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## Overview

# 1

## Why sex?

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Sex is a subject that has proved to be endlessly fascinating to generations of biologists, but recent advances in our understanding of animal behaviour, embryology, molecular biology and genetics have shed new light on some of the age-old questions. How and when did sexual reproduction first evolve? What are the advantages and the disadvantages of reproducing sexually, the costs and the benefits, and what are the consequences?

Sex is usually seen as one of the cornerstones of natural selection. The process of meiosis, in which the chromosomes in the diploid germ cells exchange genes by crossing over and then shuffle the maternal and paternal chromosomes to deal a random haploid set to each of the gametes, produces an enormous amount of genetic variability. This is increased still further when maternal and paternal gametes from different individuals meet at fertilization and fuse their two sets of chromosomes at syngamy to produce a new, genetically unique diploid organism. This variability is the substrate on which natural selection can act.

But maybe there is also a down-side to sexual reproduction and its attendant natural selection, since the whole process will always act to favour the selfish interests of the individual. Richard Dawkins has even gone so far as to propose the concept of a 'selfish gene' which dominates the life of the organism that plays host to it. But, since the gene is no more than an inert fragment of DNA until it is able to translate its hidden chemical message into some cellular function, it is difficult to see how the interests of the untranscribed gene in the nucleus could ever differ from those of the organism it helped to produce. If one acted against the other, the gene would always be the loser; if the organism suffered, the gene would not be transmitted to succeeding generations.

Even if we may have difficulty in believing in selfish genes, selfish individuals are certainly a reality; natural selection ensures that

self-interest will always reign supreme in the struggle for survival. But where will this progressive evolutionary drive lead us? Natural selection will normally ensure that a balance is maintained between the organism and its environment, and it is the environment, such as the availability of food or shelter, that is the ultimate constraint. But there is a fatal flaw in the design that could lead to runaway selection and eventual destruction of the species. This will occur if natural selection eventually results in the evolution of an organism that can assume control of its environment and can escape from these natural constraints.

Our new-found ability to transmit knowledge across time has catapulted us into this league. Suddenly, we are able to profit from the sum total of all knowledge that mankind has ever possessed; uniquely amongst all species, we have been able to escape from the slow, blind, groping, random trial-and-error of natural selection, exchanging it for the explosive potential of a Lamarckian style of evolution. The acquisition of knowledge has given us the ability to inherit acquired characteristics through non-genetic means. This accumulated wisdom has enabled us to dominate our environment; we now have the power to change it in the twinkling of an eye and Nature cannot prevent us, it can only punish us after the event. The voice of reason may make us try to exercise restraint individually by limiting our food consumption or our fertility, but reason is unlikely to prevail; we may be able to *think* rationally as individuals, but corporately we seem unable to *act* in a rational manner. Even in a democracy, our leaders are selected largely because of their own self-interest; they want the job. Put a group of selfish individuals in charge and they will usually tend to act out of self-interest, not altruism towards those whom they allegedly seek to serve, or concern for the world in which their offspring must live.

We should all have shuddered a little at the recent announcement by the world's radioastronomers that they can find no evidence of other intelligent lifeforms within 40 million light years of us. Perhaps the lifespan of a species is inversely proportional to its degree of intellectual development? The probability that a species that has evolved to be as intelligent and all-conquering as ours could survive for long is remote indeed. We may live in a silent universe for a very good reason. Paradoxically, evolution may have ensured that we have one of the shortest survival times of any species, since it has made us, effectively, our own executioner.

But these grim forebodings about our future as a species did not concern Charles Darwin. When he first published *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle*

for *Life* in 1859, he certainly saw evolution as a dynamic process, but his immediate concern was the mechanism by which the favoured individual propagated his or her desirable traits to others. Darwin realized that evolution would not occur unless the chosen few were fertile and could pass on their more desirable characteristics to their offspring. So, in *The Descent of Man, and Selection in Relation to Sex* (1871), he went on to develop his ideas about sexual selection. It is worth quoting him on the distinction between natural selection and sexual selection, since these ideas still form the basis for our understanding of the differences between the sexes, the theme of this book:

Sexual Selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; whilst Natural Selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners.

