SF Evolution Lecture 19
Altruism part 1 - Kin Selection

Until now natural selection seems straightforward
But Darwin had two worries:
1) Sexual Selection and how such mal-adaptively showy males could evolve.
   (see lecture on sex)
2) Altruism: Why animals are so often nice to each other when their direct fitness would be higher if they were selfish.

Natural selection tends to select for selfish traits, so we might think animals should put themselves first at all times.
But we see the opposite everywhere:
- Parent spiders slow themselves down with thousands of their young
- Wild dogs co-operate to kill food, then share it out among themselves
- Unrelated meerkats will look after the young while their parents are foraging.
- Even humans give blood, helping complete strangers.

These behaviours are called **Altruism**

**Altruism** is a pattern of behaviour performed by an individual that decreases the fitness of that individual, but which increases the fitness of one or more other individuals. (Skelton

**How can altruism evolve?**

One commonly suggested answer is **wrong**, but still widely suggested (including in your essays). It is called **Group Selection**.

- e.g. “The monkey looks after its sick mate because the species will survive better if it does.”
- Or “… because the group it lives in persists longer and makes more baby monkeys in the long run.”
Sharing group
Each produce 1 baby per year but never die of famine

Selfish group
Each produce 2 babies per year, but sometimes die of famine

Initially appears sharing group will survive longer. However, what if there’s mixing between groups? Suppose a selfish monkey invades the group? Now he will do better as he will get help in famines but not incur the cost, so will have 2 babies per year.

The group will gradually become selfish, even if sharing was better for everyone. Invasion by of the selfish group by a sharing monkey wouldn’t work as the sharer would give away food but not get any.

Things to notice
1) Evolution will drive the sharing trait to extinction even though the group (and the species) would survive better, if the sharing gene had persisted.

2) The immediate benefit to the individual in terms of numbers of offspring is what decides which trait persists, not the long term effects of the trait.

3) Saying anything happens “for the good of the species” is always going to be wrong because, unless it’s for the good of the immediate actor, it’s not going to persist. So traits evolve for the good of the individual showing that trait.

Traits which cannot be invaded by their alternative allele (like the selfishness allele here) are called Evolutionary Stable Strategies (ESS) (Maynard Smith 1972)

So why ARE animals so often nice to each other?
5 reasons:
1) Humans are weird
2) Reciprocal altruism
3) Kin selection
4) Best of a bad job
5) Mutualism

True altruism?

Only apparent altruism

We will discuss each of these, but not in that order.
Humans are weird.

They do air-sea rescue, adopt children, go to war, give blood, help strangers, etc. etc. Individual fitness would certainly be higher if they didn’t.

Unfortunate carry-over of our instincts from a time when all our neighbours were our relatives? (Richard Dawkins thinks so)

Is effective policing of invading selfish beings enough to allow altruism to persist?

Yes, but who benefits by being the policeman? Arguments abound.

Think about it during the rest of these lectures.

Best of a Bad Job (I)

Shelduck run a creche for all the chicks of the group.

Everyone takes their chicks to the creche, then goes off to feed, but one female stays with the chicks. Why does she stay and miss feeding time?

Answer: she doesn’t want to, but she was the last there. If she abandoned the young, there would be no-one to look after them so they’d all be eaten by the gulls, including her own.

She stays, and looks after all the chicks so that her ones (who stay closer to her) have a smaller chance of being eaten because the gulls are busy eating the other shelducks’ chicks.

Best of a Bad Job (II)

Why does the reed warbler feed the cuckoo chick even though it’s obviously not its own?

Fitness benefit to reed warbler = 0
Fitness cost = no chicks this year, fewer next year, + 1 more cuckoo.

Why doesn’t it evolve the ability to recognize the cuckoo and stop feeding it?

A cost of flight is having to be small and light. Brains are heavy and cost a huge amount of energy, so birds must cut corners.

They have “Rules of Thumb”. e.g. “If it’s in my nest, feed it.”

Rules of Thumb and releasers

These are good enough as long as the times they break down are rare. If cuckoos are rare, it’s better to take the risk you won’t meet one and keep your rules simple.

Feeding is triggered by a simple releaser such as a large gape.

This can lead to some amazingly odd behaviours such as this cardinal feeding a goldfish.

The goldfish has learned to give the releaser, and trigger the cardinal’s feeding behaviour.
Kin Selection

e.g. parental care

This stink bug will put her own body between any predator and her babies, shielding them from view as far as possible.

Several birds, like this kildeer, will pretend to have a broken wing in order to distract predators from their nest.

