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Insects and sex

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Most organisms reproduce sexually, but the evolution of sexual reproduction is not yet well understood. Sexual reproduction leads to new variation and adaptations to the environment, but sex is also costly. Some insects reproduce without sex through parthenogenesis or paedogenesis. Almost all sexual insects have two separate sexes, male and female. There are many mechanisms of sex determination. Most insects have male heterogamety (males XY, females XX). Female heterogamety and haplodiploidy (males haploid, females diploid) are less abundant. Proportions males and females in populations are typically equal, but deviations are known to occur by driving sex chromosomes and other sex ratio distorters.

Keywords: diploidy, haploidy, paedogenesis, parthenogenesis, reproductive mode, sex, sex ratio distorter

Sexual reproduction and differentiation are fundamental aspects of living organisms. Most insects reproduce sexually. This means that two individuals of opposite sex (males and females) reproduce together to form new individuals. The term 'sex' has several meanings in biology. In the 'genetic' sense it means recombination leading to new genetic variation. Recombination of genes can occur in various ways (Fig. 1). In diploid organisms (having two chromosome sets) gametes are haploid and a new individual is generated by fusion of two haploid gametes, each of a different parent. A second mechanism is the random segregation of chromosomes. Upon the formation of gametes each individual chromosome has an equal chance to segregate to one of the two division products. A third mechanism that generates variation is crossing-over, the exchange of chromosomal regions between chromosomal pairs.

Not all insects reproduce sexually. Parthenogenesis is the development of an egg without fertilization. Parthenogenetic species consist of females only. Although less widespread than sexuality, parthenogenesis occurs in many groups with low incidence, including silver fish (Thysanura), spring tails (Collembola), may flies (Ephemeroptera), grasshoppers and allies (Orthoptera), stone flies (Plecoptera), bugs (Homoptera), butterflies and moths (Lepidoptera), flies and mosquitoes (Diptera), beetles (Coleoptera) and ants, bees, wasps and sawflies (Hymenoptera) (Suomalainen *et al.* 1987).

THE PARADOX OF SEX

The widespread occurrence of sexual reproduction is not self-evident from an evolutionary point of view. It is clear that sex generates new variation that can be used by natural selection to act upon. However, sex is also costly (Maynard Smith 1978). Several costs can be distinguished, such as for example the cost of producing males, the cost of mate finding and the cost of meiosis. Due to the costs of producing males parthenogenetic populations can grow faster. The argument is explained in Figure 2. Consider a sexual and a parthenogenetic population in which individuals are equal for all other aspects. Assume that each female can lay two eggs. A sexual female will produce one son and one daughter. Each daughter will lay two eggs again, etc. Two sexual individuals (a female and a male) will therefore produce two new individuals each generation. Now consider the asexual population. Each female will produce two offspring, each of which will be female. Both daughters will produce two new daughters, etc. The net outcome is that asexual females produce twice as many offspring as sexual females in the same time. Asexual populations are therefore expected to quickly out-compete sexual ones. In other words, males are a biological waste because

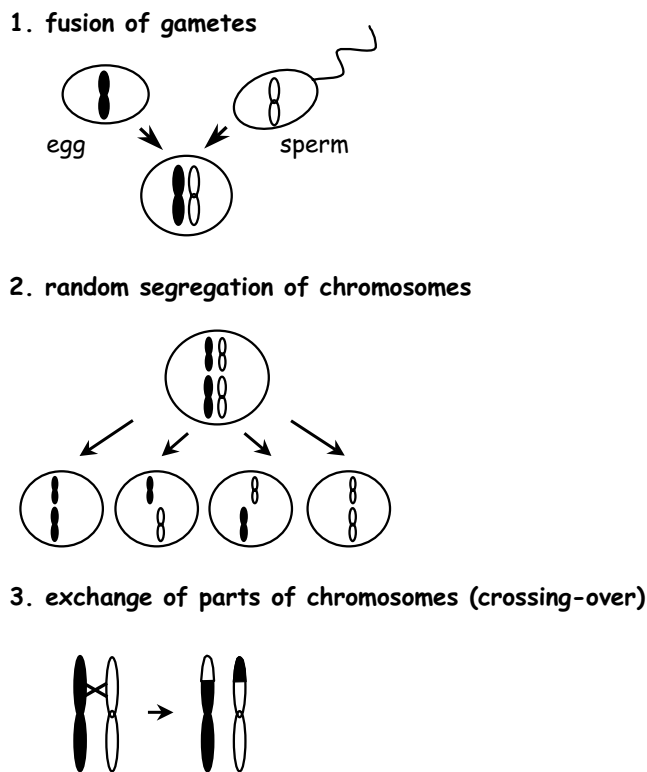


Figure 1. Three processes of sex.

they do not lay eggs. Much effort in current evolutionary biology is spent on finding short-term benefits of sexual reproduction to balance the costs of sex (West *et al.* 1999).

