Kin Selection Theory

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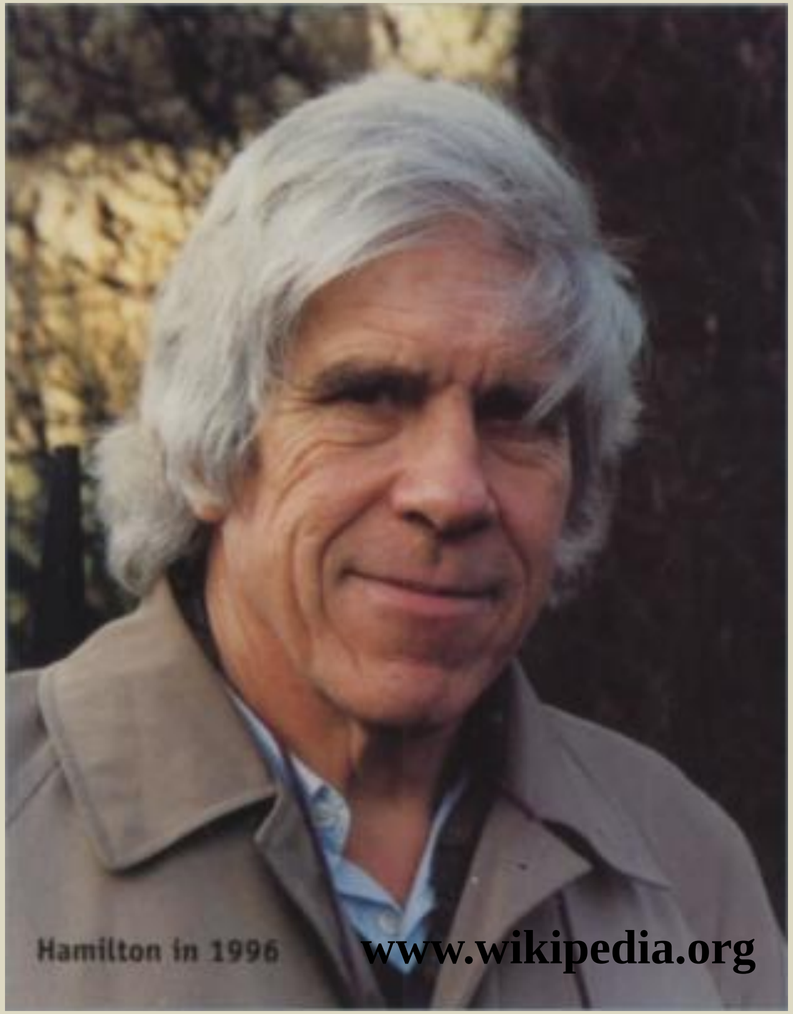
Kin Selection Theory

