the long run (of genes, individual, or group).

Evolution of cooperation

Cooperation vs. altruism

- Do factors leading to their evolution differ?
- Is cooperation (especially reciprocity) more likely between (compared to within) species?
- How can cooperation be 'enforced'?

Evolution of altruism

Two additional ways of evolving altruistic behavior

Evolution of altruism

'Sexual selection'

- Females select males *or vice versa*
- Males fight for access to females
  - success may depend on traits that are costly (handicap principle)...

A trait is 'sexually selected' if it confers increased mating at a cost to survival.

'Sexual selection'

Altruism may be such a costly trait if it increases mating opportunities:

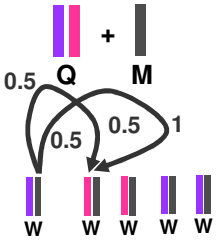
Nuptial gifts in dance flies

Status

Similarly, altruism may be a costly trait that increases status (and thus ultimately mating or access to resources).

Food sharing in Arabian babblers

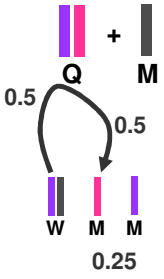
Does haplodiploidy cause eusociality?



0.25 + 0.5 = 0.75

- In complete monogamy, **workers are more related to the queen's daughters (r=0.75) than to their own (r=0.5)**
- This would explain why so many Hymenoptera are eusocial
- and why workers are always females

Does haplodiploidy cause eusociality?



- However, workers are only related to males by r=0.25 (less than to daughters) – thus average relatedness to reproductive offspring is still 0.5 (depending on sex ratio)
- Actual relatednesses measured in insect colonies are almost never 0.75 (multiple queens, polygamy)
- Recently more eusocial species without haplodiploidy have been discovered; and many haplodiploid species are not social

Alternative hypotheses for the origin of eusociality

- Parental manipulation
- Predisposition to sociality because of high b/c ratio (underground nests, extended brood care)
- Group selection