FORMS OF PARTHENOGENESIS

In species that consist of both sexuals and parthenogens, the distribution of both types need not be similar. Geographical parthenogenesis refers to the situation where parthenogens have a different geographical distribution than their sexual counterparts. In many insect species, the parthenogens occur at higher altitudes and latitudes than the sexuals. A good example is the beetle *Otiorynchus chryso-comus* which is parthenogenetic in Scandinavia and northern Great Britain, but sexual in central Europe (Suomalainen *et al.* 1987). The reason for these distributional differences is often not clear. One frequently used explanation is that parthenogens are often polyploid (more than two chromosome sets) which may allow them to occupy more harsh environments. Another possibility is that the current distribution is a consequence of the last ice-age during which most of Europe was covered by ice. Parthenogens may have been more successful in colonising new areas from southern refuges.

In some insects individuals can alternate between sexual and parthenogenetic reproduction. This is known as cyclical parthenogenesis. A well known example are aphids. The common bean aphid, *Aphis fabae*, alternates a number of parthenogenetic generations during the summer season with a sexual generation that overwinters.

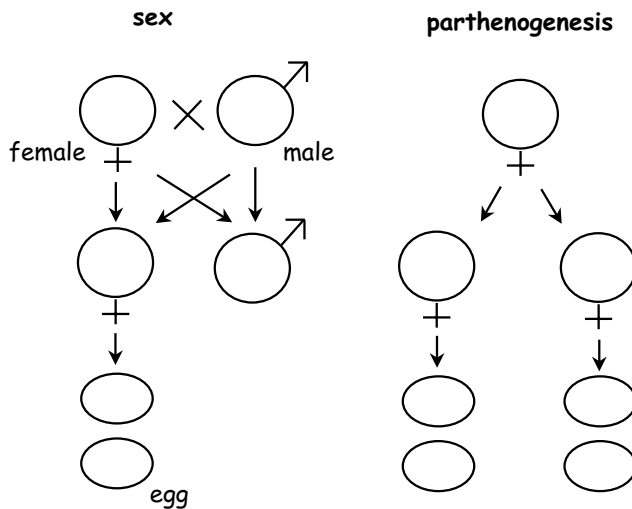


Figure 2. The cost of sex. Parthenogenetic females can reproduce twice as fast as sexual ones because they do not produce 'wasteful' males that cannot reproduce by themselves.

Paedogenesis is reproduction by larvae or juveniles. This is a rare mode of reproduction that has been found in aphids and coccids (Homoptera), some beetles (Coleoptera), gall midges, mosquitoes and hoverflies (all Diptera). In a study of B. Achterkamp at Leiden University paedogenetic reproduction was found to occur at very low frequency in the hoverfly *Eristalis arbustorum*. He placed 546 larvae individually in small containers and found in five cases two pupae, indicating that the original larva had reproduced (Achterkamp *et al.* 2000). Little is known about the mechanism of paedogenetic reproduction as well as about the conditions that may promote it.

Haplodiploidy can be considered as a mixed mode of reproduction. Under haplodiploidy, males develop from unfertilised haploid eggs and females from fertilised diploid eggs (Fig. 3). Males are therefore produced parthenogenetically and females sexually. Males in haplodiploid species only have a mother and no father, whereas females have a male and female parent. All ants, bees, wasps and sawflies (Hymenoptera) have haplodiploid reproduction. It further occurs in some beetles, coccids and thrips, as well as in some mites (Acarina). In haplodiploids, females can have control over the fertilisation process. They have a spermatheca in which they store sperm after copulation and can facultatively release sperm to fertilise an egg upon oviposition. This phenomenon is well known from the Hymenoptera.

Haplodiploidy in which males develop from unfertilised haploid eggs and females from fertilised diploid eggs is known as arrhenotoky. There exist also haplodiploids in which females develop parthenogenetically from unfertilised eggs and there are no males. This mode of reproduction is known as thelytoky.

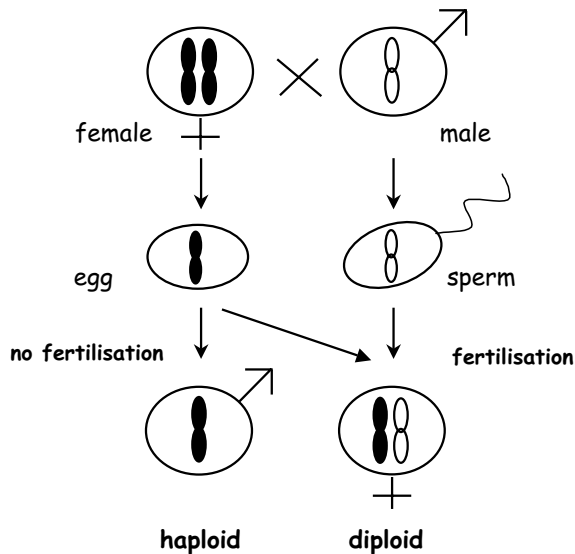


Figure 3. Haplodiploidy. Males develop from unfertilised haploid eggs and females from fertilised diploid eggs.