Also known as Hamilton's Rule or Inclusive Fitness Theory



W. D. Hamilton (1936 – 2000)

$$\mathbf{b/c > 1/r}$$

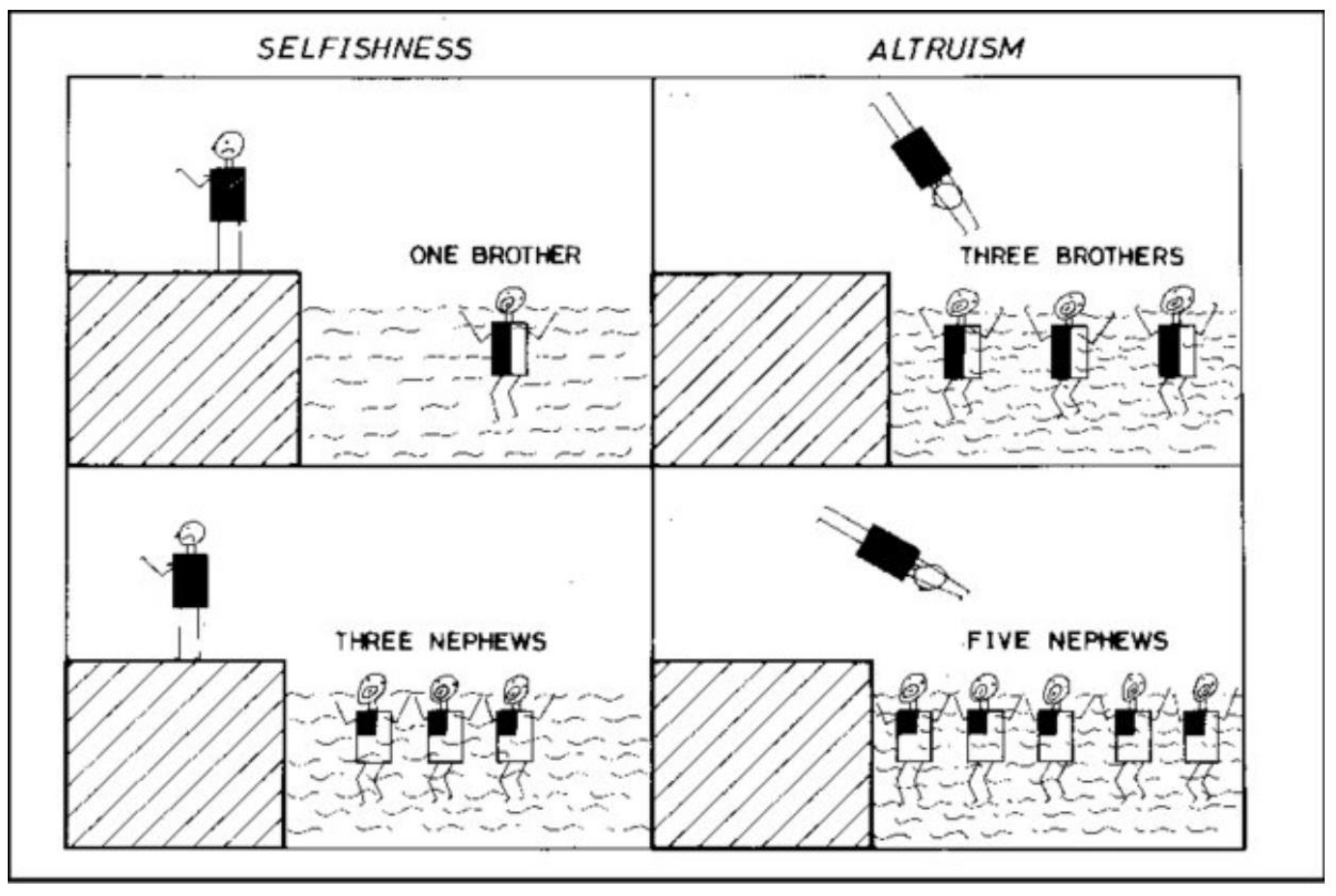
or

$$\mathbf{b.r > 1.c}$$

b = benefit to recipient
c = cost to the altruist
r = the coefficient of genetic relatedness between altruist and recipient

Note: Benefit and cost are measured in terms of surviving offspring

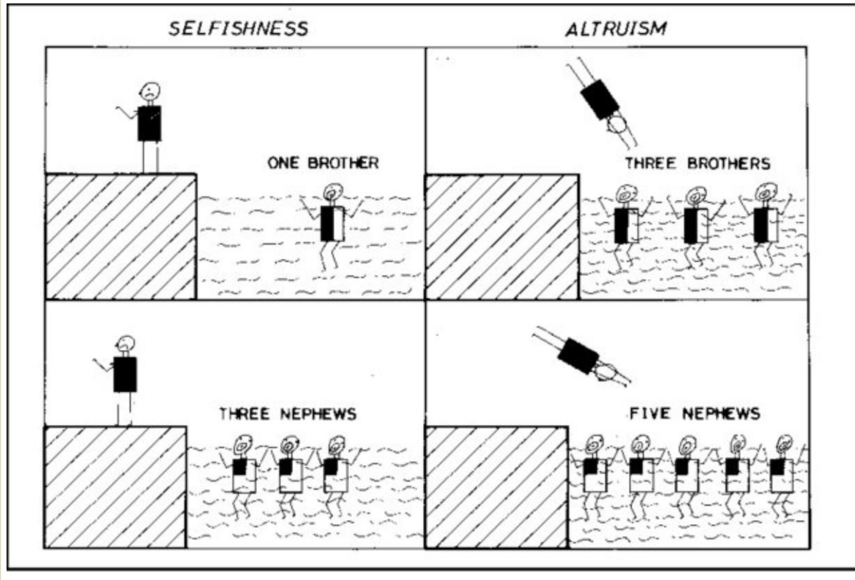
The Haldane Story



Question: When should you jump into the lake to save a drowning person?

Read the article by Prof. Gadagkar for the interesting anecdote. Also watch the “simplistic” video for the answer!

The Haldane Story



Why did Haldane come up with such a paradigm?

Humans would typically jump in save an unrelated drowning person.

Haldane used this paradigm to explain genetic relatedness and its role in the evolution of altruistic behaviour.

However, Haldane did not elaborate on his little essay on this idea further.

W. D. Hamilton used this very paradigm to propose the theory of kin selection, for his PhD thesis. However, Hamilton was unaware of Haldane’s essay.

Kin Selection Theory

How do you calculate “r”?

