# 6

Sex

A fundamental feature of human life is that there are two sexes, with one member of each sex needed in order to reproduce. Pairing up is a complex business responsible for many of the scrapes that we get into and the emotional highs and lows that we experience. Movie-makers and writers would be short of material if there were no sex. The problem of sex is made even more difficult by the fact that men and women seem to differ in certain ways, including, often, in what they want. Why are humans like this?

This chapter is about sex and, in particular, why the sexual system which humans have has evolved. Why have any sex at all? Why have two *different* sexes, rather than anyone being able to have sex with anyone else? And why should the two sexes be different from each other in aspects of their phenotype other than just their gametes? The sexual system we humans have seems so normal, so inevitable, that these questions seem almost surreal, but in fact nature shows that a great variety of different ways of organizing reproduction are possible. For this reason, the chapter will focus mainly on examples from other organisms, until the final section, where we briefly apply some of the generalizations we have made to humans. However, you can probably identify other human parallels as we go along, and the Taking It Further section points you to avenues for exploring the human literature.

Figure 6.1 Just some of the diversity of sexual systems in nature. Clockwise from top left: bdelloid rotifers have no sex at all; starfish can reproduce sexually or asexually; hamlet fish have both male and female genitalia; clownfish change sex from male to female during adulthood; pipefish males carry the eggs in a pouch or skin patch. *Top left: © John Walsh/Science Photolibrary. All other photos: © Corel.*
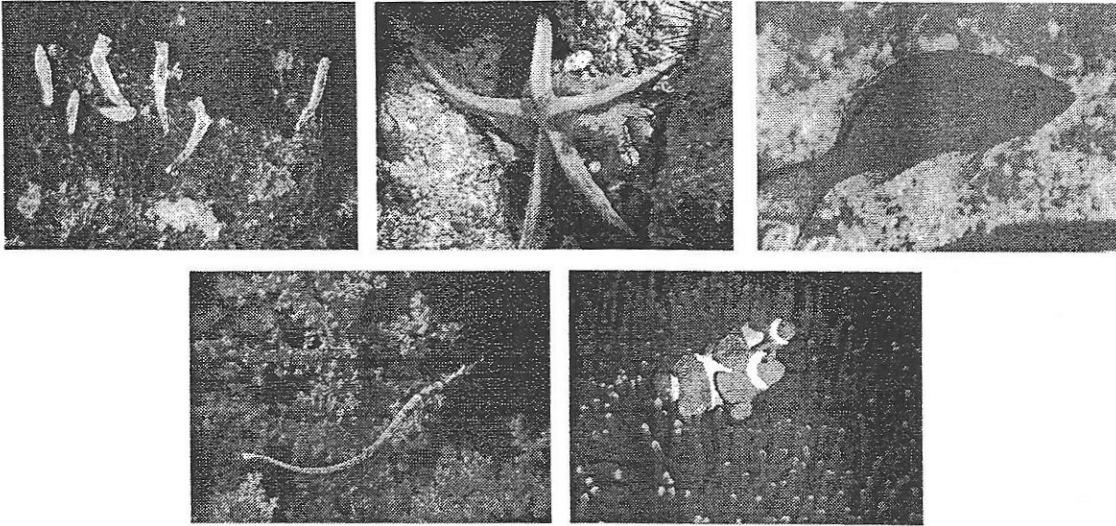
6.1 The diversity of reproduction in nature

Nature contains an enormous diversity of systems of reproduction (Figure 6.1), the chief of which are described below.

6.1.1 Asexual reproduction

First, there are creatures who do without sex altogether. That is, reproduction simply involves the parent individual producing an offspring individual that is genetically identical to itself. This is asexual reproduction. It is common in many single-celled organisms, fungi, and plants, and there are even a few animals devoted to it. Bdelloid rotifers are small, plankton-like animals that live in water and in damp ground. There are several hundred closely related species, but all of them seem to reproduce exclusively asexually. Related groups of animals all have sexual reproduction, and so it looks like the bdelloids lost sexual function at some point in their evolutionary history and have survived for millions of years without it.

6.1.2 Obligate and facultative sex

Individuals of many species are capable of both sexual and asexual reproduction. Starfish, for example, can either release embryos, which do not need fertilization, into the water, or release gametes, which need fertilization by another starfish. Thus, they have both options available to

them and their sex is said to be facultative. In facultatively sexual organisms, sexual behaviour is often most common when the population is crowded densely together or resources are scarce. These may be the times when sex is either least costly or most beneficial.

6.1.3 Isogamous sex and the number of sexes

In our system, one sex (the female) provides a large gamete (the egg) and the early parental care, whilst the other (the male) provides a small gamete (the sperm). This is not the only possibility. For example, in seahorses and pipefish, it is the male, not the female, who carries the fertilized eggs. (We still call him the male since he provides the smaller of the two gametes. This is the biological definition of maleness.) More radically, many algae and fungi display isogamy. This means that the two gametes are the same size and so there is no male or female. There is still a need to prevent gametes fusing with other gametes from the same parent, and so gametes in these organisms carry a marker and will only fuse with a gamete whose marker is different from their own. These markers define a mating type. The number of mating types is often two, but can also be much higher, and a gamete can fuse with a gamete of any mating type other than its own. In contrast to these systems, our system, featuring two strict sexes with gametes of different sizes, is called anisogamy.

6.1.4 Simultaneous hermaphroditism

Even if you have an anisogamous sexual system, there is no requirement for an individual to limit itself to just being one sex at a time. Most flowering plants are hermaphrodites, which means that they have both male and female parts. Amongst the animals, adult hamlet fish have both male and female genitalia. When they mate, they take turns in playing the male and female roles, so that each member of the pair provides both some eggs and some sperm. In the nematode worm, *Caenorhabditis elegans*, there are some individuals who are males and some who are hermaphrodites, but none who are full-time females.

6.1.5 Sex determination

In humans, which sex you are is determined genetically at conception, with males having one X and one Y chromosome, and females having two copies of the X chromosome. Even if you are going to have two anisogamous sexes and individuals can only be male or female at a given time, this is by no means the only way of arranging things. Amongst cockroaches, females are XX and males just have an X on its own. Amongst birds, it is the males who have two sex chromosomes the same (ZZ) and the females who have two different (ZW).

It is not even necessary to determine sex chromosomally. In many reptiles, the sex that an egg develops into depends on the temperature of incubation (in some species cooler temperatures producing females and in some species the opposite). Elsewhere, it depends on early experience. In the green spoon worm, *Bonellia viridis*, if the tiny larvae encounter a female in the first few days of their lives, they enter inside her and become male, thence producing sperm to fertilize her eggs for the rest of their lives. If they do not encounter a female in this early period, they grow and become female themselves. Still other organisms change sex as their lives progress. In the clown anemone fish, *Amphiprion ocellaris*, each sea anemone is home to a small group of individuals. The largest is the breeding female, the second largest the breeding male, and the rest juvenile males. When the female dies, the breeding male becomes female and the

largest juvenile becomes a breeding male. In wrasse (a type of fish), the progression through the sexes is the other way around, with individuals female when they are small and male later.

6.1.5 How to think about the diversity of sex

It should be clear from this section that there are a great many viable ways of organizing reproduction. However, some kind of sex is very widespread. It looks like the ancestral condition for all eukaryotes is to have sex, with forms of asexual reproduction arising many times over evolutionary history, but rarely lasting very long or becoming very widespread. Sex roles and sex-determining mechanisms have also undergone numerous evolutionary changes through time. Thus, there is nothing inevitable about the reproductive system we happen to have.

In this chapter, we will be following the advice of Chapter 5 and taking the adaptationist stance on sex. That is, we will be asking why the alleles leading to sexual reproduction have out-competed alternative alleles for asexual reproduction and also why alleles for the particular form of sex one sees in mammals might have done better than their competitors. Where different organisms have come up with different reproductive systems, it must be because something about the ecology and history of those species has favoured the alleles making that system rather than another one.

6.2 Why have any sex at all?

The most fundamental question regarding sex is why there should be any at all, given that, as we have seen, asexual reproduction is possible. Section 6.2.1 will argue that there is always a cost to sex and that in anisogamous organisms that cost is quite large. Sex can only persist if it is providing some benefit that more than offsets the cost. Sections 6.2.2 and 6.2.3 review the two types of benefits that are best supported by evidence.

6.2.1 The cost of sex

Let us first consider the case where sex is isogamous (both parties provide gametes of the same size) and fertilization is external, so neither parent has to gestate the offspring in their body or carry them around. I have chosen this scenario because it probably represents the ancestral asexual condition from which sex arose.

Imagine that to produce a viable embryo requires 10 units of energy and an individual has 20 units of energy to spare. This individual has two choices. Strategy A would be to produce two offspring asexually. Strategy B would be to produce four gametes each of which contains 5 units of energy, in the hope that these will unite with four gametes from another individual, to produce four offspring in each of whom each parent has a half share.

Which is going to be better, strategy A or strategy B? Strategy A leads to a fairly certain reproductive success of two offspring. Strategy B could in principle also lead to a reproductive success of two offspring, since a 50% share in four offspring is equivalent to a 100% share in two offspring. However, strategy B is much more risky than strategy A. There might not be another individual around to mate with, the gametes released might fail to meet the other gametes, there might be genetic incompatibilities or malfunctions when the gametes fuse, and so on. All these factors will mean that a smaller fraction of energy invested in gametes will lead to

offspring than would be the case for asexual reproduction. So all in all, since strategy B can at most be as good as strategy A, and is probably less good in practice, there would never be any reason to follow strategy B unless the offspring produced that way were in some way better than those produced asexually.

The situation is even worse when we come to consider the case of anisogamous sex. In anisogamous sex, the female pays essentially the full energy cost of setting up the offspring because the egg is large. Sperm, by contrast, are just DNA with a tail and so the male may pay almost nothing. Let us return to our example, where it costs 10 units of energy to make a viable embryo and an organism has 20 units of energy to spare. Strategy A would be to produce two offspring asexually. Strategy B would be to adopt the female role and reproduce sexually. As previously mentioned, an egg embodies all the energy required to set up an embryo and so costs 10 units just as an asexually produced embryo does. So strategy B is for the individual to produce two eggs, which then get fertilized by someone else's sperm. Thus, the choice is between a 100% share in two offspring, or a 50% share in two offspring. This means strategy A is giving twice the return of strategy B, even if all gametes are fertilized successfully.

