The selfish gene

- selection acts mostly for the benefit of the individual
- sometimes selection may act for the benefit of relatives
- rarely, selection acts for the benefit of the group

- in asexual organisms any mutant is linked to any other gene in the individual
- in sexual organisms genes can become un-linked and thus can become selfish (relative to other genes)
- if genes are transmitted by different way, genetic conflict arises
There is no selection for the benefit of the species or the group!

Formerly it was believed that natural selection acts for the *benefit of the species*. This idea was used to explain
- why animals do not kill each other when they fight,
- why salmon die of exhaustion after having laid their eggs,
- why animals live in groups and colonies, ...

However, this is not the case. Whenever selfishness results in an advantage, it will spread.

Theoretical example: A population of birds on an island. If each pair of bird pair produces 2 offspring, the population will not grow and resources (e.g. food) will not become limited. A mutant arises producing 5 offspring. It will leave more genes to the next generation and all of its offspring will do the same (produce 5 offspring). After some time, all birds on the island will be descendants of this mutant until a mutant arises which produces even more offspring. This happens regardless of whether the bird population will increase in size and the resources become limited. As long as the mutant has an advantage relative to other birds, its genotype will become more common.
Infanticide: Lions kill baby lions to increase their own reproductive success.

In the Serengeti National Park in Tanzania, lions live in groups of 3 to 12 adult females, 1 to 6 adult males and several cubs. Females stay in these groups while males migrate to other groups and attempt to take them over. If successful, they have 2-3 years to rear their own offspring. Then, they in turn are driven out by stronger males. To maximise their reproductive success, they kill the cubs which still depend on their mothers. By doing this, the females are more quickly receptive again and he can become father of the next generation of cubs. Females allow this, as the new group leader protects them from other males which would kill their cubs. The male benefits because he is able to produce offspring, the females benefit because once the new male is established, he protects them and his offspring.

Cannibalism: Spider females eat their mating partner.
In many spider species, females eat their partners after mating. In many cases the males do not seem to do anything about it. Why?
The evolution of sex and its consequences

Sex is common in nature and important for evolution. Here we discuss its evolution and some of the consequences:

1. The evolution and maintenance of sexual reproduction
2. The evolution of anisogamy
3. Sex allocation and sex ratio
4. Sexual conflict and sexual selection
5. Parental care and mating systems
6. Kin selection and relatedness
7. Intragenomic conflicts and genetic architecture
8. Species defined by reproductive barriers
What is sex?

About 1 – 2 billion years ago a process evolved we call today “sex” or better “genetic recombination”. There are many ways how this can be achieved, here we deal only with the iconic form of sex, i.e. the alternation of gametogenesis and syngamy.

Having equally sized gametes is called “isogamy”. This is the ancestral form of sex. Syngamy of a large gamete (ovum) with a small gamete (pollen, sperm) is called “anisogamy”. Only with anisogamy we talk about “two sexes” (zwei Geschlechter).
1. The evolution and maintenance of sexual reproduction

The paradox of sex: Sex is common despite a two-fold cost

If sexuals invest half of their resources in sons, and males only contribute sperm to the offspring, parthenogenetic individuals multiply twice as fast.

This is the cost of males!
The paradox of sex: Costs of males and other costs of sex

Costs of males: There is 2-fold cost if
- there is anisogamy (the 2 sexes have unequal investment in gametes)
- half of the resources are allocated to each sex (sex ratio 50:50)
- the father only contributes sperm to the offspring (no other resources)

A parthenogenetic lineage does not waste half of its resources investing in male function. Why are not all species asexual?

