**Kin and Group selection**

Social interactions between organisms present the opportunity for **conflict** and **cooperation**

Interaction between individuals can have 4 possible outcomes on the fitness of the 2 individuals involved:

<table>
<thead>
<tr>
<th>Performer benefits</th>
<th>Performer suffers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>Altruism</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Selfish</td>
<td>Spiteful</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- **Performer benefits**
  - Cooperation
  - Selfish
- **Performer suffers**
  - Altruism
  - Spiteful

**Social interaction**

**Cooperation**, or mutualism, results in fitness gain for both participants

Example: **symbiosis**, like between corals and zooxanthellae - hard corals cannot obtain enough nutrients by feeding - symbiotic dinoflagellates provide carbohydrates from photosynthesis in exchange for nitrogen from the coral

<table>
<thead>
<tr>
<th>Performer benefits</th>
<th>Performer suffers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>Altruism</td>
</tr>
<tr>
<td></td>
<td>Selfish</td>
</tr>
<tr>
<td></td>
<td>Spiteful</td>
</tr>
</tbody>
</table>

**Social interaction**

**Selfish** actions benefit the performer and hurt the receiver

Typical examples include predation and parasitism— one organism exploits another to increase its own fitness

Also, sexually antagonistic actions that benefit one sex at the expense of the other

<table>
<thead>
<tr>
<th>Performer benefits</th>
<th>Performer suffers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>Altruism</td>
</tr>
<tr>
<td></td>
<td>Selfish</td>
</tr>
<tr>
<td></td>
<td>Spiteful</td>
</tr>
</tbody>
</table>

**Social interaction**

**Spiteful** actions hurt both parties

- no known examples of spiteful behavior in nature

Text claims "an allele that results in fitness losses for both actor and recipient would quickly be eliminated by natural selection"— do you believe this is necessarily true? how might such an allele persist, despite hurting the performer?

<table>
<thead>
<tr>
<th>Performer benefits</th>
<th>Performer suffers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>Altruism</td>
</tr>
<tr>
<td></td>
<td>Spiteful</td>
</tr>
</tbody>
</table>

**Social interaction**

**Altruism** is the case where the performer suffers in order to benefit the recipient of the action

Example: a dolphin rams into the side of a shark that is trying to eat me

<table>
<thead>
<tr>
<th>Performer benefits</th>
<th>Performer suffers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperation</td>
<td>Altruism</td>
</tr>
<tr>
<td></td>
<td>Selfish</td>
</tr>
<tr>
<td></td>
<td>Spiteful</td>
</tr>
</tbody>
</table>
Different levels of selection

- **Individual level natural selection**: Natural selection that occurs because some individuals have higher fitness than other individuals.
- **Group selection** is defined as the evolution of traits because they decrease the chance of a population going extinct.

Group selection
Wynne Edwards theory (1961)

- His belief that animals that helped, or failed to mate, did so for the ‘benefit’ of the group, therefore such behaviours produce increased ‘survivorship’ of groups whose members acted *selflessly*.
- Thus, selection occurs at the level of the ‘GROUP’, not the level of the ‘individual’ as in Darwin’s ideas!

Why invoke Group selection?
- **Altruism in animal societies**
  - Darwin suggested animals should behave ‘selfishly’ & strive to produce as many offspring as possible.
  - Some traits exist that can’t be explained through individual level selection!
    - e.g. decreased individual fitness (decreased reproduction?)
  - Some animals behave in ways which increase the survival & reproduction of other members of the group/species, at a cost to one’s own survival/reproduction = Altruism.
  - Why else did some animals such as sterile workers of social insects (e.g. ants, termites) forego breeding altogether to help their colony!
  - Behaviours good for the group but bad for individual? Darwin wrote that this “…at first appeared to me… actually fatal to my whole theory,” because altruism is so common in nature

Examples of Altruism

- Baby-sitting in meerkats?
  - Baby-sitters don’t breed but work hard!
- Alarm calls in prairie dogs?
  - Risky behaviour - more likely to be attacked by a predator!