This problem was described by the great evolutionary biologist John Maynard Smith (Figure 6.2) as the twofold cost of males (Maynard Smith 1978). In a sexually reproducing anisogamous

Figure 6.2 John Maynard Smith (1920 – 2004), one of the greatest evolutionary theorists, applied himself to the problem of the evolution of sex. © Corbin O'Grady Studio/Science Photolibrary.

population, any female carrying a mutant allele which made her give up males and start devoting her energies entirely to asexual reproduction would seem to double her reproductive success. Yet sex has persisted in the eukaryotes for hundreds of millions of years and has not, bdelloid rotifers aside, been outcompeted by asexual reproduction.

Sex must have evolved before anisogamy, so it did not immediately face the twofold cost of males. It must, however, have had some significant advantage in terms of offspring viability or success in order to have got going in the first place. However, once anisogamy had evolved, that advantage had to be very strong in order for sex to be maintained, for now the cost of sex to females had become much higher.

There are currently two main theories for why sex persists. The first focuses on genetic mutations and the second on the selection pressures brought about by parasites. Both of the hypotheses are similar in that the advantage of sex lies in creating genetic variation amongst one's offspring.

6.2.2 Mutation and the efficacy of selection

When an asexual organism reproduces, the offspring are identical to the parent, apart from the occasional new mutation. As we saw in Chapter 2, most mutations that have any phenotypic effect are deleterious. Other things being equal, then, the biological performance of organisms deteriorates as mutations accumulate (see section 2.3.3). What stops this happening is natural selection. Individuals carrying more deleterious mutations are less likely to reproduce and so the deleterious mutations are lost from the population.

First consider an asexual lineage in which a mutation occurs. The parent will pass that mutation on to all its offspring. If that mutation is deleterious, then *all* of the offspring will be at a selective disadvantage, as will all of the grand-offspring and all of the grand-grand-offspring. There is basically no way of getting rid of the mutation except by waiting for another mutation that exactly cancels the first, which is extremely unlikely to occur. Thus, if there is selection against the mutation, the likely outcome is that the whole lineage will lose out in competition with other lineages not carrying the mutation and go extinct. The lineage itself will not be able to evolve.

Now consider by contrast a deleterious mutation occurring in a sexually reproducing individual. The individual mates and, following the principles of inheritance, around 50% of the offspring will be carrying the mutation and 50% will not. Thus, even if the 50% carrying the mutation do extremely badly, the lineage has some descendants free of the mutation, who may go on to do well.

What sexual reproduction is doing, then, is creating genetic variance between lineage members, and this increases the efficacy of natural selection to remove the least fit alleles from the lineage, and also to fix the best ones, and to generate novel combinations of alleles. There is experimental evidence that sexual reproduction does increase the efficacy of selection. Goddard *et al.* (2005) studied two types of yeast. The first, the naturally occurring type, has facultative isogamous sexual reproduction. The second strain was genetically engineered to be incapable of sexual function and was thus restricted to asexual reproduction. The researchers allowed each strain to evolve for a number of generations in a novel environment (a Petri dish with limited glucose). They then compared the growth rate of the two experimental strains (the sexual and the asexual one) with that of the ancestral strain, which had never been exposed to limited glucose, in the glucose-limited environment.

The sexual strain got better at growing in the glucose-limited environment relative to its ancestral strain, at a faster rate than the asexual strain did (Figure 6.3). In other words, in the

Figure 6.3 A sexual strain of yeast adapts to a novel environment (by increasing its growth rate compared with the growth rate of the ancestral strain) at a faster rate than an asexual strain. *Data from Goddard et al. (2005).*
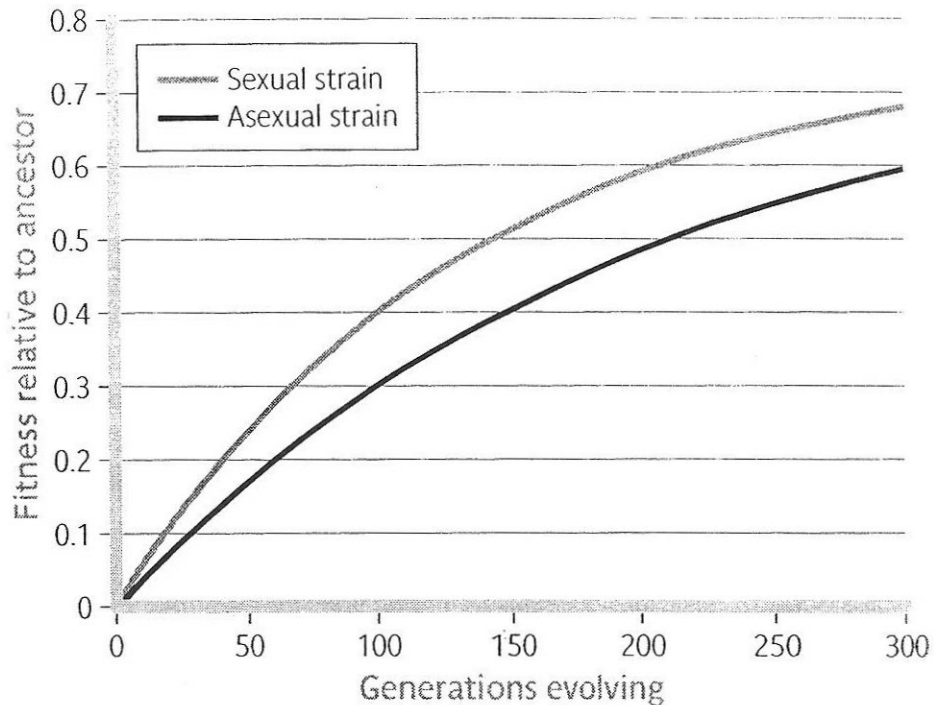
sexual strain, selection was efficient at production adaptation to the glucose-limited environment, whereas in the asexual strain less evolutionary change occurred. This is because the variation produced by sex gives selection something to work with, eliminating the alleles that are deleterious under these conditions and fixing the beneficial ones.

The message of Chapters 4 and 5 was that arguments about selective advantage must always be expressed at the level of the allele ('Why would an allele causing sexual reproduction do better than its competitors?'). So how do we phrase the selective advantage of sex increasing the efficiency of selection in terms of alleles? An allele in a sexual versus an asexual individual would have a disadvantage in competition (because of the costs of sex, see section 6.2.1). However, on the other hand, it would in the long term be more likely to occur in some well-adapted individuals (and less likely to occur in only individuals so bad that they died out) exactly because sex is always shuffling the pack of which alleles co-occur with which others. This benefit could outweigh the cost of sex under certain assumptions about the frequency of mutations and the strength of selection.
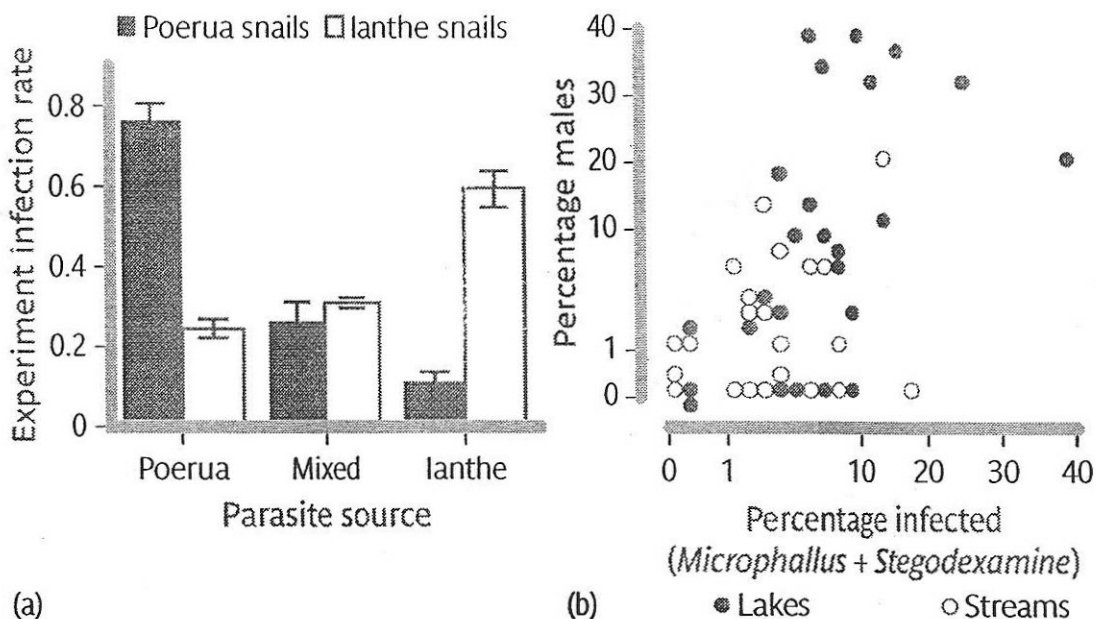
6.2.3 The 'Red Queen' hypothesis

The second hypothesis centres on the idea that individuals benefit directly from being different from their parents. The most commonly discussed reason why this might be the case is because of parasites. Parasites—things like infectious diseases—are constantly evolving to be maximally efficient at infecting hosts of the most common type that they encounter. Thus, being of a different biochemical makeup from other individuals of one's population might make one less

susceptible to infection. This provides a selective advantage to any mechanism that makes offspring different from their parents and sex does this. In fact, the selective advantage of sex is not just in the hosts, but also in the parasites; host immune systems get good at detecting the biochemical makeup of parasites, so sex will be favoured in the parasite too as a mechanism for staying ahead of the host's immune system. This hypothesis is called the 'Red Queen' hypothesis after the character in Lewis Carroll's *Through the Looking Glass* who has to run on the spot all the time just to stay still. Hosts and parasites need to change their biochemical makeup all the time just to maintain their existence level of immunity or ability to infect.

Evidence for the relationship of sex to parasites

Some of the best evidence for the Red Queen hypothesis comes from the study of a New Zealand snail, *Potamopyrgus antipodarum*. This creature exists in both sexual and asexual forms, often within the same habitat. Lively (1987) showed that the proportion of the sexual form in the population was correlated with the rate of infection by two parasites; the more parasites there were, the more common the sexual form was (Figure 6.4). In addition, Lively & Dybdahl (2000) have shown that the parasites are best at infecting whichever genotype of host is most common in their local area. This is a critical pre-condition for parasites to lead to the evolution of sexual reproduction.