Clearly, Darwin appreciated that in polygynous species, where the males mate with more than one female, the competition between males for access to the females is greater than the competition between females for access to the males, leading to an exaggerated development of those secondary sexual characteristics used in inter-male aggressive encounters (see Figure 1.1). As Darwin wrote: ‘That some relation exists between polygamy and the development of secondary sexual characters appears nearly certain’.

He even appreciated the potentially self-destructive nature of sexual selection, which he thought might sometimes act counter to natural selection, instead of in concert with it. Probably thinking of the massive antlers of the great Irish elk (which in fact are not out of proportion to its overall body size; see Chapter 6 by Gerald Lincoln, and Figure 1.2) or even the tail of the peacock, he said: ‘The development however of certain structures – of the horns, for instance, in certain stags – has been carried to a wonderful extreme; and in some cases to an extreme which, as far as the general conditions of life are concerned, must be slightly injurious to the male.’

But Darwin went to his grave still baffled by the nature of the mechanism that enabled desirable characteristics to be transmitted from one generation to the next. He was unaware of the publication in 1866

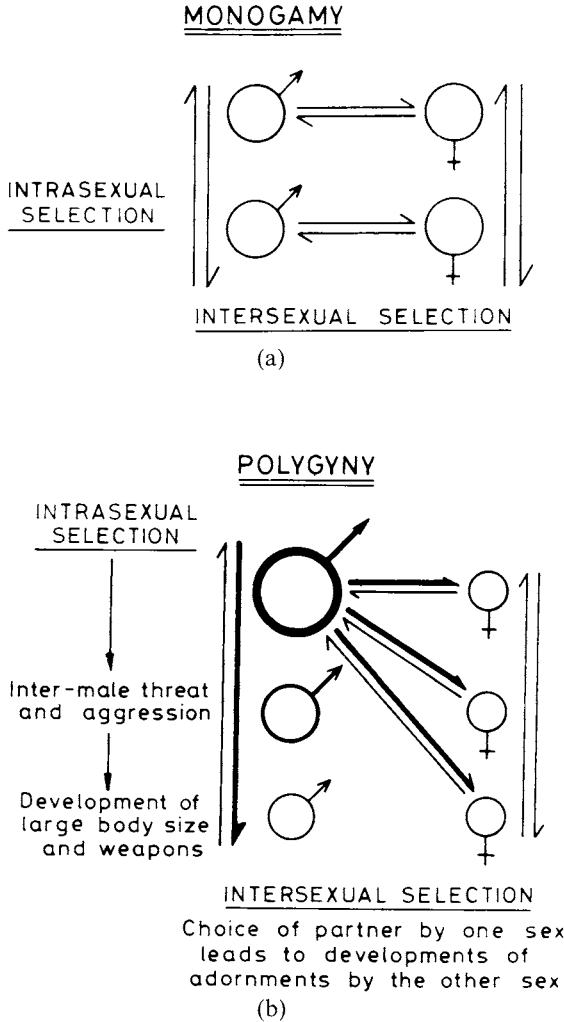


Figure 1.1. Differential effects of intersexual and intrasexual selection in (a) monogamous and (b) polygynous mating systems. (From Short, R. V. (1979).)

of his contemporary, Gregor Mendel, working away in the monastery gardens of Brno, Czechoslovakia, on the particulate nature of inheritance in plants, although Mendel had a copy of Darwin's *Origin of Species*. Mendel's work was almost completely ignored until it was rediscovered by others at the turn of the century. If only Darwin had known about genes, chromosomes and meiosis! Instead, he was forced to come up