For the good of the species or group?

- Territorial behaviour & communal displays such as leks & roosts (e.g. grouse) was once thought to exist for the “good of the species”!
- Idea that by spacing themselves out in a habitat, members of the same species avoided depleting their food resources & causing a population crash.
- Animals did not over-exploit resources but were prudent farmers!
- If in danger of diminishing their food supply, they would reproduce less!
- So individuals sacrifice themselves for the benefit of others?

Group selection to explain altruism?

- Theory of group selection is now rejected by most behavioural ecologists today.
  - **WHY?**
    - If it is the ‘survivors’ who transmit their characteristics to future generations, it’s difficult to see how does altruistic behaviour persists in population, according to group selection arguments?
Randomly distributed genes:
R = “risky” altruistic genes
e.g. those for giving alarm calls
S = selfish genes

**Group selection is only a weak force because...**

| S | S | S | R | S | S | S | S | R | S | S | S | S | R | S | S | S | R | S | S | S | R | S | S | S | R | S |

- Those individuals lacking the “risky” genes would survive (S).
- For instance, they may be warned about predators with no risk to themselves.
- Thus, their chances of reproduction would be greater.
- So selfish alleles (S) would spread rapidly, eventually eliminating risky genes (R) from the gene pool.

**Randomly distributed genes:**

- **Group selection is NOT likely to occur because...**

- Individually selected “Cheats” immediately benefit and spread through individual selection.
- The life cycle of groups is slow relative to that of individuals.
- E.g., Individuals reproduce & die much more rapidly than groups divide & become extinct.
- So selection at the level of the individual MUST override the level at the group.

So how do we account for phenomena of altruism & sterility?

**Levels of selection**

- **Individual level natural selection**: Natural selection that occurs because some individuals have higher fitness than do other individuals.
- **Group selection** is defined as the evolution of traits because they decrease the chance of a population going extinct. (mostly unlikely but think about it!)
- **Kin selection** the evolution of traits because they are passed on by the relatives (the kin) of individuals who express the traits.

**Group selection & infanticide in Lions?**

- Lions live in social groups called ‘prides’
- Prides taken over by groups of incoming males
- Incoming males kill infants in the group

**WHY?**

- Group selection arguments contend that death of infants benefits species by reducing population size & conserving resources!

www.lionresearch.org/behavior_guide/ infant.html

Craig Packer & Anne Pusey

**Selfish or individual selection & infanticide?**

However, infanticide benefits **perpetrators**!

- Incoming males receive reproductive benefits because mothers of dead infants respond by coming into estrous.
- Nursing mothers do not ovulate, so females ready to be fertilized.
- Instead of spending years rearing unrelated young, new males kills them & fathers own offspring.

- Behaviour NOT for the good of species!
- BUT exists because alleles that encourage selfish behaviour increase in frequency!

**Group selection is NOT likely to occur because...**

- Individually selected “Cheats” immediately benefit and spread through individual selection.
- The life cycle of groups is slow relative to that of individuals.
- E.g., Individuals reproduce & die much more rapidly than groups divide & become extinct.
- So selection at the level of the individual MUST override the level at the group.

So how do we account for phenomena of altruism & sterility?

**Kin selection (after Maynard Smith 1964)**

- Sexually reproducing organisms do not produce exact copies of themselves. But leave copies of part of their genome to their offspring.
- Gene copies are not only shared between parents and offspring but also with relatives by descent.
- An individual may act altruistically, even at great risk to it’s self as it helps increase the representation of it’s alleles in the gene pool by helping relatives.
- Helping closely related individuals increase the number of copies of shared genes hence the “inclusive fitness” of the helper.
Inclusive fitness

The relative number of an individual's alleles that are passed onto future generations, **both**

- **directly**, as a result of an individual's own reproductive success, and also indirectly,

- **indirectly** when the individual helps relatives, who also carry a proportion of their alleles, and who reproduce more because they receive help from this altruistic individual.