Figure 6.4 (a) In an experiment, snails (*Potamopyrgus antipodarum*) from either Lake Poerus or Lake Ianthe were exposed to parasites either from their own lake or from the other one. Parasites are best at infecting hosts they have been co-evolving with. Error bars represent 95% confidence intervals. *From Lively & Dybdahl (2000).* (b) Across different populations, the frequency of the sexual form of *Potamopyrgus antipodarum* is correlated with the frequency of parasites. *Data from Lively (1987).*

Major histocompatibility complex diversity and immunity

Another line of evidence that bears indirectly on the Red Queen hypothesis concerns a group of genes called the major histocompatibility complex (MHC). This group of genes is found in all vertebrates and is involved in how the immune system recognizes parasites to attack. There are often many alleles (e.g. in humans there are around 140 MHC genes and some of them have up to 500 alleles). A possible reason for all this diversity is that parasites become efficient at evading the immune systems made by the most common alleles and so rare types always have an advantage (this is an example of negative frequency-dependent selection, see section 5.2.2).

The relevance of this to sex is that when animals mate, they tend to prefer mates who are genetically dissimilar to them in terms of alleles at the MHC. Similarity is detected through odour. Preference for dissimilarity has been well documented in mice (Roberts & Gosling 2003). In humans, Wedekind & Furi (1997) showed that people prefer the scent of T-shirts that have been worn by people whose MHC alleles are unlike their own. By choosing a dissimilar mate, individuals are making their offspring more different from them at the MHC and thus giving them an advantage in parasite resistance.

The best evidence for such an advantage comes from Atlantic salmon, *Salmo salar*. These salmon are parasitized by small worms. Consuegra & Garcia de Leaniz (2008) compared the MHC genotypes and parasite loads of salmon in the wild from two groups. The first group's parents had mated in the wild. The second group's parents had been in hatcheries where they had no choice of mate and the young had then been released into the wild. The researchers found that the two copies of the MHC genes in the wild-mated salmon were less similar to each other than would be expected by chance. This was not true of the hatchery-mated group, which suggests that parental salmon were actively choosing mates unlike them at the MHC when they had an opportunity to do so. Moreover, the wild-mated salmon had lower loads of parasites than the hatchery-mated group (Figure 6.5), which turned out to be due to their greater MHC diversity.

This study does not compare sexual with asexual reproduction. However, it is relevant to the benefits of sex, in that it shows that combining genetic material with an individual different from oneself provides an advantage against parasites. An asexual salmon would be in an even worse position than the hatchery-mated group in the study since they would be genetically identical to their parent.

6.2.4 The pluralist approach

From the above discussion, you might be wondering what the difference is between the efficacy of selection hypothesis and the Red Queen hypothesis. They both seem to say that it is better to be different from your parents than be identical to them and so sexual reproduction evolved. However, there is a subtle difference. The efficacy of selection hypothesis does not require that sexual offspring have higher reproductive success than asexual offspring, only that the *variance* in their reproductive success must be greater. In the long term, this can lead to sexual reproduction winning out. The Red Queen hypothesis, by contrast, requires that the mean reproductive success be higher for sexual versus asexual offspring.

It is difficult to find evidence that conclusively dismisses the importance of either mechanism. For example, sex becomes more common the longer the generation time of the organism. It is ubiquitous in relatively long-lived organisms such as mammals, whereas many fast-reproducing single-celled organisms are asexual. Long generations increase the rate of mutation and so could make the role of sex in removing deleterious mutations more critical. On the other hand, long generations also means plenty of time for parasites to adapt to one's biochemical environment

Figure 6.5 The number of parasite worms (*Anisakis*) in salmon whose parents had no choice of mate or free mate choice. The hourglass shape represents the inter-quartile range, the central notch represents the median and the vertical bars represent 90% of the values. The advantage of the free mate choice group stemmed from greater MHC dissimilarity between the parents. *From Consuegra & Garcia de Leaniz (2008).*
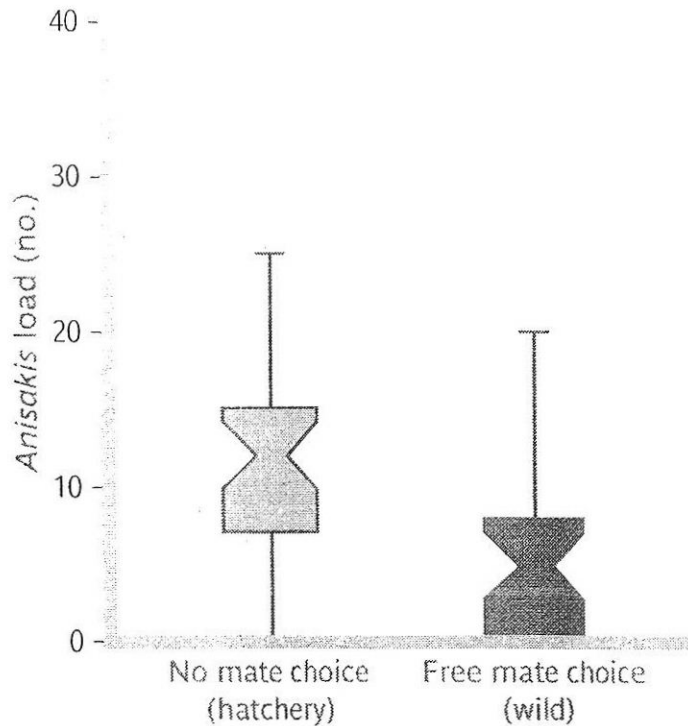
and thus makes the Red Queen advantage of sex all the greater. Thus, the relationship of sex to generation time is not decisive.

West et al. (1999) argue for a 'pluralist' approach, which stresses that both types of mechanism can operate. The efficacy of the selection hypothesis suggests that asexuals will experience greater likelihood of extinction in the very long term (as they fail to evolve), whereas the Red Queen gives them a handicap in the short term (as their offspring have higher rates of mortality due to infection). Thus, the reason that there is not more asexuality in the eukaryotes might be that when it occurs, its spread is slowed by greater vulnerability to parasites, and when it does spread, for example in environments where parasitism is rare, it eventually goes extinct because of reduced efficacy of selection.

This seems a plausible position. However, there are many questions unanswered about the origin of sex, including why sexual organisms tend to do it so often. Most models show that the advantage of sexual reproduction (particularly the mutational advantage, section 6.2.3) could be had by generations of asexual reproduction interspersed with occasional sexual events. There are facultatively sexual species, but in many others—all the mammals, for example— sexual reproduction is obligate in every generation. Why this should be the case is still a topic for investigation.

There are many fascinating further questions—beyond our scope here—concerning how to allocate energy to sexual functions, for example whether to be hermaphrodite or to specialize in one sex, whether to change sex during one's lifetime, and what is the best system (genetic

versus environmental) for determining to which sex an individual belongs, all of which can be fruitfully approached from the adaptationist standpoint (see Questions to consider).

6.3 The evolution of anisogamy

The evolution of anisogamy is clearly a key development in the history of sex, since only once gametes are different sizes can there be said to be males and females. Both isogamous and anisogamous sexual reproduction are widespread and the exact conditions for one to be favoured over the other are still a matter of some debate (Randerson & Hurst 2001; Bulmer & Parker 2002). This is because anisogamous reproduction seems so obviously unfair. In isogamous reproduction, both parties get a half genetic share in the offspring and both pay equally for this. In anisogamous reproduction, the female gets a half share and pays almost all the cost (in cases where, as is common, there is no parental care from males). It is not difficult to see what the advantage is to the male, who gets the benefit of reproduction cheaply, but it is more difficult to see how females might have evolved to tolerate this apparent exploitation.

There are a number of models which suggest conditions under which anisogamy can evolve. Although they differ in details, they tend to share the following assumptions:

1. There are initially two mating types with equal gamete size.
2. Other things being equal, gametes that are larger than average have some advantage, for example they survive longer, are more likely to be found by the other gamete, or can build more viable offspring because they contain more raw materials.
3. Producing larger gametes means an individual produces fewer of them because more energy is required to produce each gamete if they are larger.
4. There is some random, heritable variation in gamete size to start the process off.

In such models, there is a trade-off between quantity of gametes produced and their size or the energy they contain, such that an individual producing many gametes has to reduce the size and energy of each one, and an individual maximizing their size or the energy contained can only produce a few. Crucially, the optimal compromise for one mating type in terms of size and number of gametes depends on what the other mating type is doing. Thus, if one mating type happens to have fewer, relatively larger gametes, the other is selected to specialize in producing more numerous smaller ones. Once this process of specialization has become established, it is very difficult to reverse. Any individual female in an anisogamous species who produces smaller gametes than other females will have reduced reproductive success, for example through her offspring having less energy to start their development, given that the sperm have become so small that they provide very little. Thus, once one mating type has a small gamete, the other is constrained to go on providing a large one. Similarly, any male who produces fewer, larger sperm will produce fewer than his male rivals and they will have no real advantage given the trivial energy contribution of the sperm to the fertilized egg.

Anisogamy is generally common in multicellular organisms and isogamy in single-celled ones. One possibility is that multicellular development, which requires that a lot of energy be present in the fertilized egg to power the process of embryonic development, selects strongly for increasing gamete size, and if one mating type happens to respond more quickly to this pressure, the other can become a quantity specialist or, in other words, male (Bulmer & Parker 2002).

6.4 Sex differences

In species with two sexes, the two sexes often look very different from each in ways that do not follow directly from their reproductive physiologies. For example, the male mandrill is twice the size of the female and has spectacular facial colouring, and in peacocks, males are brightly coloured with a splendid patterned train which is longer than their bodies, whereas females are more drab and lack the train (Figure 6.6). The difference between male and female forms of the same species is called sexual dimorphism. Why should sexual dimorphism exist? Darwin himself speculated that differences between males and females could often arise through what he called sexual selection. Sexual selection is natural selection on the ability to gain mates. If males with a particular trait, such as larger-than-average size or brighter-than-average colouring, can gain more mates than their rivals, then these traits will increase, even if they are detrimental to other aspects of fitness, such as the ability to avoid predators.

   This section deals with sexual selection, examining exactly how it works, why it can lead to extravagant traits like the peacock's train, and why it so often (but not always) produces males that are larger and more showy than females. However, to understand sexual selection, it is essential first to clarify how the stakes in the game of reproduction differ between the sexes.