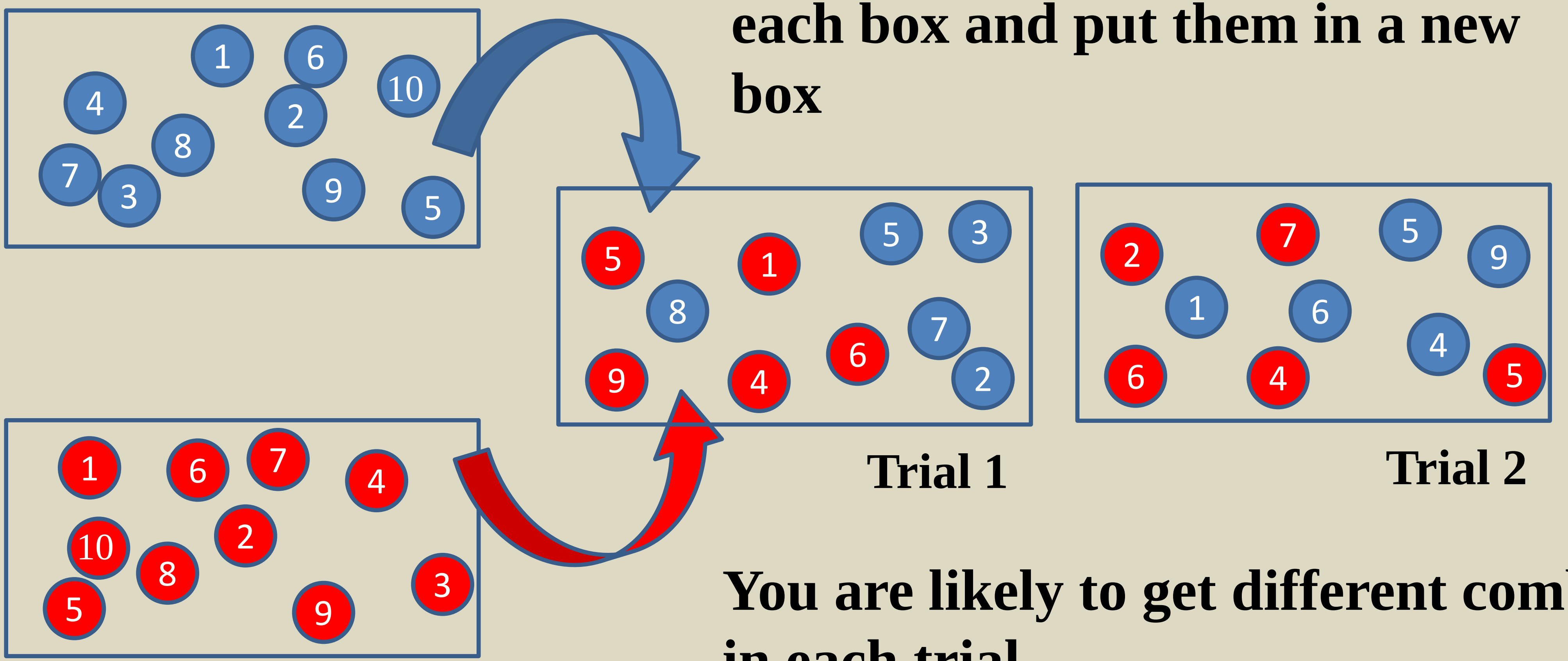
The genetic relatedness between two individuals is given by the proportion of genes shared between them.

In a diploid system of reproduction, every individual is 2n, having received half the set of their chromosomes from each parent. Hence we are all related to our parents by 0.5.

Let’s play a game!

Consider two boxes as below:

Randomly draw 5 balls from each box and put them in a new box

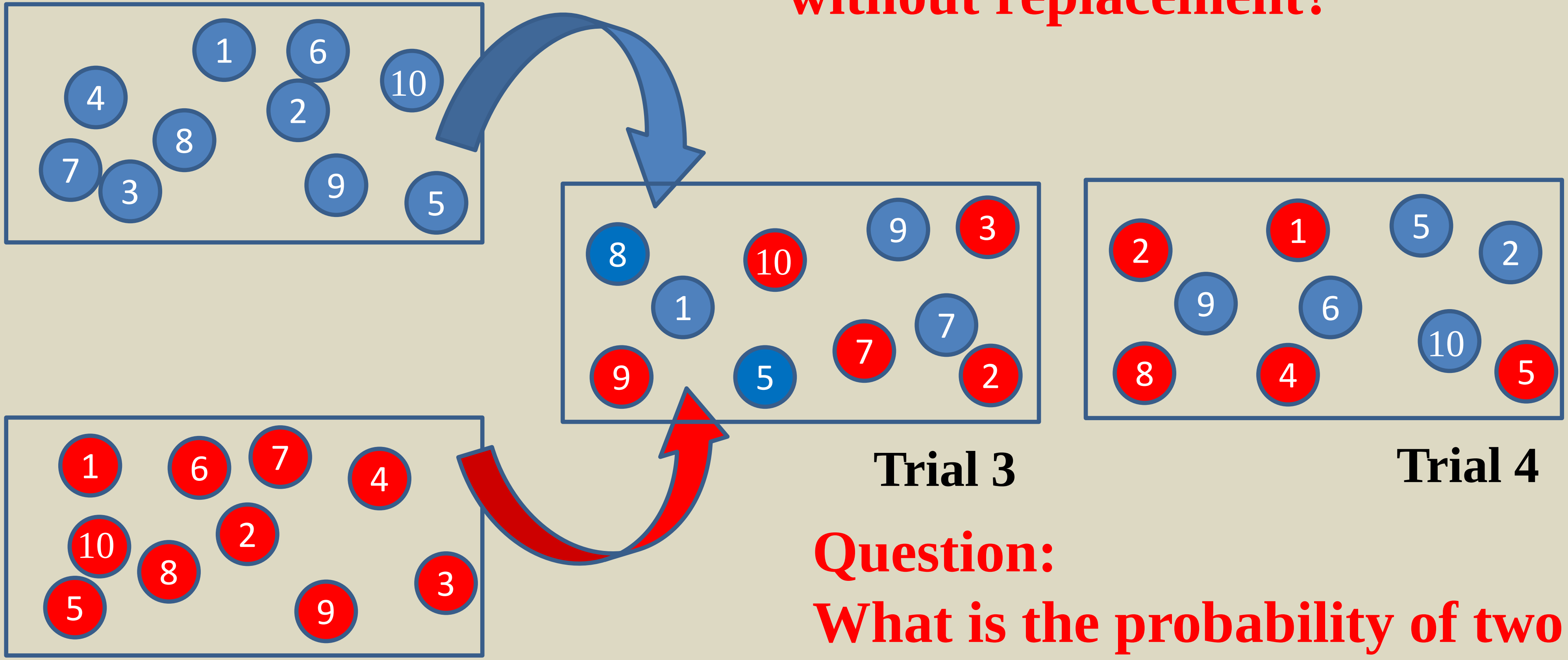


You are likely to get different combinations in each trial.

Let's play a game!

Consider two boxes as below:

Question:
What is the probability that you will draw the same ball again, if you do sampling without replacement?