Evolution of altruism

Traits that lower personal fitness can survive natural selection if they increase fitness of close relatives

You only pass 50% of your alleles to each offspring

On average, you share 50% of your alleles with each sibling

Therefore, when your parents produce another child, it's the same as if you reproduced yourself: a new individual is created that shares 50% of your alleles

Similarly, if a sibling produces 2 offspring it's equivalent to you producing one offspring yourself

Kin selection

- If recipient of the altruist's help are kin to the altruist, it is likely to carry the same alleles, including the 'allele' for altruism.
- The allele for altruism can be reproduced by the individual who receives help.
- It may be reproduced so much that it increases in the population, even though the altruist itself does NOT reproduce it very much.
- Since the most closely related animals share most genes by common descent, expect altruism to be common amongst closely related individuals.
- To understand this better need to know concept of the Coefficient of relatedness, \( r = \frac{\text{proportion of one individual's genes (or alleles) that are identical by descent with those present in another}}{1} \)

Diploid species

Female A has exactly half her genes in common with her mother B

In common with her sister, she has, on average, half the genes inherited from her father and half of those from her mother

Coefficient of relationship

Genetic model was proposed in 1964, showing how an allele that promoted altruism could spread

Depended on the coefficient of relationship, \( r \)

- Probability that 2 copies of an allele, in 2 different individuals, are identical by descent from a common ancestor

A coefficient of relationship, \( r \), is calculated using a pedigree that shows how the performer and recipient of the action are related
Path analysis:

1. Start with the performer
2. Trace all paths of descent through the pedigree to the recipient
3. Determine odds that an allele was passed along each arrow
4. Multiply the odds for each path
5. Add the odds for all paths together

--the odds that an allele was passed from the common parent to both siblings is just \( r = \frac{1}{4} \)

--since we have only one path, the odds that an allele was passed from the common parent to both siblings is just \( r = \frac{1}{4} \)
---with full siblings, there are two ways the same allele can be passed to both offspring: through the mother or the father

\[
\begin{align*}
\text{mother} & \rightarrow 1/2 \rightarrow 1/2 \\
\text{father} & \rightarrow 1/2 \rightarrow 1/2 \\
\end{align*}
\]

\[
(1/2)(1/2) = \frac{1}{4}
\]

\[
(1/2)(1/2) = \frac{1}{4}
\]

add the probabilities for each path: \( r = \frac{1}{4} + \frac{1}{4} = \frac{1}{2} \)

---

**Coefficient of relationship**

<table>
<thead>
<tr>
<th>full siblings</th>
<th>mother</th>
<th>father</th>
<th>mother</th>
<th>father</th>
</tr>
</thead>
<tbody>
<tr>
<td>performer of action</td>
<td>⬅️</td>
<td>⬅️</td>
<td>⬕️</td>
<td>⬕️</td>
</tr>
<tr>
<td>recipient</td>
<td>⬕️</td>
<td>⬕️</td>
<td>⬕️</td>
<td>⬕️</td>
</tr>
</tbody>
</table>

---

**When altruism? Hamilton's rule**

(1964)

- Selection favours genes for altruism if
  \( r b - c > 0 \)

if \((\text{benefit})(\text{degree of relatedness}) - (\text{cost}) > 0\), the allele spreads

where \( r \) is relatedness to beneficiary

- \( b \) is benefit in fraction of **additional** offspring resulting from helping
- \( c \) is cost to altruistic individuals from helping (what opportunity is given up)

---

**What makes \( b \) and \( r \) larger and \( c \) smaller?**

- Ecological constraint: Shortage of food or good breeding sites are scarce, for example, individuals may not be able to reproduce very much without ‘help’ (low \( c \))
- High Benefit to helping: (high \( b \))
- Genetic system & resulting relatedness?