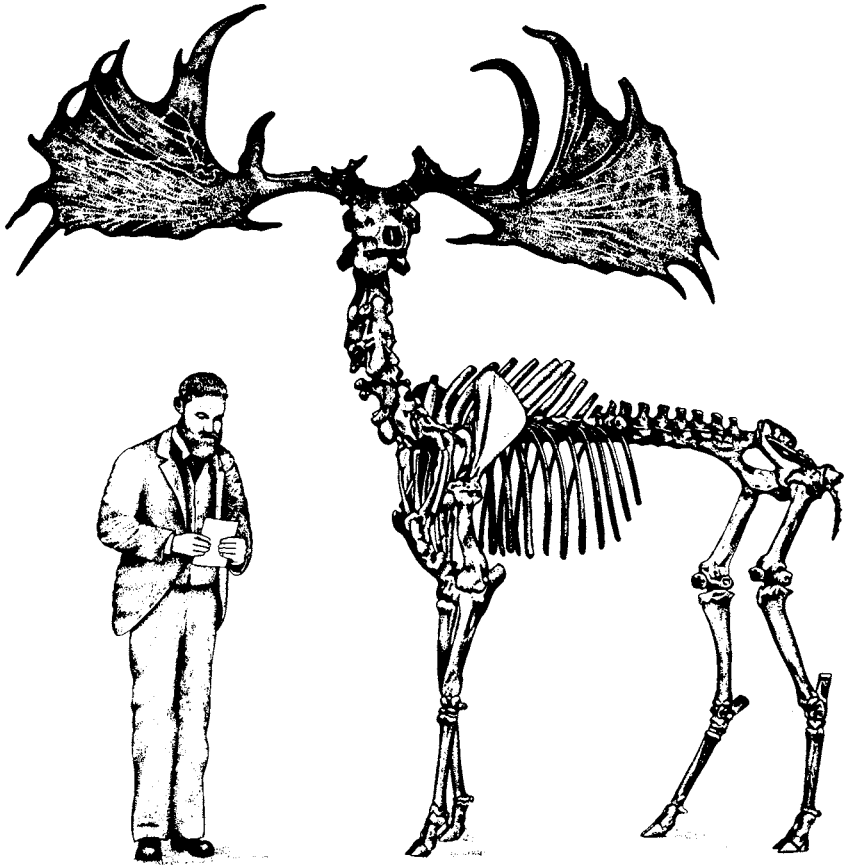


Figure 1.2. The great Irish elk. (From Short, R. V. (1976) *The origin of species*. In *Reproduction in Mammals*, Book 6, *The Evolution of Reproduction*, p. 112. Eds. C. R. Austin and R. V. Short. Cambridge University Press.)

with a concept he named pangenesis to explain how characteristics might be inherited. He developed this idea at length in his 1868 publication *The Variation of Animals and Plants under Domestication*, but few people were attracted to it, for obvious reasons. This caused him bitter disappointment. He summarized his pangenesis hypothesis in *The Descent of Man, and Selection in Relation to Sex*: 'According to this hypothesis, every unit or cell of the body throws off gemmules or undeveloped atoms, which are transmitted to the offspring of both sexes, and are multiplied by self-division. They may remain undeveloped during the early years of life or during successive generations; and their development into units or

cells, like those from which they were derived, depends on their affinity for, and union with other units or cells previously developed in the due order of growth'.

Darwin's 'gemmules' were thus the product of the cell, unlike our concept of a gene as a chemically coded message that goes to make the cell in the first place. And in the absence of any understanding of hormones, Darwin was forced to explain the development of sexual dimorphisms in secondary sexual characteristics as being due to the dormancy of the appropriate gemmules in one sex or their development in the other.