In the parasitoid wasp *Venturia canescens*, which parasitises pyralid moth larvae, both arrhenotokous and thelytokous females occur in the Mediterranean area. In a detailed study of its population structure we found that both forms have overlapping distribution ranges (Schneider *et al.* 2002). They also appear to occasionally exchange genes, but we do not yet know how.

SEX DETERMINATION

Most insects have separate sexes (genders), males and females are different individuals. In contrast to many other invertebrate groups, hermaphroditism, *i.e.* individuals with both male and female organs, is absent or very rare in insects. Genetic mechanisms of sex determination appear to be very diverse (Bull 1983, Traut 1999). In most insects, the male is the heterogametic sex (Fig. 4, see also Beukeboom 2003). This means that they have two different sex chromosomes, X and Y, of which the Y chromosome is male determining. Females are homogametic, *i.e.* they have two identical sex chromosomes, XX. The opposite pattern, female heterogamety, is less abundant and occurs in Lepidoptera and Trichoptera. In the housefly, both male and female heterogamety is known to occur (Dübendorfer *et al.* 2002), which makes it an ideal organism for studying the evolution of sex determining mechanisms. In haplodiploids, there are no separate sex chromosomes. Sex is somehow determined by the number of chromosome sets (haploid = male, diploid = female).

Sometimes aberrations occur during the development of an organism which can lead to individuals in which sex determination is disturbed. Such individu-

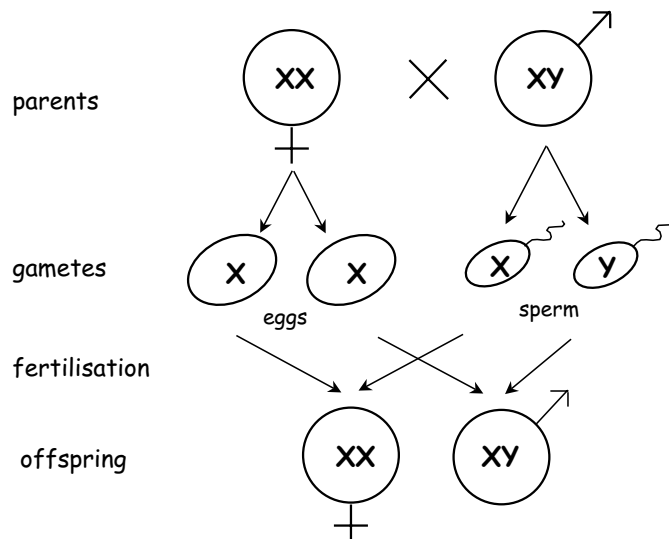


Figure 4. Sex determination by male heterogamety. Males have one X and one Y chromosome and females two X chromosomes. The Y-chromosome determines maleness.

als can sometimes be found as gynandromorphs. Gynandromorphs are individuals that have both female and male characteristics (Fig. 5). They are typically sterile. They are exceptions to the normal development of separate sexes and should therefore not be confused with functional hermaphrodites. A recent example is the Asiatic butterfly *Papilio memnon* in the Emmen Zoo [De Telegraaf 6 december 2004]. This butterfly was female on the left side of the body and male on the right side of the body.

Gynandromorphs can originate in different ways (Fig. 6). Under male heterogamety loss of one sex chromosome in some cells could result in tissues with and without a Y chromosome. Since the Y chromosome is male determining, those tissues without a Y chromosome will be female. Another possibility is double fertilisation. Occasionally, the egg divides before being fertilised and both nuclei become fertilised by a different sperm cell. The nucleus fertilised by a Y-bearing sperm will give rise to male tissues and the one fertilised by an X-bearing sperm to female tissues. Under female heterogamety, such as in butterflies, gynandromorphs can also originate through loss of a sex chromosome. However, double fertilization cannot cause gynandromorphism because all sperm are identical and female determining (see Fig. 6). In haplodiploids gynandromorphs can arise in an analogous fashion by loss of a complete chromosome set or double fertilisation.