---

**Kin Selection**

When natural selection favors the spread of alleles that increase **indirect** fitness, **kin selection** results

- kin selection = natural selection based on indirect fitness gains
- most instances of apparent altruism result from kin selection

Example: alarm calling

- in many mammals, individuals that see a predator approach produce an alarm call to warn others of their species
- often, this exposes the caller to added danger

---

**Alarm calling: Belding’s Ground Squirrel**

- Highly social mammal; breeds in colonies
- Females tend to breed near their birthplace
- Neighbors are often closely related
- Produce alarm calls when predators approach

13% of alarm-callers are chased by predators; only 5% of non-callers are chased

How did this evolve?…
Females were much more likely to call than males.

Females were much more likely to call when they had a close relative nearby—thus, altruistic actions are not randomly distributed.

Mothers-daughters and sisters were also more likely to cooperate in chasing trespasser squirrels off their territory.

Thus, the degree of cooperation depends on the degree of relatedness between females.

John Hoogland dragged a stuffed badger through Prairie dog colony & recorded identity of alarm callers & listeners during 125 expts.

At least 200 bird species with young fed by more individuals than just the breeding pair.

Most cases ‘helpers’ are close relatives; often offspring of that pair from previous broods.

Example: white-fronted bee-eaters

Merops bullockoides

Emlen (1990); Emlen, Wrege & Demong (1995)
Kin Selection in White-Fronted Bee-Eaters

In many birds, young will help their parents rear new offspring, rather than go off and reproduce themselves.

New offspring may be full or half-siblings of the young helpers.

Common in species where opportunities for breeding or new nest construction are limited.

In these cases, the young helping their parents may be making the best of a bad situation.

Emlen (1990); Emlen, Wrege & Demong (1995)

An extended family

- At the heart of bee-eater society is the extended family.
- This is a multi-generational group of 3–17 individuals.
- Typical family is 2–3 mated pairs plus an assortment of single birds (unpaired & widowed).
- 15–25 families (100–200 birds) nest in a colony.

Emlen (1990); Emlen, Wrege & Demong (1995)

Mating system & Colonial breeders

- Nests are excavated in sandy cliff faces.
- Birds dig metre long tunnels that end in enlarged nest chambers.
- Late in the afternoon all bee-eaters congregate at their colony to socialize & roost.
- Once paired, bee-eaters are socially monogamous, exhibiting high mate fidelity.
- Males are philopatric (stay at home) & females disperse (so are unrelated to her mates family).

Emlen & Wrege (1992) Nature

bee-eater ‘helpers’?

- Some first-year males do not reproduce. Instead, they feed & defend the brood produced by their father’s.
- In harsh years, fathers actively destroy their son’s nest &/or clutch. Following this act of destruction, their son will act as a helper’s to its father & his mate (sometimes, but not always his mother).
- Why should sons forego reproduction & help?
- Calculate fitness costs & benefits for participants to clarify why parents recruit & helpers ‘help’.

Emlen & Wrege (1992) Nature

Kin Selection in White-Fronted Bee-Eaters

(1) Unrelated birds that have “married” into a clan are much less likely to help than a blood relative born into the clan (= natal, or by birth)

birds that haven’t yet reproduced

(2) Young selectively help adults they are more closely related to -coefficient of relatedness predicts how help will be distributed

This makes a huge difference to parents.

Half of bee-eater babies starve to death before leaving the nest.

Each 1-yr old helper results in 0.47 more offspring being successfully raised --major boost to inclusive fitness.

Kin Selection in White-Fronted Bee-Eaters

(1) Unrelated birds that have “married” into a clan are much less likely to help than a blood relative born into the clan (= natal, or by birth)

birds that haven’t yet reproduced

(2) Young selectively help adults they are more closely related to -coefficient of relatedness predicts how help will be distributed

This makes a huge difference to parents.

Half of bee-eater babies starve to death before leaving the nest.

Each 1-yr old helper results in 0.47 more offspring being successfully raised --major boost to inclusive fitness.
3. Feeding of juvenile bee-eaters & survival

Food varies unpredictably (flying insects) so it’s not easy for a pair to find sufficient food for their brood near the colony, so ‘helpers’ are crucial.