Trial 3

Trial 4

Question:
What is the probability of two such sets being the same?

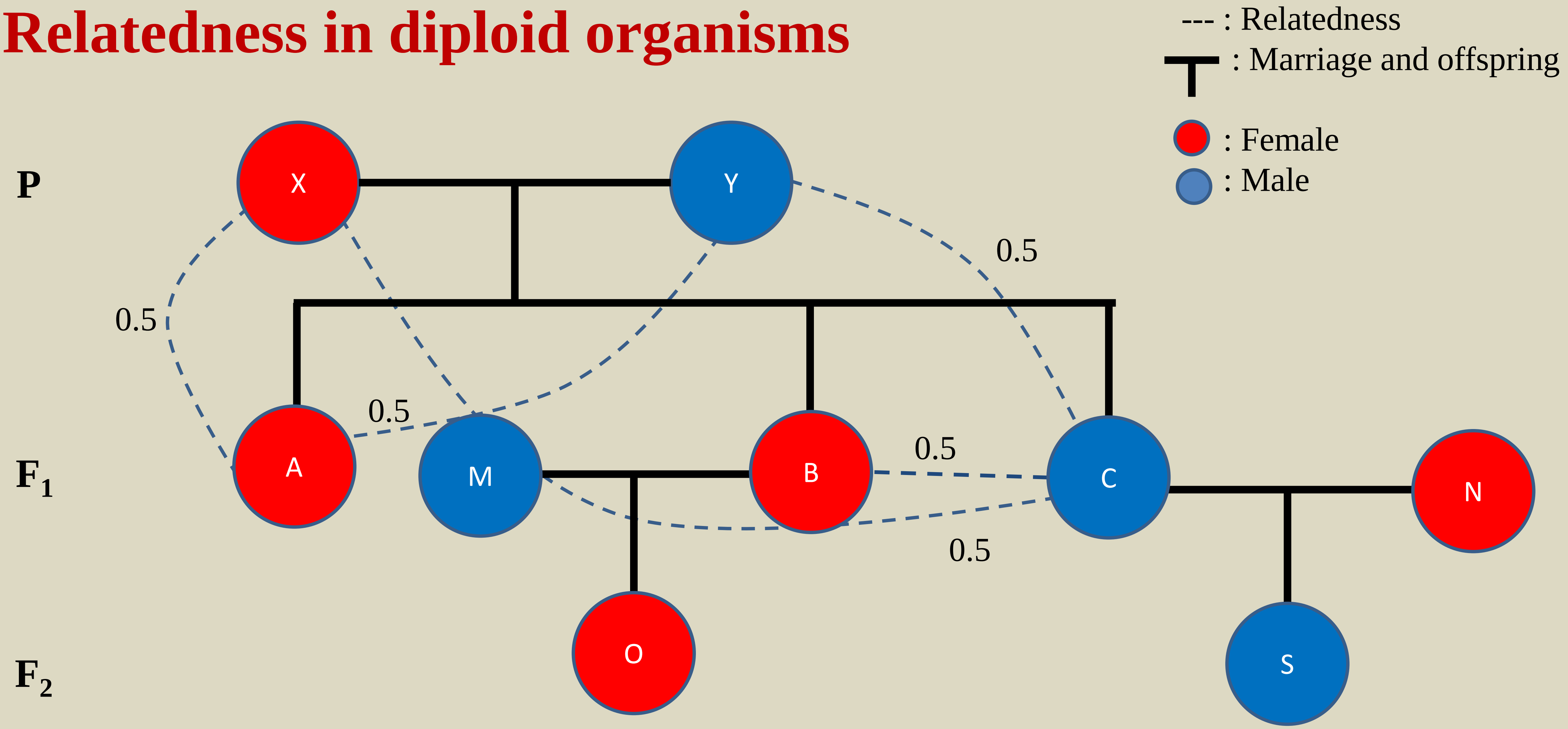
Let's play a game!

If we carried out a large number of trials, we would find 50% overlap between any two of the "offspring" boxes produced by such trials.

Since we draw half of the balls from each box in a trial, any "offspring" box would have 50% overlap with each of the "parent" boxes.

In case of diploid systems, you can simply replace these balls by chromosomes/genes, and the logic will remain unchanged.

Relatedness in diploid organisms



Each offspring carried 50% of the mother's and father's genes, each event of meiosis is sampling with replacement.

Relatedness in diploid organisms

What is the probability that A receives the same set as B from X? 0.5 X 0.5 = 0.25

What is the probability that A receives the same set as B from Y? 0.5 X 0.5 = 0.25

Therefore, probability of A and B sharing the same set of genes (two events occurring together) = 0.25 + 0.25 = 0.5

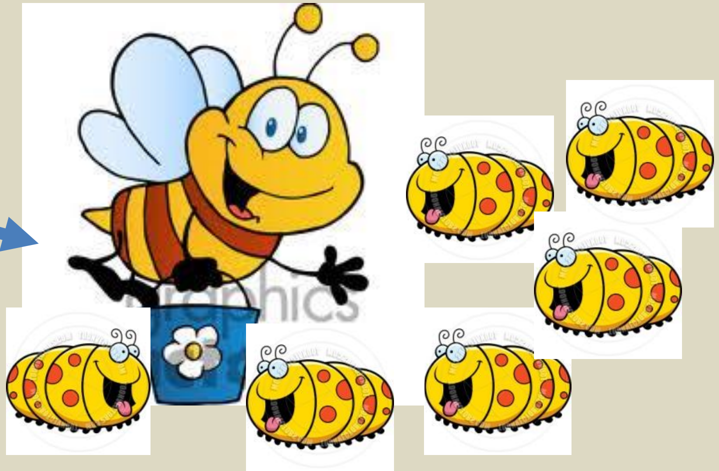
Thus all sibling are related to each other by 0.5, irrespective of their gender.