6.4.1 Bateman's principle

Recall that male gametes are very much smaller than female ones. For a male, producing some extra sperm takes little time and is not very costly in terms of energy. This means he could in principle father almost limitless numbers of offspring and his reproductive success will be limited by how many females he can persuade to mate with him. For a female, by contrast,

Figure 6.6 Males and females are often different: left, male mandrills are twice the size of females and have spectacular facial colouring which the females lack; right, peacocks have bright coloration and an elaborate train, absent from the peahen. *Left: © Corbis/Digital Stock; right: © Photodisc.*
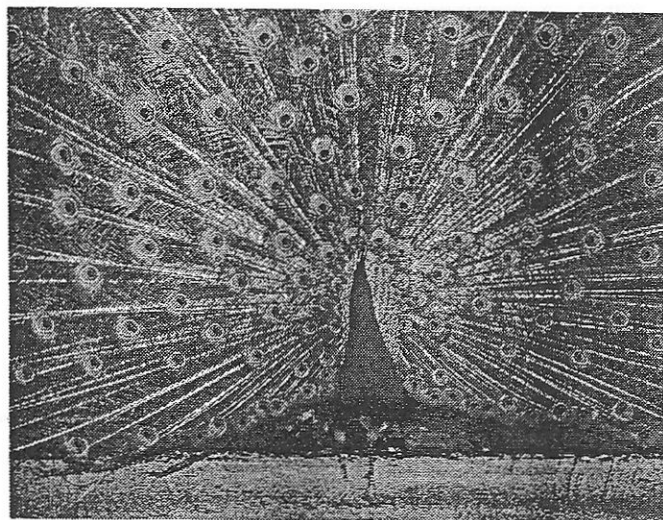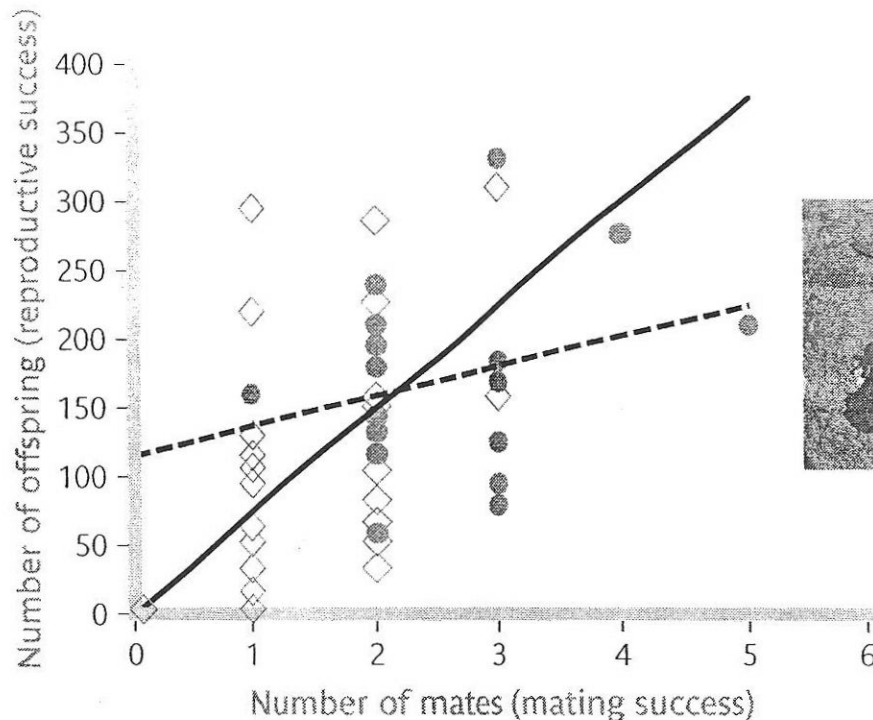
Figure 6.7 Bateman's principle in the rough-skinned newt (*Taricha granulosa*). Male reproductive success (sold line, diamonds) increases more strongly with each additional female mated than female reproductive success (dashed line, circles) does with each additional male mated. *From Jones et al. (2002). Photo © Goldenangel/Fotolia.com.*

producing extra eggs has a significant cost. She can only produce a certain number in her lifetime. There is no reproductive success advantage for her in mating with more partners than are necessary to fertilize the number of eggs she can produce.

This leads to the prediction known as Bateman's principle (after Bateman 1948), which is the following: male reproductive success increases with each additional partner mated to a greater extent than is true for females. Bateman's principle can be tested empirically. For example, Jones *et al.* (2002) studied the rough-skinned newt, *Taricha granulosa*. They used DNA fingerprinting techniques to establish the paternity of all the eggs produced in a pond. For males, the number of offspring sired increased sharply with the number of females mated (Figure 6.7). For females, by contrast, the increase in offspring production with increasing number of males mated was more modest.

A related principle is that the variance in reproductive success is greater for males than for females. A female will always find someone to mate with her, but has an upper limit on how many offspring she could ever produce. Males, on the other hand, have almost no upper limit, but they are faced with females that are choosy and will only mate with the best specimens. Thus, many males will manage no matings at all and a few high-quality individuals will manage to mate with a large number of partners and have very large numbers of offspring. For example, Clutton-Brock *et al.* (1988) studied lifetime reproductive success (number of surviving calves) for male and female red deer, *Cervus elephas*, on a Scottish island. Females who lived to breeding age had between 0 and 9 calves over their lives, with a mean of 5.03 and a variance of 9.09, whereas males who lived to breeding age had between 0 and 32 offspring (with many having 0), with a mean of 5.41 and a variance of 41.9 (Figure 6.8).

Figure 6.8 Male and female variances in lifetime reproductive success in red deer (*Cervus elephas*). Many males had no reproductive success at all, but the most successful males were much more successful than the most successful females. *Data from Clutton-Brock et al. (1988). Photo © Martin McCarthy/istock.com.*
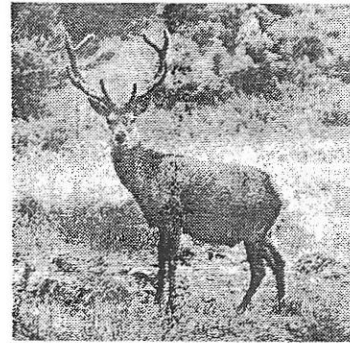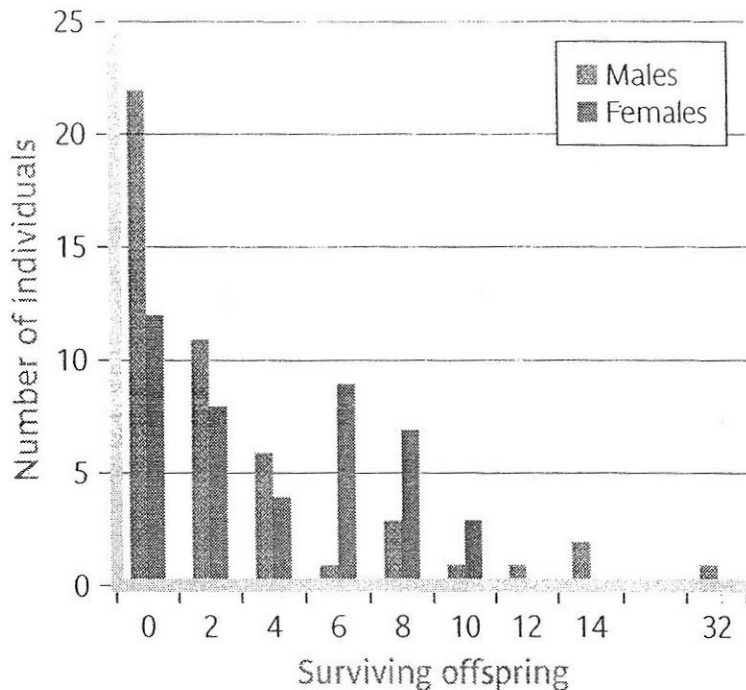
Because of Bateman's principle, other things being equal, males should always seek and take any extra matings available (since the cost is low and the benefit relatively high), whereas females should be more choosy (since the cost is higher and the benefit smaller). This pattern is indeed common in nature. For example, grouse gather every breeding season on display grounds called leks. The males fight with each other for central positions, from whence they puff up their feathers, strut, and call. Females lurk, inspecting the talent on offer, and finally mate with one of the best specimens. Males, on the other hand, will accept all offers. Thus, females spend a long time choosing quality, whilst males maximize the quantity of their matings.

Since an extra mating is usually worth more to a male than to a female, there is generally more benefit for him than for her in investing in anything that might bring about an extra mating. This has consequences for how males compete with other males (section 6.4.2) and how they evolve to please females (section 6.4.3).

6.4.2 Intrasexual competition and sexual dimorphism in size

In many species, males fight with each other much more than females do. Fighting between males is an example of intrasexual competition. The reason males fight each other more than females (and intrasexual competition is generally more intense) follows directly from Bateman's principle. Fighting is a risky business and should only be undertaken to the extent to which the benefit is greater than the cost. The benefit of fighting will often be gaining access to more mates (by ousting or driving away one's rivals). Because of Bateman's principle, every extra mate gained will have a greater effect on reproductive success for males than for females. Thus, fighting is more often a worthwhile endeavour for males than for females.

Figure 6.9 In seals, sexual dimorphism in size increases with the number of females that a male controls. Each data point represents a species. *From Alexander et al. (1979).*
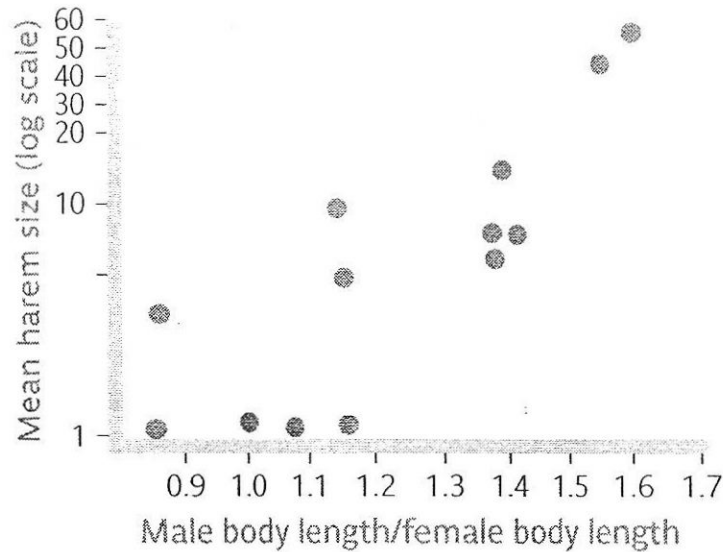
This has a consequence for the evolution of body size. Having a larger body is advantageous in combat. However, growing large takes time and energy. A creature that carried on growing for its whole life would have a size advantage, but it would have no time or energy for reproduction. Thus, a trade-off point is reached where the returns to growing any more are not sufficient to outweigh the costs and organisms are selected instead to cease growth and begin reproducing. However, since for males the potential fitness benefits of successful combat are larger than they are for females, this trade-off point is reached later. In other words, to the extent that Bateman's principle is true, it is economic for males to invest in increasing their body size for longer than it is for females. This is why males are bigger than females in so many species.