<table>
<thead>
<tr>
<th>Number of adults at the nest</th>
<th>Total provisioning rate to nest (feeds per hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>5</td>
</tr>
</tbody>
</table>

No. of adults at the nest affects rate at which juveniles are fed & is closely associated with no. birds that survive to fledgling.

Evidence ‘helping’ in bee-eaters evolved via Kin selection:

1) Both males & females help but MANY more males than females.
   - Why?
     - Males are philopatric (stay at home) & females disperse so live in groups that are unrelated to her mate's family.
   - Thus, many first-year males do not reproduce. Instead, they feed & defend the brood produced by their father’s.

2) Individuals do not gain anything other than ‘inclusive fitness’ by helping.
   - ‘helpers’ are not more successful when they become breeders themselves than those birds that did not help.
   - In harsh years, fathers actively destroy their son’s nest &/or clutch. Following this, their son will always act as a helper’s to its father.

4. Relatedness & altruism in bee-eaters

• Helper’s gain in indirect reproductive benefits (i) is proportional to degree of genetic relatedness between helper & juvenile being helped.
• Degree of genetic relatedness = strong predictor of probability that one bee-eater will help another.

Summary: Relatedness & helping

• As with all diploid animals, bee-eaters are closely related to it’s siblings as it is to it’s offspring (r =0.5), so benefits will accrue from rearing either.
• So helping to produce an extra brother/sister has exactly the same impact on fitness as producing a son/daughter.
• Degree of genetic relatedness is strong predictor of probability that one bee-eater will help another.
• Kinship very important component in white fronted bee-eater society.

Evolution of altruism does not depend only on r but also b & c

When to help?

\[ r b - c > 0 \]

b = high
Benefit is high for males (philopatric; so rear extra kin) but low for females (disperse, unrelated to pairs)

\[ c = \text{low} \]

1st yr bee-eaters = poor parents, restricted food, unlikely to succeed loss of reproduction not large

Measuring relatedness?

• Given the importance of kinship in evolutionary theory need accurate relatedness.
• Females mate with more than 1 male; extrapair matings, & these can’t always be observed.
• Genetic methods such as DNA fingerprinting (Jeffreys et al. 1985) can be used instead
• based on minisatellite repeats, same short sequence repeated many times (like a bar code on food in Supermarkets)
• Sequences are identical within individuals but highly variable (hypervariable) between individuals
• Close relatives share many sequences & hence bands on a Fingerprint gel
Evolution of Eusociality & kin selection

Eusociality in hymenopterans, ants, termites, mole rats. ‘Ultimate altruism’ is applied to a group displaying 3 traits:

a) cooperation in caring for young

b) reproductive division of labour, with more or less sterile individuals working on behalf of the individuals engaged in reproduction

c) overlap of at least 2 generations of life stages capable of contributing to colony behaviour

Why are hymenoptera social?

Sex determination? Haplo-Diploid species?

The unusual genetic system of social insects makes eusociality a likely consequence of kin selection

In haplodiploidy, sex is determined by chromosome number

- males develop from unfertilized eggs, are haploid
- females develop from fertilized eggs, are diploid

Sons do not have fathers, only mothers

Sisters get the same set of chromosomes from their father, but have a 50% chance of getting the same allele from their mother

Why are hymenoptera social?

Sex determination? Haplo-Diploid species?

Unfertilized eggs hatch into haploid males

Fertilized eggs hatch into diploid females

Sisters are more related to each other (0.75) than they are to their mothers (0.5) !!!