Now, consider Haldane’s story and Hamilton’s Rule.

While Hamilton proposed this Rule as a general theory for the evolution of altruism, he said that Hymenopterans (the family of insects to which ants, bees and wasps belong) are a special case with a genetic predisposition for the evolution of altruism, due to their haplodiploid genetic system.

Kin Selection Theory

Imagine a honeybee colony



Workers

Queen

WHY Do The Workers Work For the Benefit of the Queen?

Haplodiploidy

Bees, Wasps, Ants have a special genetic system called **Haplodiploidy**.

Males: n (produced by parthenogenesis from the mother's egg)

Females: 2n (produced by meiosis followed by fertilization)

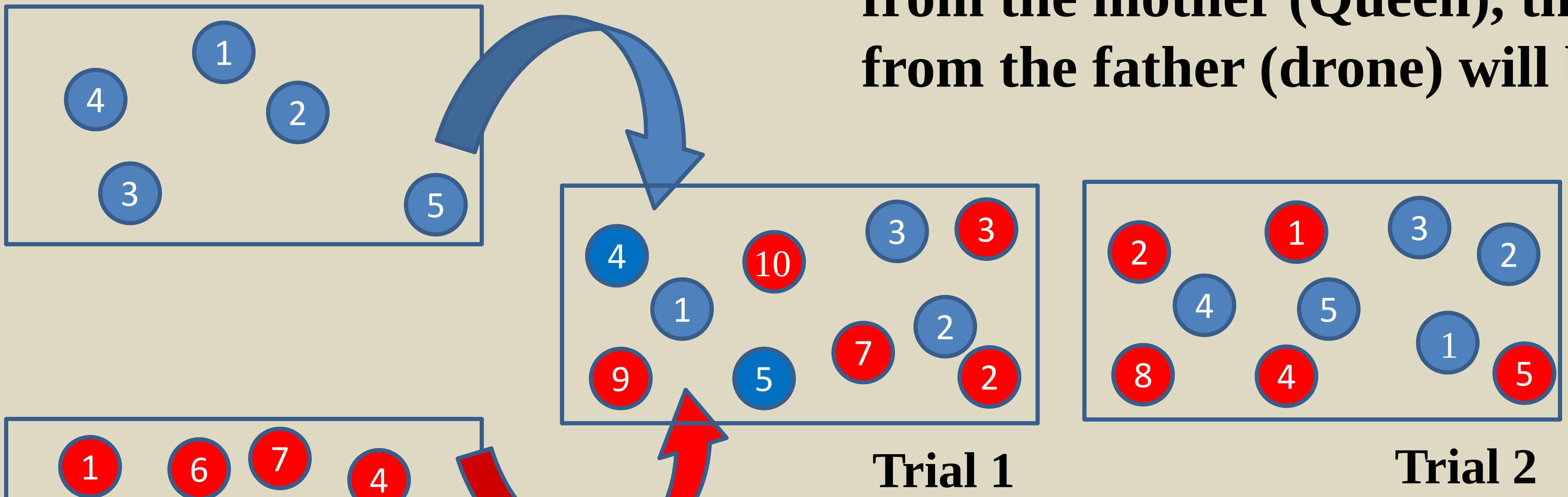
Males have no sons and no fathers, they are clones of their mother's eggs

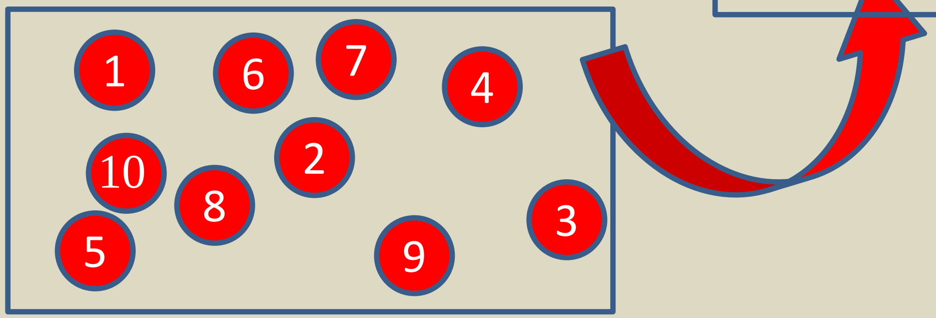
Why do you think Hamilton considered haplodiploidy to provide a special condition for the evolution of altruism?

Imagine the honeybees

Consider two boxes as before:

- Males are haploid, females are diploid.
- All sperms are clones of the male.
- Irrespective of the set of genes received from the mother (Queen), the set of genes from the father (drone) will be fixed.