This hypothesis can be tested directly because organisms differ in the extent to which the male reproductive variance is greater than the female one (for reasons we will discuss in Chapter 7). For example, male seals of some species defend large harems of females during the breeding season (and thus the male reproductive variance is large), whilst males of other species have smaller harems or do not defend harems at all, which means that the male variance is closer to the female variance. Alexander *et al.* (1979) showed that the greater the harem size, the greater the extent to which the male is bigger than the female (Figure 6.9). In elephant seals, with large harems, an adult male can be twice as long as a female and six times as heavy. Male–male fighting is very common and intense in this species in the run-up to the breeding season. In harbour or common seals by contrast, there are no harems, less male–male fighting, and the male and female are only modestly different in size. Thus, there is good comparative evidence that it is greater variance in male than female reproductive success that drives the evolution of sexual dimorphism in size and male–male aggression.

6.4.3 Female choice and ornamentation

A second way males may compete for extra matings is by their attractiveness to females. Darwin himself hypothesized that highly ornamented male traits such as the peacock's train

might have evolved because it made the male bearing it more attractive to females. This hypothesis has been largely confirmed. However, it raises further questions. Why would females prefer ornamented males? And why would many of the sexual ornaments we see in nature, like the peacock's train, be so exaggerated? In this section, we first review some evidence that male ornaments are indeed the product of female choice, then look at the evolutionary mechanisms that lead to male ornaments becoming exaggerated.

Do male ornaments function to attract females?

The first step in showing that male ornaments exist because they attract females is to show that females actually prefer males with the ornaments. In a classic study, Møller (1988) examined tail length in the barn swallow, *Hirundo rustica*. Males of this species have elongated tail feathers compared with the females. Møller cut a section off the tail of some males and glued it onto the tails of others. Thus, he had birds with shortened tails and birds with artificially elongated tails. He compared the time it took from arrival at breeding grounds to find a mate for these two types of male, and also two control groups: males whose tails had not been manipulated and males who had had a section of tail cut off and glued back on again. Males with elongated tails paired up more quickly than the controls and males with shortened tails took a long time to find a mate (Figure 6.10). Thus, the long tail really does make males more attractive to females.

The tails of the elongated group were actually longer than any tail the females would ever have seen occurring naturally. This raises the question of why males do not just evolve tails of that length, given the mating advantage. The answer is that it is costly to do so. Males with the elongated tails caught less food and as a consequence were in poorer condition the next season. Thus, males have evolved tail elongation to the point where any extra mating success they gain from growing the tail any further will be outweighed by the costs to their flight and feeding.

Figure 6.10 **Male barn swallows (*Hirundo rustica*) find a mate more quickly than usual if their tail feathers are artificially elongated and less quickly than usual if they are shortened.** *Data from Møller (1988).*
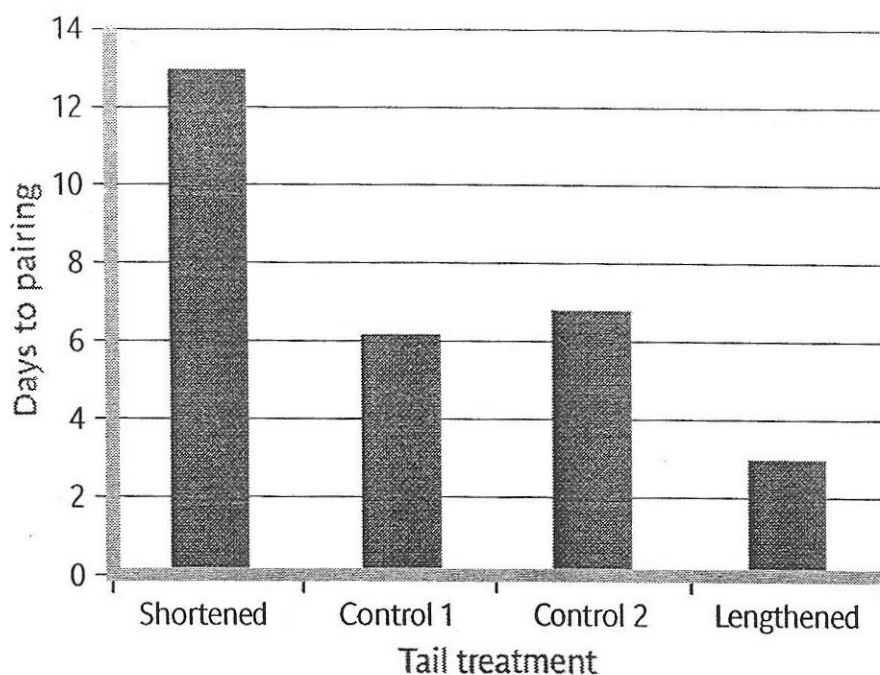
Results similar to those for the barn swallows have been found for many different types of male ornament in many different species. The ornament can be a behavioural as well as a bodily structure. For example, in a songbird, the European sedge warbler, Catchpole (1980) showed that males who sang the most elaborate songs were the ones who mated most quickly.

Why are male ornaments attractive to females?

The evidence that male ornaments are attractive to females is compelling, but why should they be so? What benefit is there to females in choosing the most ornamented males? Historically, there have been two approaches to this problem: Fisher's (1930) and Zahavi's (1975). These are known colloquially as the 'sexy son' hypothesis and the 'good genes' hypothesis. We will review each in turn and then conclude that they are not mutually exclusive and are usually likely to operate in tandem.

The sexy son hypothesis

The sexy son hypothesis is a great example of how evolutionary processes can be at once very simple and also extremely hard to understand. It basically states that if there is any initial slight preference amongst females for males with longer tails, then the preference for the long tail and the length of the tail itself co-evolve to both become ever greater over time.

The key to understanding this runaway is the following. Females who choose a mate with a longer than average tail will have sons who have longer than average tails (because the sons will inherit it from their fathers). Thus, there is a fitness advantage to choosing a long-tailed mate if only because one's sons will thereby be attractive. Fine, but how does this lead to tail length becoming exaggerated? In general, those females with the strongest preference for long tails will mate with those males who have the longest tails. This creates a genetic correlation between the preference for the trait and the trait itself. As we saw in section 5.4.3, when selection acts on one of a pair of genetically correlated traits, the other is changed too, so as selection favours a stronger preference (because females with a stronger preference have sexier sons), the length of the tail is dragged along as a correlated trait. However, as tail lengths get longer, the sons of the longest-tailed males get sexier and the fitness payoff for having a stronger preference becomes greater. The trait and the preference are in a positive feedback loop.

Fisher's hypothesis has nothing to say about where the initial slight preference for longer tails came from, but it only needs to be slight. It could be as simple as males with longer tails being easier to see or to identify as males. The point of the Fisher process is that the slight initial difference can be amplified by selection into a strong female preference and an exaggerated male trait without having to postulate any further functional effects of long tails.

The good genes hypothesis

The good genes hypothesis starts from a slightly different point of view. What male ornaments such as long tails, bright coloration, or energetic singing all share is that they are costly, that is it would be difficult to allocate enough energy to doing them well unless one had energy to spare, meaning that one was feeding effectively, not too infested with disease, not carrying too many deleterious mutations, and so on. Thus, females choose males with the largest ornaments because those males are proving that they have the quality to do well in the current environment (hence 'good genes'). Lower-quality males simply cannot produce signals as elaborate as those produced by higher-quality males. Males invest in ornaments as much as they can to signal their quality to females. The reason that the ornaments tend to be so exaggerated is that if they were not costly, all males could produce them and they would not discriminate the high- from the low-quality ones.

In the good genes model, the female is choosing males of high quality because quality is heritable. This makes a subtly different prediction from the Fisher hypothesis. Under Fisher's hypothesis, the (male) offspring of long-tailed males need to also have long tails and this needs to make them more attractive to females. Under the good genes model, all the offspring of long-tailed males need to be of better quality in general, that is you would expect them not just to be more attractive, but to survive better and have lower parasite loads.

Evidence for good genes and sexy sons

There is evidence for sexy son effects and for good genes effects on female mate choice. One of the key predictions of the Fisher model is that there should be a genetic correlation between preference for the ornament and the ornament itself. Bakker (1993) studied sticklebacks, amongst whom red coloration is a sexually selected male ornament. He was able to measure experimentally the strength of the preference that females have for red coloration in males. He showed that the stronger a male's red coloration, the stronger his sister's preference for red coloration in males (Figure 6.11). This shows that the alleles for the preference and the trait are indeed assorting together, as Fisher's model requires.

As for good genes, a number of studies have shown that the offspring of highly ornamented males survive better or have lower parasite loads than the offspring of males with small ornaments. Amongst the barn swallows, the offspring of long-tailed males' resistance to parasites is heritable. Møller (1990) showed this by an adoption study in which he moved chicks into different nests (to eliminate effects of shared environments). He found that the parasite of the biological parent predicted that of the offspring and moreover that chicks whose fathers had