Sex determination in social insects

Sisters are highly related to each other in haplodiploidy

Path #1

Path #2

Odds that one of sister A’s alleles came from mom = 1/2
Odds that mom gave an allele to sister B = 1/2
-odds of identical-by-descent allele for Path #1 is \( (1/2) \times (1/2) = 1/4 \)
Sex determination in social insects
Sisters are highly related to each other in haplodiploidy

Path #1
- mother (diploid) x father (haploid) = 1/2
- sister

Path #2
- mother (diploid) x father (haploid) = 1/2
- sister A x sister B = 1/2

Odds that one of sister A’s alleles came from dad = 1/2
Odds that dad gave an allele to sister B = 1 (his haploid genome)
- odds of identical-by-descent allele for Path #2 is
  \[
  \left( \frac{1}{2} \right) \left( 1 \right) = \frac{1}{2}
  \]

Combined odds of sisters sharing identical alleles:
(Path #1 odds) + (Path #2 odds) = (1/4) + (1/2) = 3/4

Because of this system, females are more related to their sisters
\((r = \frac{3}{4})\) than they are to their own offspring
\((r = \frac{1}{2})\)

Sex determination in social insects
Sisters are only distantly related to their brothers:
\((1/2)(1/2) = 1/4\) (only one path links sisters and brothers)

In haplodiploidy, females maximize their inclusive fitness by investing in the production of reproductive sisters, who are closer relatives than their own offspring or brothers

Evolution of cooperation among eusocial insects (ants, bees & wasps)
Haplo-Diploid species
- As sisters are more related to each other than to their daughters they cooperate & forego breeding themselves.
- They aid the Queen to produce more sisters, who are more closely related (75% related) than potential offspring (50% related).
- Allows the Evolution of queens, workers ..etc

Evolution of Eusociality? Termites?
- While haplo-diploidy appears to pre-dispose hymenoptera to high degree of sociality, sex determination is NOT the only factor in evolution of eusociality!
- High degree eusociality in termites? WHY?
  - diploid mating system
  - sterile workers of both sexes, with \(r = 0.5\)
  - King & queen long-lived (live for 60-70 years) & monogamous
  - Queen lays up to 36,000 eggs per day
- King & queen have millions of offspring in their lifetime but only a tiny fraction will ever reproduce!

Why are termite workers sterile?

Conflict of interest between queen and non-reproductive workers

Queen is equally related to sons and daughters \((r = 1/2)\)

Workers have \(r = 3/4\) with sisters, but only \(r = 1/4\) with brothers

Their fitness will be maximized when the queen produces a 3:1 sex ratio (more daughters than sons)

Who wins the conflict?

- in one species of ant, the queen laid eggs in a 1:1 ratio, but at hatching the sex ratio was biased towards many more females
- workers selectively destroyed male larvae
- assert their own reproductive agenda over the queen’s
Why are termite workers sterile?
• 3 variables in Hamilton’s equation: 
  When to help? 
  \[ r - b - c > 0 \]
  altruism does not depend only on \( r \) but also \( b \) and \( c \)
• High \( r \) predisposes towards helping as it increases \( b \)
• But even low \( r \) leads to helping if \( b \) were high enough & \( c \) low enough!
• \( C \) to each worker of being sterile = loss of offspring they would have had if they had not been helping the colony
• Given a pair of termites on their own would not survive, let alone reproduce, \( c \) of helping must be small (no hope of reproducing means no cost of losing it!)
• Monogamous nature of termite breeding = workers have a long series of brothers & sisters
• King & queen offer no parental care to young, without workers young would die!

How does this work still?
• Workers make a difference to the survival of close relatives
  BUT actual \( b \) for each worker is still small.
• Remember: 
  - Benefits of helping the colony are SUBSTANTIAL, 
    - \( c \) low
  - \( r \) at least as high between diploid parents & offspring
  BUT
• Termites live in deserts (or in very dry & arid regions)
• Can only do so as they live in mounds
• Mounds built by collective labours of millions of workers!
• Enables them to create their own microenvironment to survive
• Single pair of termites removed from this environment stands no chance!

This fact alone effectively reduces \( c \) & increases \( b \) of helping the royal pair in the colony!