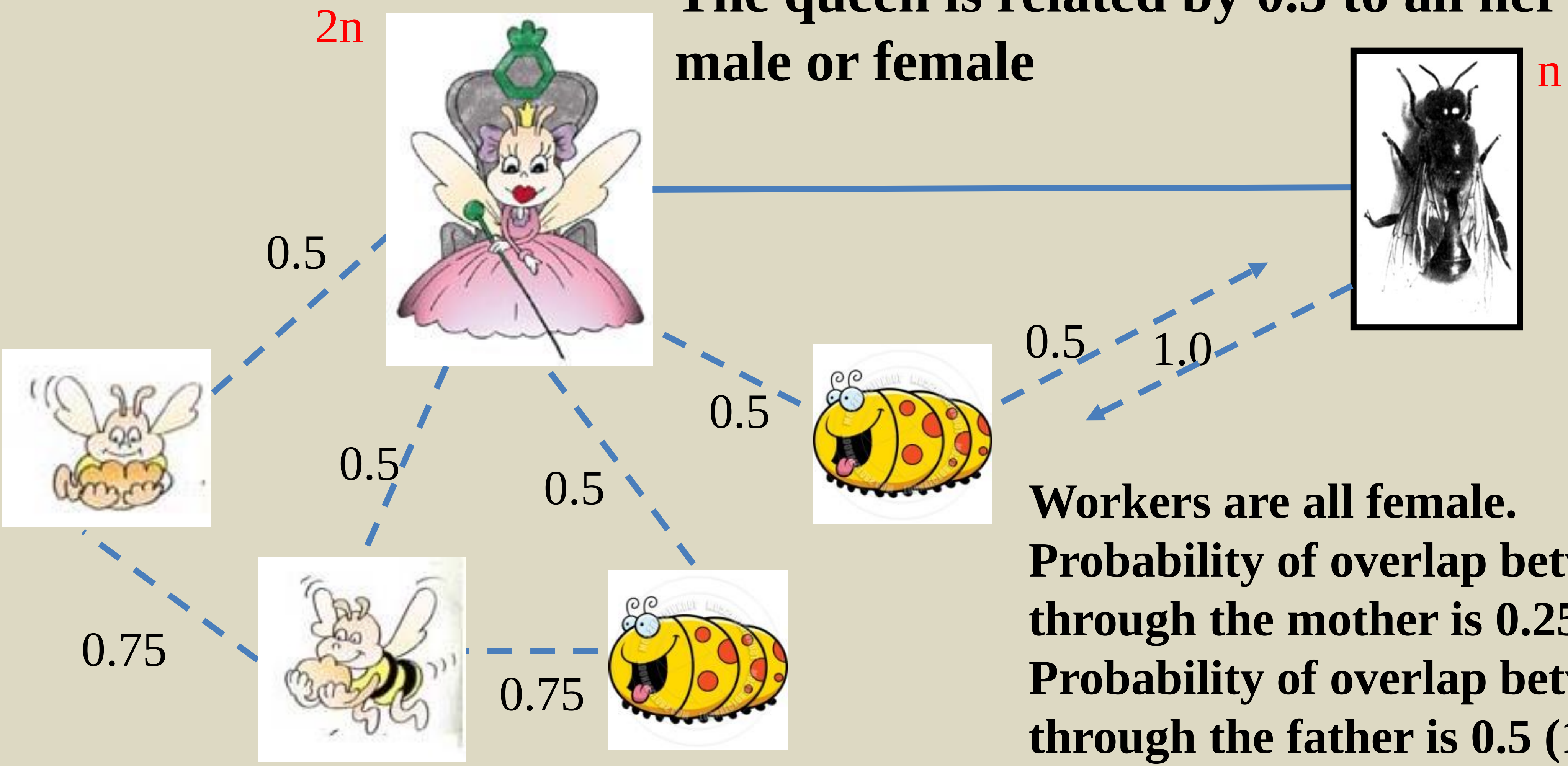




Relatedness will be skewed due to Hapldiploidy.

Imagine the honeybees

The queen is related by 0.5 to all her offspring, male or female



Workers are all female.
Probability of overlap between 2 workers through the mother is 0.25
Probability of overlap between 2 workers through the father is 0.5 (1/2 of 1)
So relatedness between 2 sisters: 0.25 + 0.50 = 0.75

Haplodiploidy

Using this logic, workers are related more to their sisters (Queen's brood) than to their daughters (0.5).

Workers are related to their sons by 0.5 and to their brothers (Queen's brood) by 0.25.

The queen is related to her brood by 0.5

The workers are related to their sisters by 0.75

If they could produce daughters, they would be related to their daughters by 0.5

Haplodiploidy

Thus, Hamilton proposed, that for a worker, helping to raise a queen's daughter is more beneficial than raising her own daughters (0.75 < 0.5)

If a worker sacrifices the opportunity to raise a daughter, her cost is 0.5 X 1, if she raises a sister instead, her benefit is 0.75 X 1. Thus b X r = 0.75, c X 1 = 0.5.

This gives them a genetic predisposition towards altruism.

If we consider male brood, the inequalities are reversed, as a worker would be related to her brother by 0.25 (only related through the mother) and to her own son by 0.5. She would be related to her sister's son by 0.125.

Haplodiploidy

So, in principle, a worker would gain by laying unfertilized eggs, that would produce sons.

However, in a system where workers are responsible for taking care of the brood, it would not be beneficial for the workers to tend to their sisters' sons.

Hence they would try to kill the sisters' sons. In fact, this kind of **worker policing**, where workers eat up each other's eggs, in the rare cases of workers laying haploid eggs, soon after they are laid, has been reported in honeybees.

In honeybees and many other social insects, workers cannot mate and are thus sterile, but can lay male (haploid) eggs.

Genetic predisposition

Solitary wasp

She needs to build the nest, lay eggs, forage to feed the brood, protect the brood from predators.

If a predator attacks when she is away, her fitness becomes 0.

Might produce 10-20 offspring (r = 0.5) in her life.

Workers don’t have any direct fitness.