Figure 6.11 In sticklebacks (*Gasterosteus aculeatus*), the intensity of males' red coloration is correlated with the strength of their sisters' preference for red coloration in males. Fisher's runaway theory predicts that such genetic correlations will exist. *From Baker (1993).*
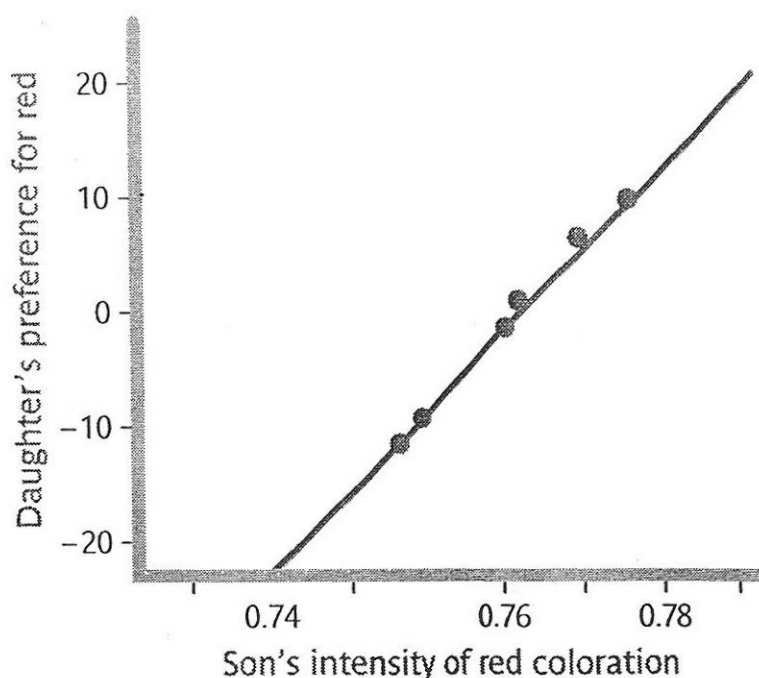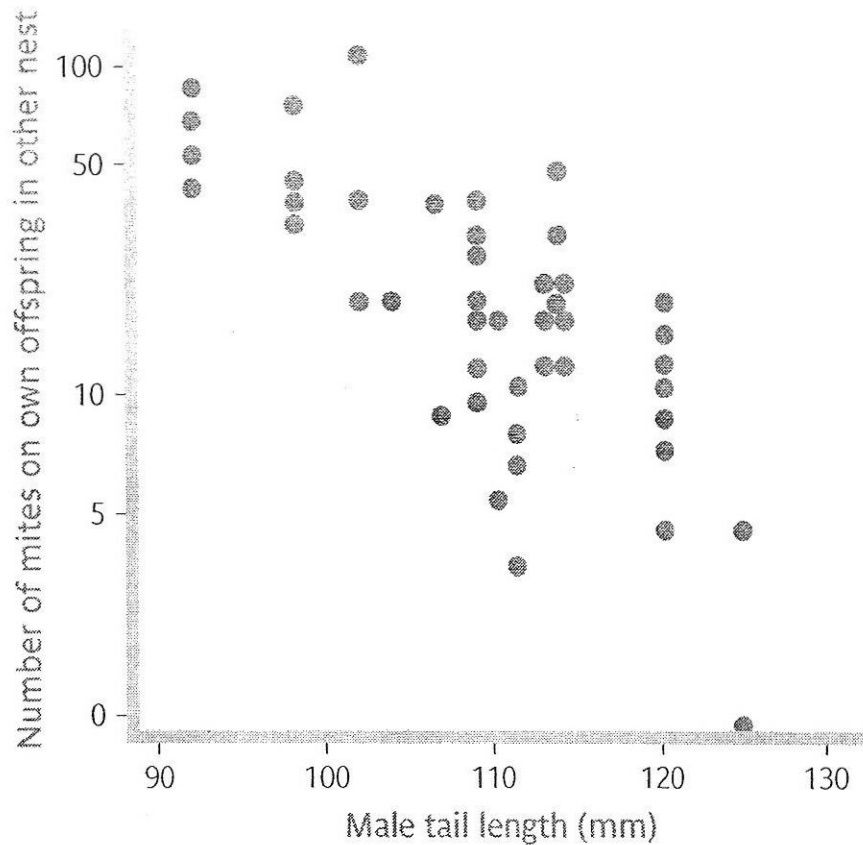
Figure 6.12 Male barn swallows with longer tails sire offspring with fewer parasites. This is true even if the offspring are raised in other nests, suggesting that heritable genetic quality is the explanation. *From Møller (1990).*

longer tails grew up with fewer parasites (Figure 6.12). These findings are consistent with the idea that males, through their long tail feathers, are signalling their heritable genetic qualities such as parasite resistance.

Complementarity between good genes and sexy sons

The good genes and sexy sons models are often framed as alternatives, but in fact they are not mutually exclusive. Moreover, they are both likely to operate. Choosing a male who is signalling good genes will benefit a female both through making her offspring more healthy in general and making her sons more attractive to females in particular. Also, as a trait becomes more and more exaggerated through the Fisher process, it becomes more and more costly to produce it and males will vary in their ability to do so. A trait under Fisherian selection is therefore likely to become revealing of male quality because some males will be able to allocate enough energy to displaying it and some will not. Theoreticians have thus realized that the two processes are tightly connected and may often occur in tandem (Kokko et al. 2002).

6.4.4 Sex-role reversal

Is Bateman's principle always true, producing choosy females and males that compete for mates in every anisogamous species? Our discussion of Bateman's principle focused exclusively on the

costs of producing the gamete. However, these are not always the only costs of reproduction. Parents of many species feed their young after conception or even develop them inside their bodies. Trivers (1972) pointed out that, in considering the costs and benefits of mating, what matters is the *total* cost to each sex of a reproductive episode, not just the cost of the gamete.

In mammals, it is the female that gestates the offspring inside her body, the female that lactates, and often the female that provides other care too. Mostly, males do nothing for the offspring apart from mating. Thus, the difference between the costs for the two sexes is made even greater by considering the costs of post-conception parental investment as well as those of the gamete and Bateman's principle holds true. However, there are organisms—many penguins, for example—where mating pairs share the raising of offspring more or less equally. This means that the difference in cost of a reproductive episode for a male and a female is slight, and, accordingly, males tend to be neither larger nor more ornamented than females in these species.

There are also species where the male does all the post-fertilization care. This more than offsets the initially lower gamete cost and means that the cost asymmetry between the sexes is exactly reversed. Accordingly, we should predict that in these species it will be females who have the larger variance in reproductive success, females who will be larger and more ornamented, and males who will be more choosy.

Jones *et al.* (2001) studied mating success in a pipefish, *Syngnathus scovelli*, off the coast of Florida. In these animals, the female transfers the fertilized eggs to a patch or pouch on the male, who carries them around until they hatch, and so the male invests more time and energy in a clutch than the female does. Using DNA fingerprinting, Jones and colleagues showed that the variation in reproductive success was also the reverse of the usual pattern. All males held just one brood (from one female), whilst the most successful females had broods with four males and many had none (Figure 6.13). The variance in female mating success was around seven times the variance in male mating success, which is an asymmetry as strong as that seen

Figure 6.13 Sex-role reversal. In the pipefish (*Syngnathus scovelli*), the variance in reproductive success is greater for females than males, and accordingly females are larger and more brightly ornamented. *From Jones et al. (2001). Photo © Corel.*
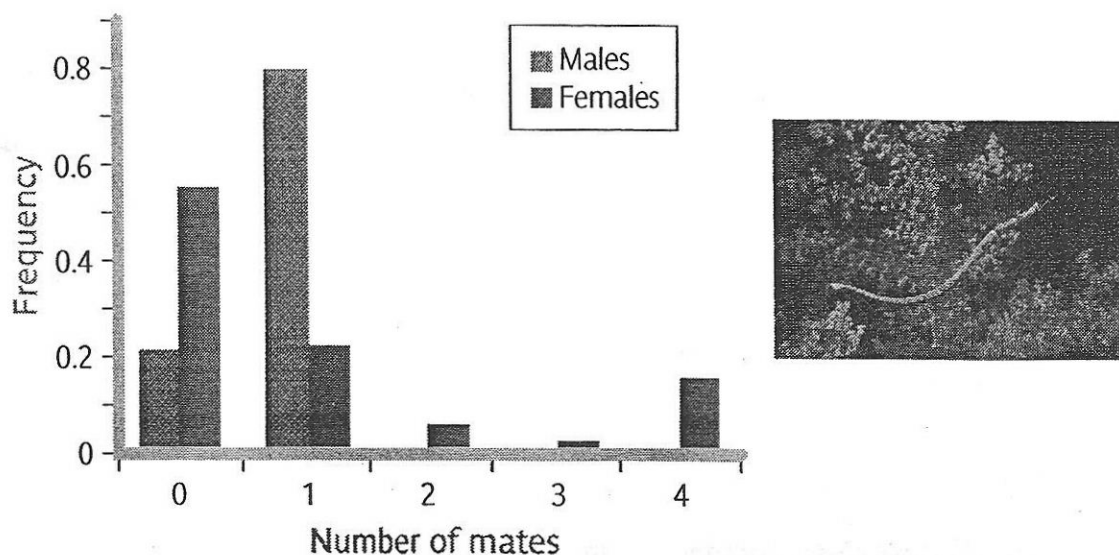
the other way around in sexually dimorphic mammals. Satisfyingly, in this species of pipefish, females are larger than males and have brilliant stripes, which the males lack. The researchers were also able to show that, amongst the females they captured, those that had managed to mate were larger and more brightly ornamented than those who had not, which demonstrates sexual selection in action.

Pipefishes and other sex-role-reversed species are examples of 'the exception which proves the rule'. That is, typical sex differences are reversed, but this is because the difference in costs of reproduction is reversed and so theory predicts that the females should be larger and more ornamented. Their existence does mean, however, that we need to formulate Bateman's original principle slightly more carefully. Rather than saying that the male will always have a larger variance in reproductive success than the female and will therefore compete for mates, we need to say that whichever sex invests less per episode of reproduction will have the larger variance in reproductive success and will therefore compete for mates.

6.5 Pluralism in sexual strategies

Our discussion so far has stressed how the sex with the lower parental investment grows as large as possible and competes for mates, whilst the sex with the higher parental investment is choosy and only seeks one mate. This picture is a slight simplification for two reasons. First, females do often seek more mates than necessary to fertilize all their eggs (section 6.5.1) and, second, males often have alternative tactics for gaining mates (section 6.5.2).

6.5.1 Female multiple mating and extra-pair copulation

Most birds and some mammals form long-term pair bonds and biologists used to believe that females in these species only mated with one male. DNA fingerprinting has allowed us to understand that this is not so; females often mate with multiple males, even if they have a social pairing with just one. Matings that take place with a male other than the social partner are called extra-pair matings. Extra-pair matings are quite common in many pair-bonding species, and female multiple mating in general more common still. Some people have argued that the existence of multiple mating by females is a challenge to Bateman's principle, but this is not strictly correct. Bateman's principle only states that the benefit of an extra mating is greater for a male than for a female; it does not state that there is no benefit for the female.

Females mate with multiple males for several reasons. Where there are pair bonds, the best males may already be paired up and so a female has to settle for a male that is available and prepared to choose her. It might still be worthwhile for her to accept even quite a low-quality male as a social partner because having a social partner may aid in parenting or territory defence. However, in terms of genetic makeup of her young, she will do better to be fertilized by the highest-quality male (or the one most dissimilar to her at the MHC) than by her social partner.