Darwin's ideas on intrasexual and intersexual selection were developed further by the English geneticist and statistician R. A. Fisher in his monumental 1930 publication *The Genetical Theory of Natural Selection*. Fisher was intrigued by the genetic control of sexual dimorphisms. Although an obvious solution might seem to be to locate the genes controlling all mammalian male secondary sexual characteristics on the only male-specific chromosome, the Y, Fisher was quick to see that Nature had usually opted for a far more subtle strategy. The Y chromosome was used simply to code for the presence of a testis; once made, the testis could then produce hormones that could act both locally and systemically to induce the development of a spectacular array of male secondary sexual characteristics. Therefore, the genes for these male secondary sexual characteristics did not need to be located on the Y chromosome, but could be on any of the autosomes. They would be expressed only under the activating influence of male sex hormones (see Chapter 8 by Jean Wilson). Thus antler growth is usually confined to male deer, but the genes regulating the antler do not need to be sex-linked and confined to the Y chromosome. We know that they are present, but dormant, in the female; if you implant a female with the male sex hormone testosterone, she too will develop antlers. Thus, the genes for most sexually dimorphic characteristics are hormonally sex-limited, not genetically sex-linked. This has made it much easier to develop a wide array of different sexually dimorphic characteristics in different species, since it is easier to develop hormone-dependent expression of an autosomal gene than to translocate it onto the Y chromosome. No wonder we see such spectacular and diverse forms of male secondary sexual characteristics such as body size, brain development, hair growth, teeth, horns or antlers in different species, whereas the Y chromosome appears to be highly conserved across all mammals and almost devoid of genetic information, apart from genes which determine spermatogenesis and the presence of the testis.

Since exceptions to rules demand an explanation, it is fascinating to discover that in marsupial mammals some sexually dimorphic structures such as the scrotum, pouch and mammary gland are under direct genetic, rather than indirect hormonal, control. The genes in question seem to be on the X rather than the Y chromosome, so that their differential expression is dosage dependent – one X chromosome codes for a scrotum, whereas two X chromosomes result in the development of a pouch and mammary gland instead (see Chapter 9 by Marilyn Renfree). Why did marsupials choose to do things differently when they sailed away from the rest of the world on Gondwanaland, some 150 million years ago?

Just as Fisher championed and expanded Darwin's view of sexual selection, so Julian Huxley was able to use his wide practical experience as an ornithologist and field naturalist to clothe the theories of Darwin and Fisher with practical examples. He realized that all aspects of the male and female reproductive tract were likely to be involved in intersexual selection, from the gametes themselves to the gonads, the male and female copulatory organs, ducts and accessory glands, any structures facilitating the discovery or recognition of one sex by the other, and any behavioural display that stimulated reproductive activity. Huxley gently chided Darwin for his modesty in not referring to the copulatory organs themselves, and re-emphasized the point made by Darwin and Fisher that polygynous mating systems would maximize sexual dimorphisms, whereas monogamous systems would minimize them.

Biologists were slow to develop ideas about the biological costs and benefits of sexual reproduction, although this has now become a happy hunting ground for sociobiologists (see Chapter 15 by Tim Clutton-Brock). It was the American, R. A. Trivers, who first pointed out that an animal's reproductive strategy in terms of the type of mating system it adopts is dictated by the relative energy investment of the two parents in rearing their young. Thus in birds, where the absence of lactation enables both sexes to play an equal role in feeding the young, monogamous mating systems are generally desirable, therefore sexual dimorphisms in body size are unlikely to develop. However, even in monogamous species, the sexes may still be distinguishable by plumage characteristics; recent evidence from DNA fingerprinting of progeny suggests that they may not be as monogamous as we had imagined and this is further borne out by the relatively large size of the testes in so-called monogamous birds. The smallest relative testis size is actually found in birds that lek, where the females seldom mate with more than one male.



It is also of interest that in birds, where the male is the homogametic sex (ZZ), the neutral or default state appears to be the gaudy plumage of the male, on which femaleness is superimposed by ovarian oestrogens. Many people still find it difficult to believe that in spectacularly dimorphic species like chickens, peacocks, pheasants and ducks, an ovariectomized female will develop the male's gaudy plumage, which is normally suppressed in the female by her oestrogens; her dowdy appearance is presumably of adaptive significance, since it will provide better camouflage when she is sitting on the nest. Peahens have been shown to select as a mate the peacock with the largest number of eye-spots in his train, which is a measure not of his androgen-induced virility, but of his lack of oestrogen-induced femininity. Since peahens with diseased ovaries can develop the male's plumage, the train is not a very reliable indicator of the male's reproductive potential. Oestrogen also seems to be the factor responsible for transforming the indifferent avian gonad into an ovary, since female chicken embryos, given an aromatase inhibitor, develop testes rather than ovaries. But the testosterone secreted by the cockerel's testes is nevertheless still responsible for his aggressive and sexual behaviour and for the development of such male secondary sexual characteristics as the comb and spurs.