SEX RATIO

The sex ratio is defined as the proportion males versus females. The number of females and males in a population is usually equal. This is not to say that both sexes are also equally likely to be observed; in many insect species one sex, usually the male, is often more conspicuous than the other. From a genetic point of view, however, both sexes are normally produced in equal numbers. The reason is that the sex-determining mechanism ensures the production of equal numbers of offspring with the male and female sex. Under male heterogamety, for exam-



Figure 5. Gynandromorphy. The butterfly (*Papilio memnon*) is female on the left and male on the right [De Telegraaf 6 december 2004]. The parasitoid wasp (*Nasonia vitripennis*) developed from a haploid egg and has a male abdomen, but female antennae, legs and wings (indicated by arrows).

ple, males produce 50% gametes with an X-chromosome and 50% with a Y-chromosome.

However, exceptions to this rule are known. In some organisms sex chromosomes are not inherited at an equal rate. Such sex chromosomes are referred to as meiotic drive sex chromosomes. Both the X and the Y can show drive. A male with a driving Y-chromosome will produce >90% sperm with the Y-chromosome and <10% with the X-chromosome. Although the exact mechanism has not been uncovered yet, it appears that sperm cells with X chromosomes degenerate. The effect is that males with a driving Y-chromosome produce almost exclusively sons among their offspring. Depending on the frequency of the driving Y in the population, this can lead to strongly male-biased sex ratios (Hamilton 1967). Conversely, driving X chromosomes can cause more females than males in populations. Meiotic drive chromosomes are known from several dipteran species, such as mosquitoes, *Drosophila*, tsetse flies and stalk-eyed flies, and butterflies.

Haplodiploids form a group of insects in which the sex ratio appears much more flexible (Wrensch and Ebbert 1993, Hardy 2002). The reason is that haplodiploids do not have separate X and Y chromosomes that determine sex. As mentioned, females can manipulate the sex ratio of their offspring by having

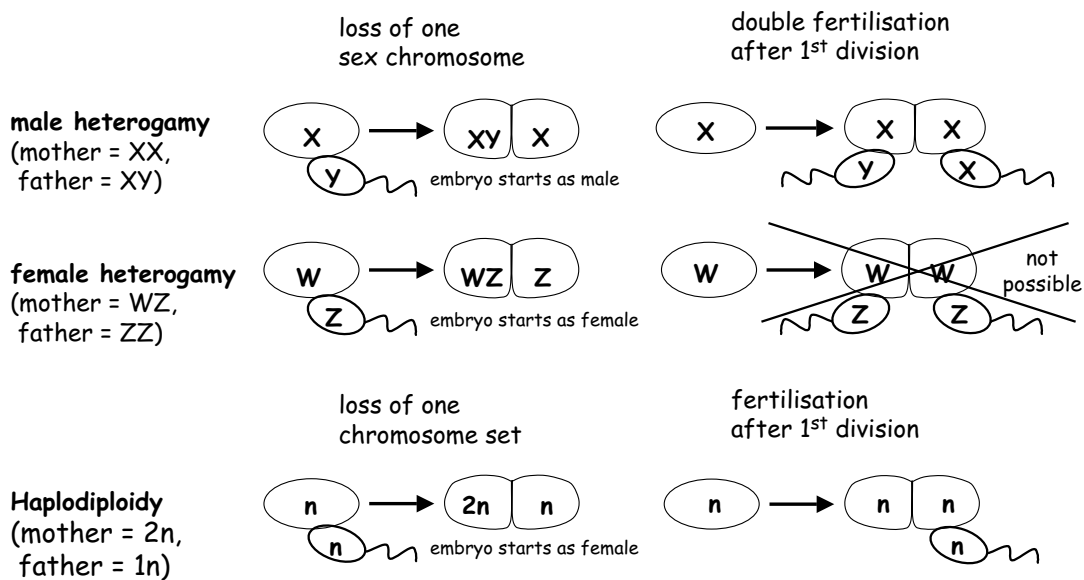


Figure 6. Possible origins of gynandromorphs through loss of a sex chromosome or double fertilisation after the first egg division. Under female heterogamety gynandromorphs cannot result from double fertilisation. Under haplodiploidy gynandromorphs can occur through loss of a complete chromosome set or fertilisation of one of the two egg nuclei.

control over fertilisation; unfertilised eggs develop into males and fertilised eggs into females. However, haplodiploids appear to be prone to infection with microbial sex ratio distorters. One such group of sex-ratio distorters are *Wolbachia* bacteria (Werren 1997). These are intracellular bacteria that reside in the reproductive tissue of invertebrates. They are transmitted through eggs of infected females and occasionally appear to move from one species to another. They have been found in 15-20% of all insect species. They can have a variety of effects on host reproduction, ranging from causing incompatibility, parthenogenesis, killing of sons, to feminisation of males. In all cases the effect is an increase in the production of females. Although the number of reported cases is still low, there is reason to believe that such sex-ratio distorters are much more widespread than previously thought.

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