In both cases it would be safer to run away, but parental care seems obvious, as the young ARE the fitness of the adult.

However, i) this year’s kids are traded off against next year’s.

ii) Our empathy with the parents just indicates we are evolved to do the same. It doesn’t explain why.

Care level (= altruism) depends on how closely related you are.

Willie Hamilton 1964 described this quantitatively with his coefficient of relatedness (r)

It is the chance that one of your alleles is present in a relative’s genotype.

Inclusive fitness

It is not only your immediate family who may share your genes.

All your “blood relatives” do, but the more distant the relation, the lower the chance of them sharing genes with you.

So their fate is part of your inclusive fitness.

Inclusive fitness is the effects of an individual on gene propagation

1) Directly in the bodies of surviving offspring that owe their existence to the parent’s actions, not to the efforts of others, and

2) Indirectly via non-descendent kin that owe their existence to the altruist’s helpful actions.

Alcock 1993
Calculating the Coefficient of Relatedness ($r$)

$$r = n(0.5)^L$$

where:
- $n$ = number of routes along which a gene could be passed
- $L$ = number of generation links between them

Full siblings

$$r = 2(0.5)^2 = 0.5$$

Grandparent and grandchild

$$r = 1(0.5)^2 = 0.25$$

You don’t always die being altruistic!

The cost of the action, and the benefit to the recipient are important as well as how related they are to you.

**Hamilton’s Rule**

“Be altruistic if the cost to you is less than the benefit to the recipient times your coefficient of relatedness to them.”

i.e. when $C < rB$

$C = \text{cost to the altruist in terms of genetic investment lost}$

$B = \text{benefit to the recipient in terms of fitness gained}$

$r = \text{coefficient of relatedness}$

$rB$ is actually the inclusive fitness benefit of the action to the altruist

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Aphids release an alarm pheromone when attacked. This cannot save them, and costs energy to make.

It is an altruistic warning to the others, who run away.

Aphids are parthenogenic so 100% of their genes are shared with their offspring. So if the chemical saves one offspring, it’s equivalent to saving the attacked aphid’s life, so it’s worth making.

Lord Robert Winston asked 2 groups of people to hold their head underwater for money. The longer they stayed, the more they earned, but the money was given in Group 1 to their sibling or in Group 2 to their best friend.

Even if they liked their friend better than their relative, they always held on longer for the sibling.

**Kin Selection in Belding’s Ground Squirrel**

Give alarm calls warning of approaching predators.

Carries a cost as predator’s attention is attracted to caller.

Not everyone calls equally often and kin relatedness explains why.

Young males never call, because they disperse to a new group, so have no relatives in the group.

Older males occasionally call as some of the young are theirs.

All females usually call, as young females make burrow close to mother’s so most females in the colony are close relatives.

So cost incurred in direct proportion to relatedness to colony.
If animals are to be altruistic in proportion to how related they are, they need some method of **kin recognition**

This has to be a whole lot more sophisticated if you leave your offspring in a massive creche.....

... than if you block them into a hole from which they can’t escape. A simple rule of thumb is likely to be fine here!

Animals use odours, colours, position, timing. Parasites and predators exploit these to get the benefits aimed at kin. It’s a fun topic, dealt with in my Behavioural Ecology 3rd yr class, but look up “kin recognition” and you can read about it in any animal behaviour textbook.

**Naked Mole Rat**
Diploid but highly eusocial with queen producing all babies and others specialised for other jobs.

Why don’t the other females leave and breed themselves?
Inclusive Fitness is higher if they produce siblings. This is because high levels of inbreeding has reduced genetic variation, so whole colony has very similar genes. So siblings have $r > 0.5$.

If breed with a neighbour (who has different genes), then the offspring will have $r = 0.5$ with mother.
I.e. better inclusive fitness to raise siblings

Sociality in hymenoptera is partly explained by coefficients of relatedness
Haplodiploidy = males haploid, females diploid

![Diagram of relatedness](image)

The workers are more related to their sisters than they would be to their offspring, so helping create sister queens is better than breeding themselves.

Kin selection explains a lot of cases of altruism but what about cases where unrelated animals help each other?

**Before next lecture** read “Born to Trade” by M. Ridley, New Scientist 26th Oct. 1996

**Also read at least two of:**
Freeman and Herron Chapter 11
Skelton Chapter 6
Krebs and Davies Chapter 11
*Unravelling Animal Behaviour* 2nd ed. by Marian Stamp Dawkins1995; Longman, Chapter 3

**Highly Recommended:**
"Indiscriminate Altruism: unduly nice parents and siblings" by L. Keller, TREE 12, March 1997