But they can contribute to raising a large number of sisters (r = 0.75) and some brothers (r = 0.25).

Genetic predisposition

Hamilton proposed that due to haplodiploidy, the Hymenopterans had a genetic predisposition for the evolution of altruism.

Due to the skew in relatedness between females, it would be advantageous for workers to help their mothers raise more daughters.

Honeybees, ants and some wasps have reached an extreme level of such evolution, becoming **highly eusocial**. In such species, the queens and workers are morphologically different and the workers are functionally sterile.

This means that the workers are incapable of mating and producing daughters.

Evolution of sociality

However, not all Hymenopterans are highly eusocial.

Various species of wasps and some bees represent varying levels of social organization.

In **primitively eusocial** species, the queens and workers are morphologically identical and the differences are behavioural.

All workers are capable of mating and laying eggs, but they do not do so, when a healthy queen is present in the nest.

The level of queen control varies across species.

Evolution of altruism

This suggests that the extreme level of altruism (worker bees committing suicide to defend the nest) and highly eusocial conditions must have evolved from less social conditions.

Hamilton proposed the term **kin selection** to explain the benefits of altruism when the help is extended to genetically related individuals or kin.

According to kin selection theory, if a behaviour leads to a situation such that the benefit accrued by helping relatives is higher than the cost of not producing one's own offspring, then such "altruistic" behaviour would be naturally selected.

However, not helping or helping non-kin will not provide an advantage.

Criticism of kin selection

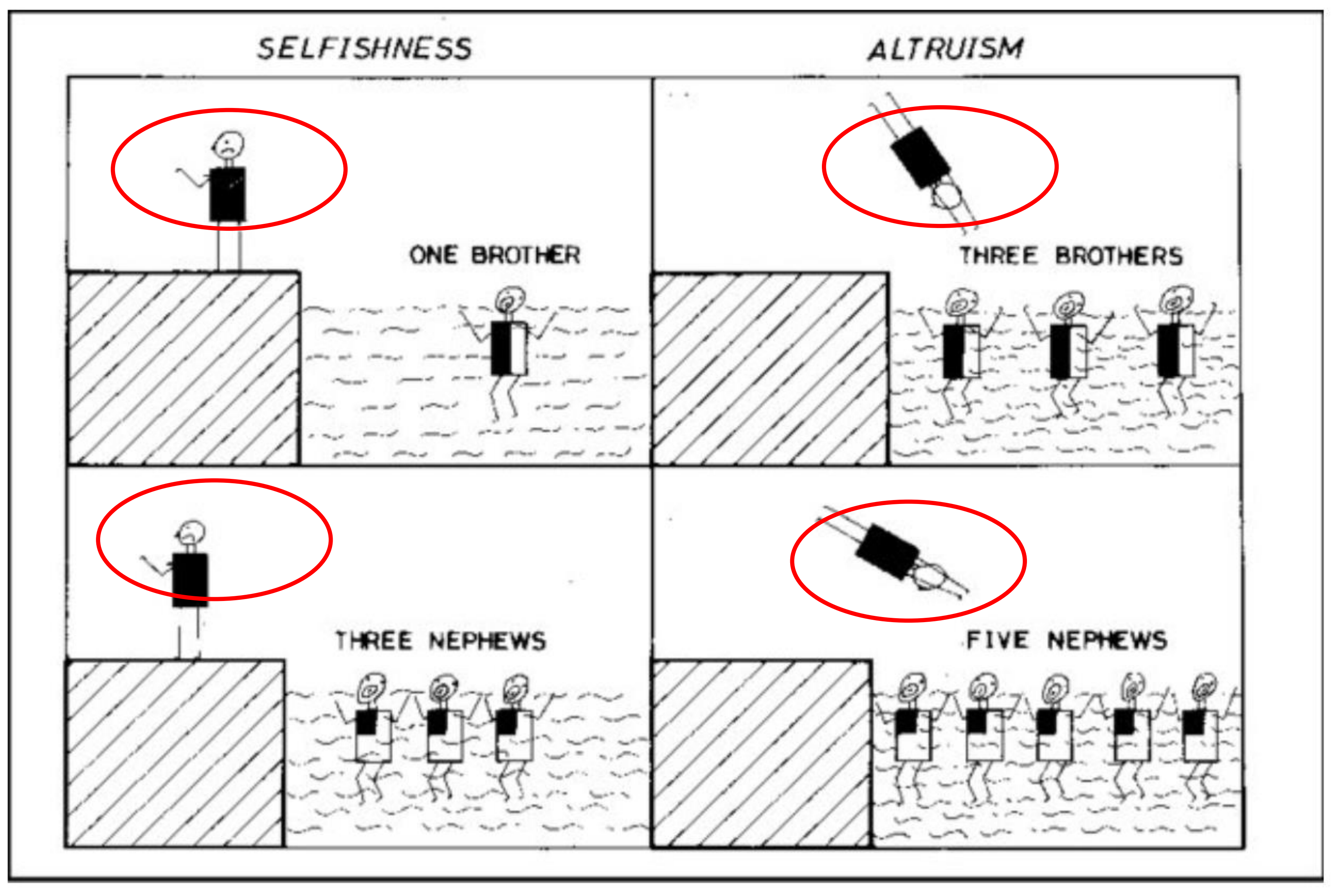
Several studies have measured r in social insects and found the average relatedness in colonies to be 0.5 or less.