The cost of sex is less than two-fold if
- males contribute resources to the offspring (e.g. paternal care)

Other costs of sex:
- trouble finding partner (takes time and energy, exposes to risks, ...)
- sexually transmitted diseases
- risk of obtaining bad genes from the partner
- ...
Direct consequences of sex: segregation

Segregation = independent assortment of alleles into gametes

Mendelian segregation creates and destroys favourable allele combinations within loci:

- A favourable mutation can easily become homozygous in a diploid sexual population; in a diploid asexual organism both copies of the allele have to mutate in the same genetic lineage.
- Asexual reproduction can preserve a beneficial heterozygous genotype but in a sexual population 50% of the offspring will be homozygous.
Direct consequences of sex: recombination

• independent segregation of chromosomes into gametes
• crossing-over during meiosis

Recombination allows (partial) independent inheritance of alleles at different loci.

Recombination creates and destroys favourable allele combinations between loci

Epistasis: fitness effects of an allele depending on the genotype at other loci (= on genetic background).

Another consequence of sex:
Recombination reduces linkage disequilibrium:

Linkage disequilibrium is present when a carrier of allele A carries a particular allele at another locus more or less often than expected by chance. Recombination reduces linkage disequilibrium by recreating other allele combinations.
Examples of loci interactions

A haploid example

Additive interactions

Epistasis

A diploid example
Advantages of sex: Sex against the accumulation of deleterious mutations (Müller's ratchet)

Müller's ratchet = accumulation of deleterious mutations in asexual lineages

In sexuals, Müller's ratchet is prevented because genotypes with few mutations are created by recombination.
Advantages of sex: Sex against the accumulation of deleterious mutations (Müller's ratchet)

Sexual recombination results in offspring with a higher variance in the number of deleterious mutations. Some offspring may be without deleterious mutation.
Advantages of sex: Sex against the accumulation of deleterious mutations (Müller's ratchet)

Asexual lineages accumulate deleterious mutations. In an asexual lineage, the spread of a beneficial mutation will cause the spread of the entire genetic background on which the mutation originally happened, together with any deleterious mutations it had previously contained. In a sexual population, recombination will free a beneficial mutation from its genetic background.
Advantage of sex: Sexual populations evolve faster
Sexual populations have more genetic variation and therefore evolve faster.  
(Fisher-Müller Hypothesis)

Recombination brings together mutant alleles that appeared in different individuals.

In a more or less constant environment this is a long-term advantage and is unlikely to prevent the evolution and short-term evolutionary success of asexual taxa.
Advantage of sex: Sexual populations evolve faster
Sex as a means to speed up coevolution (Red Queen hypothesis)

“Now, here, you see, it takes all the running you can do, to keep in the same place.” (Lewis Carroll, “Through the Looking Glass”)
Advantage of sex: Sexual populations evolve faster

Sex as a means to speed up coevolution (Red Queen hypothesis)

Red Queen Hypothesis (Van Valen 1970): each population has to evolve constantly because its resources (food species), competitors, predators and parasites also evolve all the time.

Premises of the Red Queen hypothesis applied to sex and parasites (Hamilton 1980):

• Parasites typically have much larger populations and shorter generations than their hosts. Therefore, they are expected to evolve faster than their host. Parasites evolve to exploit their hosts.
• Everyone has parasites => parasites exert strong selection on their hosts
• Parasite virulence and host resistance depend on the interaction between parasite genotype and host genotype
• Parasites will adapt to attack the most common host genotypes
• Resistance often depends on having a particular combination of genes

Therefore, sex is advantageous because recombination creates new gene combinations which may be resistant to parasites

Sex is additionally advantageous where parents may transmit parasites to their offspring – sexually produced offspring have a different genotype than their parents did and thus may be resistant to the parasites to which their parents were susceptible.
Evidence for the Red Queen hypothesis

Distribution of sexual and asexual forms of snail *Potamopyrgus antipodarum* in relation to parasite (*Microphallus* sp.) prevalence

Sexual and parthenogenetic females coexist in this snail population. Only sexual females produce males, so the proportion of males can be used to measure the frequency of sexual vs. asexual forms. Lakes with greater prevalence of infection have a greater frequency of males, i.e., a greater frequency of sexuals.