Paper wasps: case of non-sterile workers
In many eusocial insects, workers are sterile and thus obligately non-reproductive (they don’t have a choice)
In paper wasps, workers are fertile, but usually don’t reproduce
3 possible strategies for a female wasp:
  1. start her own nest (be a founder)
  2. help at an existing nest (be a helper)
  3. wait for a later opportunity to breed (wait and see)
Multi-founder nests have the best chance of surviving, because if one founder dies, another can keep the nest going
  -21/51 multi-foundress nests survived loss of a queen
  -only 5/54 single-foundress nests survived loss of a queen

Facultative Eusociality
Multi-foundress nests grew fastest when there was a big difference in body size between the dominant queen and her subordinates
  -less time lost to challenges to the dominant queen by her underlings (fighting for the right to lay more eggs)
Why help instead of starting your own nest?…
Subordinates are close relatives of the dominant foundress

Facultative Eusociality
Possible strategies:
  -strike out on your own, risk it
  -help a close relative, thereby increasing your inclusive fitness
  -sit and wait: don’t help anyone, but wait for chance to steal a nest should a foundress die or you can beat her up later
  -leave nest in early spring, hibernate, try again next season
  --reproductive altruism is facultative, meaning it can be adopted depending on the conditions faced by a particular female
    -relatedness
    -body size
    -nest availability
    -time of year (season)
Why do unrelated individuals may behave altruistically?

- Kin selection helps us explain altruistic behaviour among relatives BUT what about between non-relatives? e.g. existence of danger warnings, sharing of food & grooming among unrelated individuals?
- Such behaviour can evolve through Reciprocal Altruism
- That is, if helpers are in turn recipients of beneficial acts by individuals they have helped (cooperation).
- If there is a genetic basis for these acts, then natural selection may increase the frequency of alleles governing these behaviours.

Reciprocal Altruism

In order for Reciprocal Altruism to be a significant evolutionary force several social conditions MUST be present:
- Individuals must associate for long-enough period of time to develop reciprocal interactions.
- Likelihood of one individual performing some social exchange with another should be predicted on the basis of their past associations
- The roles of giver and receiver should reverse at least once
- Short-term benefits to the recipient are greater than the costs to the donor
- Givers should be able to recognise and expel cheaters

- Examples: Man & primates

Reciprocal Altruism

Game Theory and Reciprocal Altruism

Developed by von Neumann and Morgenstern in the 1940s to model the behaviour of individuals in economic and adversarial situations
Adapted by Maynard Smith for cooperation
Individuals behave rationally and choose the action yielding the highest payoff
Individuals always benefit more than others if they cheat

This is a major barrier to social evolution
**Hawk-dove game**

Maynard Smith & Price 1973

- **Player 1**
  - Dove: 0
  - Hawk: -B

- **Player 2**
  - Dove: B
  - Hawk: -C

---

**Game theory**

- Optimal (rational) behaviour in conflict situations?
- “players” (genes, individuals, groups)
- may each choose a “strategy”
- Each pairs of strategies is associated with a “payoff”

---

**Prisoners Dilemma**

<table>
<thead>
<tr>
<th>Player B</th>
<th>Player B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Co-operates</td>
<td>R=3.3</td>
</tr>
<tr>
<td>Defects</td>
<td>–</td>
</tr>
</tbody>
</table>

- **Player A**
  - Co-operates
    - T=5.0
    - Reward for mutual cooperation
  - Defects
    - P=1.1
    - Punishment for mutual defection

---

**Summing up**

- Group selection is not a strong force in evolution
- Taking into account the genes shared by relatives (Kin selection) resolves the apparent paradox of altruism
- Altruists help spread their genes by helping their kin
- Altruism can exist between non-relatives under special conditions of reciprocal altruism

---

**Any gene that permits a cannibalistic bearer to recognize kin should be selectively favored**

<table>
<thead>
<tr>
<th>No kin recognition</th>
<th>Kin recognition</th>
</tr>
</thead>
<tbody>
<tr>
<td>after five generations: 6 survive</td>
<td>after five generations: 12 survive</td>
</tr>
</tbody>
</table>

By Hamilton’s rule, avoidance of inbreeding will be selectively favored when \( C = 1 - 1/D \).