We know that honeybee virgin queens mate with upto 20 males on their nuptial flight and store their sperm in her spermatheca. Hence, workers in the colony are mostly half sisters. This brings down the average relatedness between the workers in the colony. **Why do they still cooperate? THINK!**

Some authors have provided population genetic level explanations for the evolution of altruism, that does not require kin selection theory.

Also see: https://evolutionnews.org/2011/05/eo_wilson_disavows_his_own_kin/

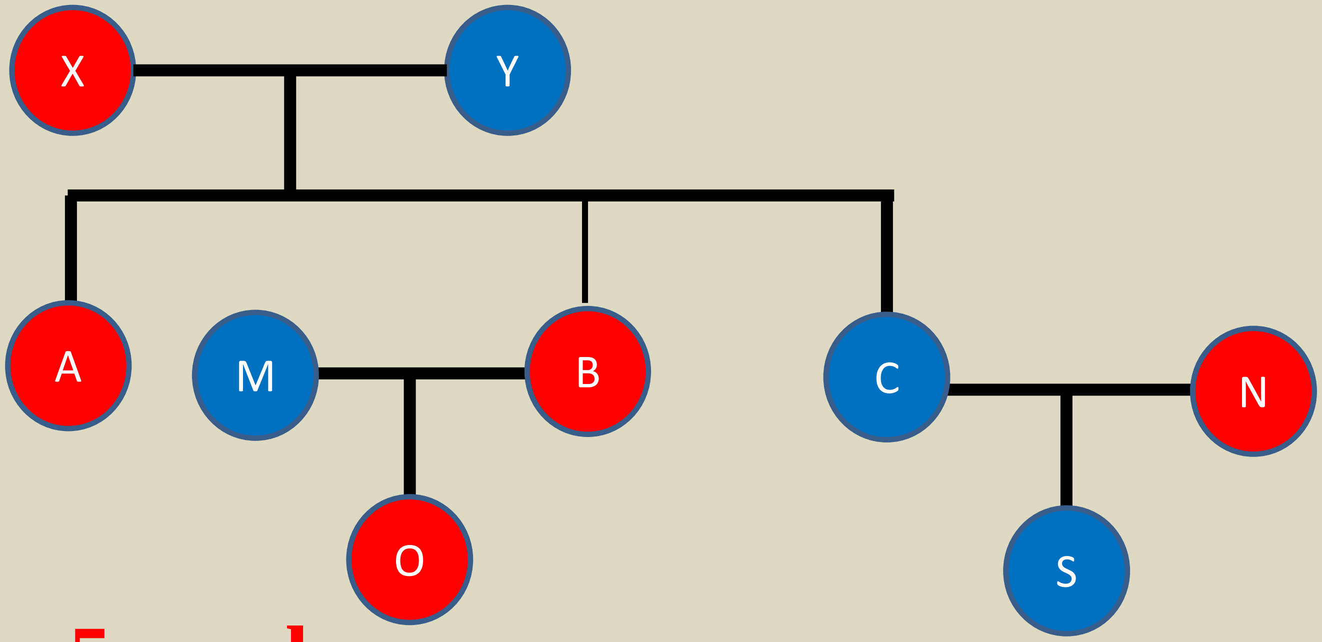
To do…



Think of Haldane’s anecdote.

Can you now calculate the benefits and costs that Haldane might have considered, to come up with these situations, from the perspective of the actor (marked in red)?

Calculate the genetic relatedness between (i) A and S
(ii) Y and O
(iii) A and C
(iv) O and S
(v) O and X.



For each, show the logic of the calculation using the diagram. – 5 marks

Arrange in descending order of relatedness to the workers, the various possible broods (of the queen and any workers) that could be possible in the colony. - 5 marks

Time: 20 min

Calculate the genetic relatedness between a honeybee worker and her sister's son. (2)

Arrange in descending order of relatedness to the workers, the various possible broods that could be possible in the colony. (3)

Time: 15 mins

Some important points to remember

When you calculate relatedness between two individuals, you are considering the probability of overlap of **genes**, considering meiotic cell division during gonad formation, followed by fertilization.

This is why, you share 50% of your genes with your parents.

However, when we consider genetic similarity between species, we consider the overlap of the **genomes** between the two species. For example, bonobos and chimpanzees share 99.6% of their DNA. This confirms that these two species of African apes are still highly similar to each other genetically, even though their populations split apart in Africa about 1 million years ago, perhaps after the Congo River formed and divided an ancestral population into two groups. So, here, populations of individuals are being considered.

Some important points to remember

While considering kin selection theory, the altruist receives the benefit (B) for only those individuals that have received the benefit of altruism. For example, if parents can raise two offspring by themselves, and with the help of a son, they raise three, the son gets a benefit of 0.5 for one extra sibling it has helped its parents to raise. The cost for the son in that season might be 1, because it has lost the opportunity to produce two offspring. However, it has been shown that helping sons become better fathers and have higher lifetime fitness. Read the paper on Fathers harassing sons.

Hence, though there are thousands of brood in a honeybee colony, worker’s B should be calculated based on the number of larvae she has fed or taken care of.

Fitness gained, according to kin selection theory, is termed **Inclusive Fitness**, which includes both direct fitness (through own offspring raised, who in turn reproduce) and indirect fitness (gained through kin raised, who in turn reproduce).

Some important points to remember

Remember:

Inclusive fitness cannot be accrued if the offspring are not viable (capable of reproduction).

Inclusive fitness cannot be accrued for offspring that are not cared for.

Inclusive fitness cannot be accrued by helping non-relatives, as genetic relatedness with the recipient of altruism will be 0.