Evidence for effects of this kind comes from the blue tit, *Cyanistes caeruleus*. Kempenaers *et al.* (1997) showed that between one-third and one-half of all nests contained chicks fathered by an individual other than the social partner of the female. It was rarely the case that all the chicks were the result of extra-pair matings. Rather, the females were obviously mating with both the partner and another male in close succession and raising mixed broods. The researchers

Figure 6.14 Extra-pair copulation in the blue tit (*Cyanistes caeruleus*). Male partners with short songs are disproportionately likely to lose paternity to extra-pair males. The strophe is a unit of song. *From Kempenaers et al. (1997). Photo © Andrew Howe/istock.com.*
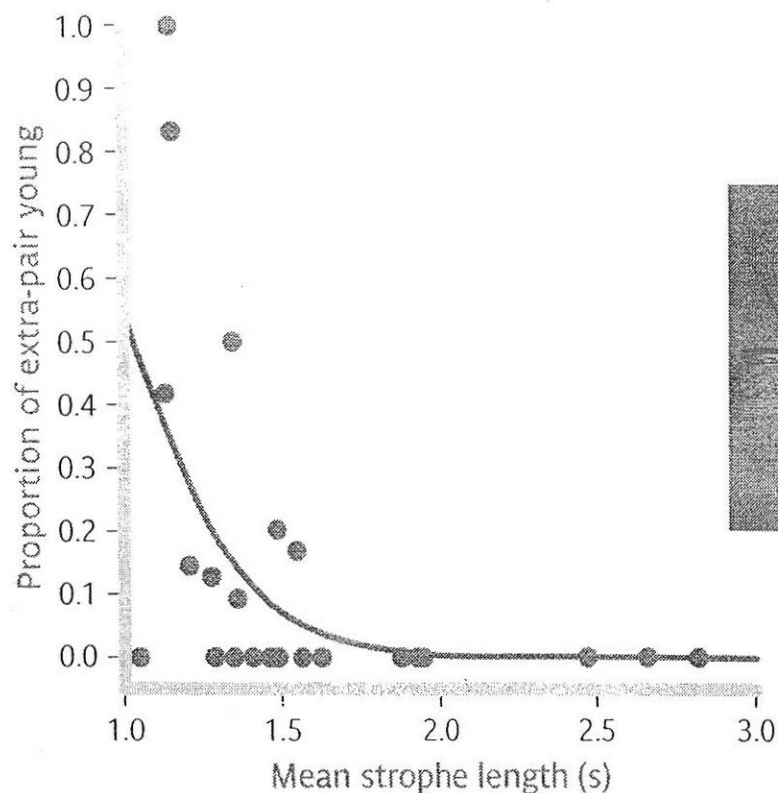
showed that it was low-quality males who lost paternity to an extra-pair male. For example, males who sang long songs fathered all the offspring in their nests, whereas males with short songs had extra-pair offspring in theirs (Figure 6.14). The mechanism for this seems to be that females with a neighbour who is more attractive than their social mate seek extra-pair matings. The reasons for them doing so are also clear: in this species, the offspring resulting from extra-pair copulations are more likely to survive than their nest mates fathered by the social partner. Thus, females are using extra-pair mating to choose good genes.

The dynamics of these situations are very interesting. It is still worth low-quality social partners investing in their partnership because at least some of the offspring may be theirs. However, higher-quality males gain a disproportionate fraction of all extra-pair matings, which amplifies the variance in male reproductive success and strengthens the operation of sexual selection.

6.5.2 Alternative male reproductive strategies

The best outcome for a male seeking to maximize his reproductive success is to be the largest male, the most dominant in contests with other males, and the most ornamented. However, by definition, not every male can be these things. Males often have secondary tactics for gaining some matings if they are not doing well in the primary competition. For example, in a colonial bird called the great-tailed grackle, the largest males hold a territory and sire offspring via

both social partners and extra-pair matings. Smaller males are unable to defend a territory successfully. They either remain in one colony seeking the occasional extra-pair mating and waiting for a territory to become available or else they become transient, roaming from colony to colony picking up occasional extra-pair matings and providing no further investment. The reproductive success of these transient males is very much less than that of the successful territory holders (Johnson *et al.* 2000). However, they are making the best of a bad job and it is at least greater than zero. Such alternative male tactics are very widespread.

6.6 Sexual selection and mate choice in humans

You have probably been wondering through sections 6.3 and 6.4 to what extent principles like Bateman's, and the concomitant sex differences in mating strategy, apply to humans. In this final section, we establish how humans fit in to the pattern described for other organisms.

6.6.1 Bateman's principle in humans

A first question to ask is whether the variance in male reproductive success in humans is greater than that in female reproductive success. Table 6.1 shows estimates of male and female variance in reproductive success (number of offspring) for several different societies. For contemporary Britain (at the age of 45 years), the male variance is only around 6% higher than the female variance, whereas for the Kipsigis, a group of Kenyan farmers amongst whom rich men have many wives and poor men tend not to have any, the male variance is around 15 times the female variance. Two groups of hunter-gatherers are intermediate between the British sample and the Kipsigis. Thus, such cross-cultural evidence as there is suggests that the variance in male reproductive success does tend to be higher than the variance in female reproductive success, but

Table 6.1 **Variance in human male and female reproductive success in four very different societies. In contemporary Britain, male variance is only slightly higher, although these data are from 45 years of age, and the difference may become more marked as the men get older, whereas for the Kipsigis, an African society where rich men have many wives, the disparity is vast.** *Data from Daly & Wilson (1983), Borgerhoff Mulder (1988), and Nettle (2008).*

| Society	Description	Male variance	Female variance	Ratio male:female variance
!Kung	African hunter-gatherers	9.27	6.52	1.42
Xavante	Brazilian hunter-gatherers	12.1	3.6	3.36
Kipsigis (Nyongi cohort)	Kenyan farmers	54.03	3.62	14.93
Contemporary Britain	Industrial and service economy	1.74	1.64	1.06

that the local economic and social situation modifies the extent of the difference (see Chapter 8 for why different societies might have different marriage systems). However, the difference is always in the direction of red deer, not of pipefish, and thus we should expect humans to have evolved the corresponding pattern of larger male size and greater female choosiness.

6.6.2 Big males and choosy females

Within the primates, as in the seals and their relatives, the degree of sexual dimorphism in size covaries with the intensity of male–male competition. Gorilla males, who defend harems, are about twice the size of females, whereas amongst gibbons, who are extremely monogamous, males and females are the same size. Humans are intermediate and rather closer to the gibbon pattern, with males around 10% bigger than females. This suggests an evolutionary history of men experiencing slightly larger variances in reproductive success than women, as corroborated by the hunter-gatherer data described in section 6.6.1.

Human males are much more likely to be involved in violence than human females, and both the victims and the perpetrators of homicide are overwhelmingly unmarried young men (Wilson & Daly 1985). Men compete with each other more riskily than women do, leading to greater male than female death rates from accidents and violence. This is particularly pronounced during the period of peak reproductive competition, from about 16–25 years (Figure 6.15).

Figure 6.15 The male death rate relative to the female death rate in the USA, broken down by age. Amongst the very young and very old, there is no sex difference in death rate, but in the peak years of reproduction, men are three times more likely to die than women. Breaking the causes of death down into deaths attributable to disease versus those attributable to violence and accidents shows clearly that the sex difference is due to greater risk-taking and aggression through the reproductive years. *Data from Wilson and Daly (1985).*
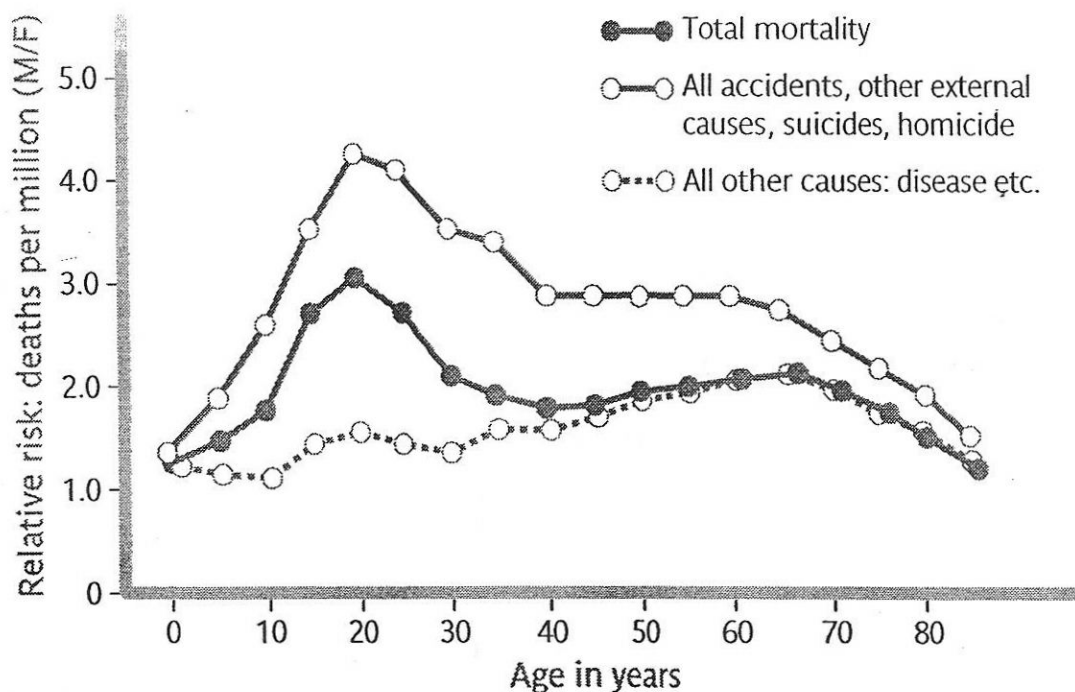
Choosy females

Bateman's principle suggests that human females should be choosier when it comes to mating, whereas males should be more interested in gaining additional mating partners. There is cross-cultural data showing this pattern. Schmitt *et al.* (2003) showed that, in 52 countries from across the globe, men express a desire for a greater number of sexual partners in the future than women, whilst women report requiring a longer period of acquaintance with a man before consenting to sex than men do for sex with a woman (Figure 6.16). There are very interesting local differences in these attitudes and in the size of the sex difference, but the direction of the sex difference is never reversed. Clark & Hatfield (1989) illustrated the difference vividly in a famous study on a university campus, where men or women were approached by an attractive stranger of the opposite sex and asked if they would like to go to bed with them that night. None of the women, but a sizeable fraction of the men, said that they would.

6.6.3 Parental investment

There is a slight paradox in data showing that men desire partner variety and are not choosy. This is because humans pair for long periods and human males make large investments in their offspring. Thus, mating represents a very considerable investment for men, almost as much as for women, and thus one might expect that both sexes would be choosy in humans.