Why should birds have evolved a completely different sex-determining mechanism from mammals? Not only are females the heterogametic sex (ZW) and oestrogen the dominant hormone, but the Z and W sex chromosomes are not even homologous to the X and Y chromosomes of mammals (see Chapter 18 by Jennifer Graves and Chapter 20 by Claude Pieau and colleagues). Perhaps we should be looking for an avian W-linked ovary-determining gene, SRW, to compare with the mammalian Y-linked testis-determining gene, SRY.

### **Sexual selection in humans and the great apes**

When Darwin first put forward the concept of sexual selection, he considered the way in which it acted to develop general bodily characteristics, but was too modest to extend his argument to the genitalia themselves. Therefore, I undertook a study of gonadal and genital development in humans and the great apes. This showed clearly that somatic size and genital development are not necessarily related to one another. Male gorillas weighing around 250 kg, although twice as big as females, nevertheless have minute 10 g testes, whereas 50 kg male chimpanzees that are only slightly larger than females nevertheless have

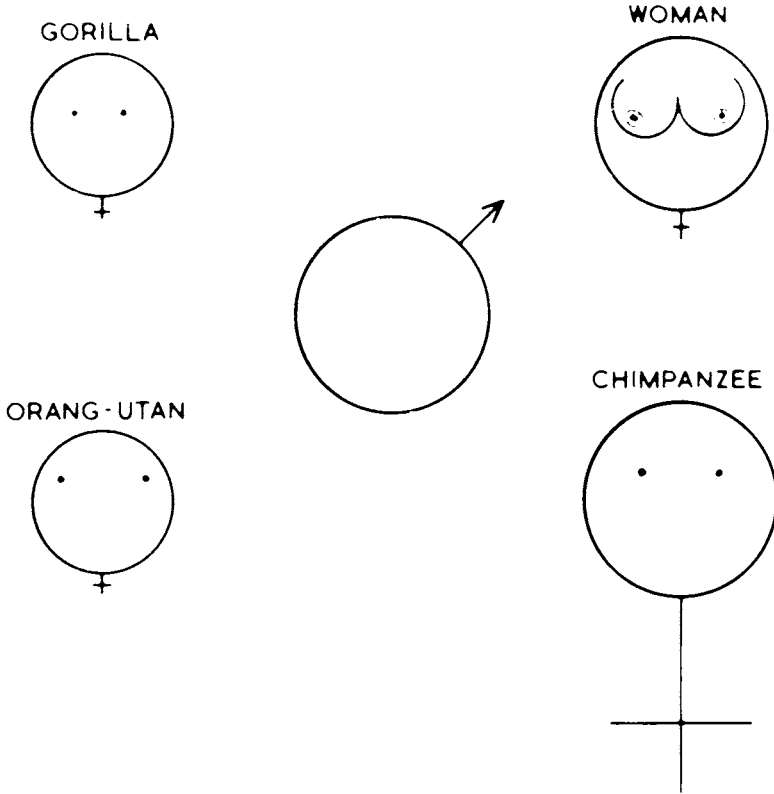


Figure 1.3. The male's view of the female, illustrating the relative sizes of the nulliparous breast and the external genitalia. (From Short, R. V. (1979).)

enormous 60 g testes. In order to explain this apparent paradox, we have to understand the different mating systems of the species in question, since these can have quite different effects on somatic and genital development (see Figures 1.3 and 1.4).

Somatic selection for body size is concerned with successful inter-male competition for a mate, as Darwin suggested originally. Genital selection, on the other hand, is far more complex; although influenced by the mating system, it is ultimately a reflection of the frequency of copulation and the number of sexual partners. Thus, in monogamous species that pair for life there is little or no somatic dimorphism in overall body size; since copulatory frequencies are also low, the testis is relatively small and the female does not have to advertise her sexual state to all-comers by developing pronounced sexual swellings. Marmoset monkeys and gibbons are good examples of monogamous primates that illustrate these points.