Source: Lively, C. Evolution 46:907-913
Evidence for the Red Queen hypothesis

Hobbling the Red Queen. Researchers can study the impact of parasite-host interactions on the evolution of sexual reproduction by conducting experiments that create different host-parasite populations, and allowing them to evolve over many generations. In this example, if researchers allow a nematode worm host (H) and a parasite (p) to coevolve (top series of boxes), then high rates of sexual reproduction are sustained (graph, right). If they use frozen parasite stocks to reinfect each new generation of the host with a fixed, nonevolving ancestral strain of the parasite (p^0 bottom series of boxes), rates of sexual reproduction can decline. Such experiments can also replace the host, rather than the parasite (11).

Moran et al, Science 2011
Brockhurst, Science 2011
Phylogenetic distribution of asexual forms
Most multicellular asexual (parthenogenetic) lineages are evolutionarily young, suggesting they have a higher extinction rate.

Some old asexual lines are known:
- Glomales (primitive fungi, >130 Myr old)
- Bdelloid rotifers (>35 Myr old)
- Darwinulid ostracods (70 Myr old)
Geographic and ecological distribution of asexual forms: Geographic parthenogenesis

Asexuals tend to occur in marginal habitats, in more extreme environments (colder, dryer, higher altitude) than their sexual relatives. This habitats have low population density and low prevalence of parasites – compatible with the Red Queen hypothesis.

But there are alternative explanations – asexuals may be favoured in such places because

- it is difficult to find a sexual partner (population density is low);
- clonal reproduction can maintain gene combinations locally adapted to marginal habitats, which would otherwise be diluted by gene flow from better habitats.
Conclusions Part 1: The evolution and maintenance of sex

- The common occurrence of sex needs an explanation because of its costs.
- Theory is well developed, but data are scarce and difficult to obtain.
- The Red Queen (RQ) hypothesis currently has the best empirical support.
- Mutational hypotheses (e.g. Müller’s ratchet) cannot be excluded.
- Pluralistic approach: the various advantages of sex may work at the same time and may reinforce each other (parasites and deleterious mutations).
- Short-term versus long-term advantages of sex:
  - Only in the RQ hypothesis is the disadvantage of asexual reproduction immediate.
  - Other mechanisms work after some generations (mutation accumulation requires time). Thus, asexual lineages are predicted to be initially successful, but predisposed to deteriorate later.

The paradox has not yet been solved!!!
2. The evolution of anisogamy

Why are there males and females?

Sexual reproduction is the alternation of a haploid and a diploid stage. Diploid stages result from the fusion of two gametes. The gametes may be of equal or unequal size.

**Isogamy**: Both gametes are of equal size. Most certainly the ancestral state. This is still found today in certain ciliates, algae, and fungi. There are often two (sometimes more) mating types (+/- or A/a) and only different types can form a zygotes (reduces inbreeding).

**Anisogamy**: A zygotes is formed with a large and a small gamete. We define male as the sex which produces the small gamete (sperm, pollen) and females as the sex which produces the large gamete (ovum).
Females are defined to be the gender with the larger gametes.

*Daphnia*
Ovum 600 µm
Spermium 5 µm

Chicken sperm 0.1 mm

Chicken egg

*Drosophila bifurca*, the species with the largest sperm.
3. Sex allocation and sex ratio

Why are there mostly equal numbers of males and females?

The sex ratio in most species is usually 50:50 (Humans: 980 females : 1000 males).

Why not produce more females (daughters) than males (sons)? R.A. Fisher showed that in bisexual species where males and females have to contribute equally to offspring, the sex in the minority would have an advantage. This is because individuals of the minority sex would contribute more to the production of the offspring than would individuals of the other sex. Thus, it would pay for a couple to produce more of the minority sex, because they would have more grandchildren. Therefore, the sex ratio will approach 50:50.

Strictly speaking, the ratio of investment in males and females should be equalised.

There are exceptions to the 50:50 rule under special conditions. For example in fig wasps (Feigenwespen) and some mites (Milben) sex-ratios can be strongly female biased. This occurs when mating occurs among brothers and sisters.