In fact, survey evidence suggests that both sexes are choosy, particularly when selecting a long-term partner, and both sexes place kindness and reliability high on their lists of desired

Figure 6.16 **In surveys across 52 countries, men report desiring more sexual partners than women (left) and women report being less likely to consent to sex after having known an individual for a month than men (right).** *From Schmitt et al. (2003).*
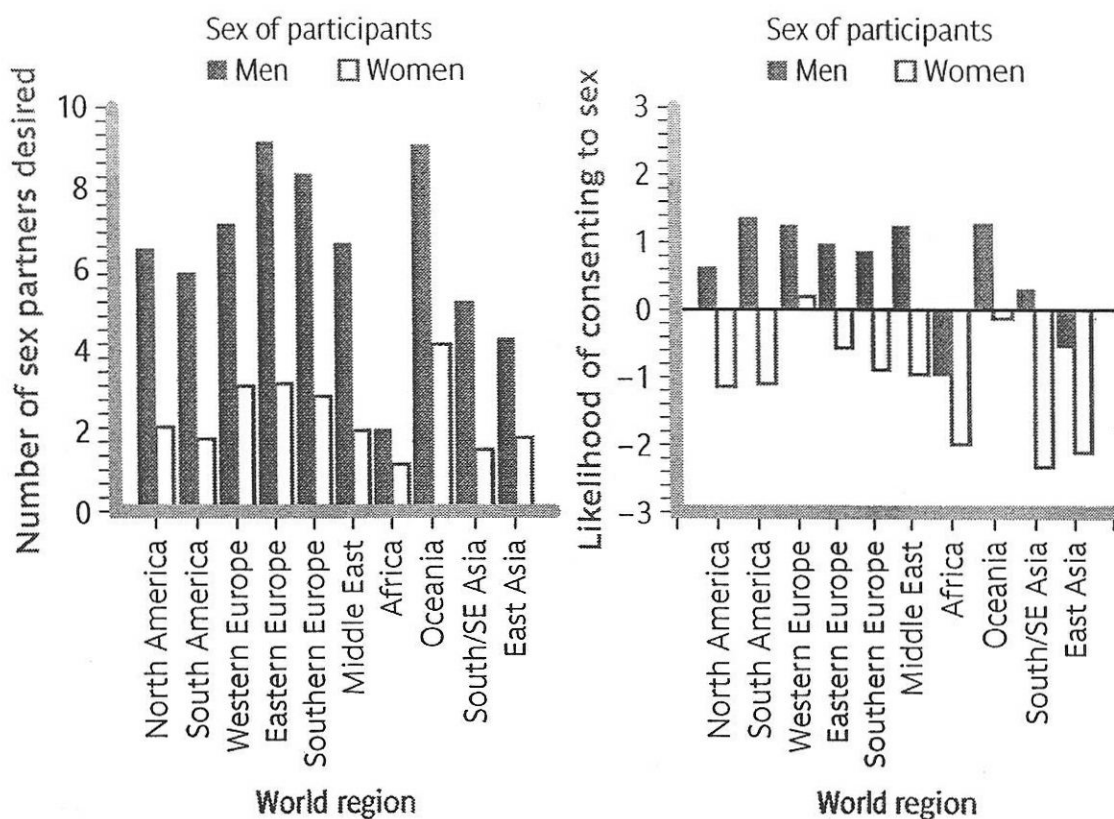
Figure 6.17 Reported mate preferences in different countries. (a) On a scale of 0 – 3, how important are good financial prospects in a potential mate? (male respondents, grey bars; female respondents, blue bars). (b) How important are good looks in a potential mate? (male respondents, grey bars; female respondents, blue bars). *Data from Buss (1989), which includes many more countries.*
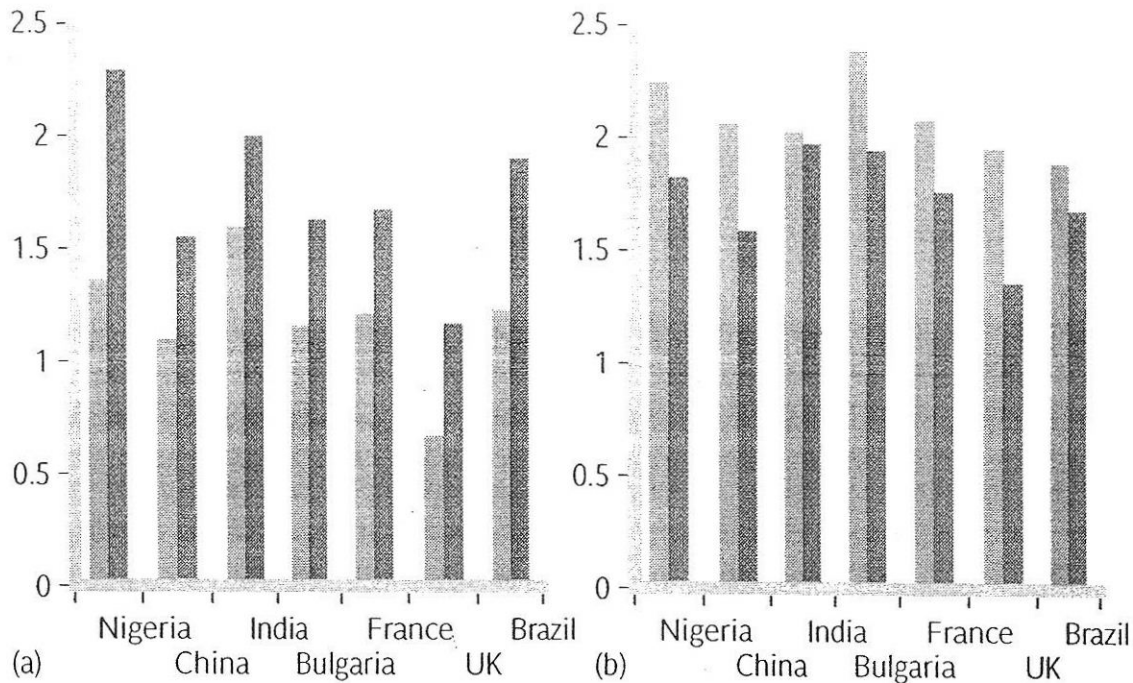
characteristics. However, the two sexes may be choosy in subtly different ways. Men need to know that the women they are investing in will be fertile and produce healthy offspring, and they place a relatively high value on physical appearance, particularly such characteristics as symmetry and body fat distribution, which signal health and fertility. Women have different priorities. Human children are extremely costly and require a long period of material investment, and women in many cultures prefer men with material resources (income or wealth) to offer. Buss (1989), in another cross-cultural survey study, showed that, across 37 countries, women put a higher value on income in a potential mate and men a higher value on physical appearance (Figure 6.17). Once again, the precise attitudes and the magnitude of the sex difference vary considerably with local ecology, but the sex difference is never reversed.

These patterns may explain why ornamentation takes the forms it does in humans. Unlike peacocks and mandrills, men do not have brightly coloured or ornamented bodies, but they do exploit cultural opportunities to signal their wealth and status, whilst women's fashions often emphasize their body composition and cues of youth and health.

6.6.4 Strategic pluralism in human mating

How do we reconcile the data showing that men desire partner variety and consent to sex at low acquaintance with the argument of section 6.6.3 that human males are high investors who ought to be choosy? The answer lies in recognizing that there are alternative mating strategies available to both males and females.

Male short-term mating

Mating can be an expensive decision for a man, if he is going to devote himself to the relationship and the offspring it might produce, but it is not *necessary* that it be costly. Unlike the woman, he can produce an offspring with no cost beyond that of copulation itself. Thus, although men might be choosy for a long-term relationship in which they plan to invest, they also have available to them a short-term mating strategy with no post-conception investment, which they might resort to if the context favours it. The male reports of desire for sexual variety and for willingness to consent to sex at low acquaintance may reflect the operation of this short-term alternative strategy.

Female extra-pair mating

Just as men have an alternative strategy available to them, so do women. In choosing a social partner, women have to accept someone who is also available and prepared to invest, and this may not represent the maximal genetic quality they could achieve. Surveys show that a sizeable fraction of women at least sometimes have sex outside of their established relationship (Koehler & Chisholm 2007) and genetic studies reveal that a small fraction of children are not fathered by their mother's long-term partner.

Like the blue tits, then, women sometimes seek genetic quality by extra-pair mating. Further evidence that this is the case comes from studies showing that highly symmetrical (i.e. high-quality) men report having more often been a partner in an extra-pair mating (Gangestad & Thornhill 1997). Moreover, at the point of their menstrual cycle where women are most fertile, they show more interest in and fantasize more about men other than their current partner (Gangestad et al. 2002), as well as being more likely to actually commit an extra-pair mating (Bellis & Baker 1990).

✅ Summary

1. Sex of some kind is extremely widespread in nature, but there are many different types of sexual system.

2. Sex is adaptive because of some combination of increasing the viability of offspring (e.g. through their resistance to disease) and increasing the variance amongst them, which makes natural selection more efficient.

3. Because of anisogamy and differential parental investment, the two sexes often benefit to different extents from gaining an additional mate. This leads to the evolution of one sex that is larger, more aggressive, and more highly ornamented than the other.

4. Male ornamentation is attractive to females in many species because the offspring of such males do better through some combination of overall higher quality and greater attractiveness.

5. There are often multiple mating strategies available to both sexes, such as territory-holding versus mobility or in-pair versus extra-pair mating.

6. Many of the principles seen elsewhere in nature, such as greater male than female variance in reproductive success, greater male aggression, female choice, and extra-pair mating, also characterize humans.

? Questions to consider

1. What factors do you think might determine whether an organism evolves to be simultaneously hermaphrodite like the hamlet fish rather than exclusively male or female like humans?

2. In many organisms, the optimum size in terms of reproductive success for males is larger than the optimum size for females. For this reason, males are often larger than females. However, there are at least three different ways of bringing this about. One is the pattern seen in many mammals, including humans, where sex is determined genetically and males grow for longer than females. The second is seen in a shrimp-like creature, *Gammarus duebeni*, where day length when the eggs are laid determines which sex the egg develops into. This results in eggs laid early in the year becoming males, who are then larger when the breeding season comes around. Another is the pattern seen in wrasse, where all individuals grow on the same trajectory, but are female when they are small and then change their sex to male as they get bigger. What kinds of factors would favour one of these systems over the others?

3. In Møller's barn swallow experiments, why do you think he had a group of birds where a section of the tail had been cut off and stuck back on again?

4. In Britain, a man is only allowed to be married to one woman and yet the variance in male reproductive success is higher than the variance in female reproductive success. How can this be?

→ Taking it further

The sheer diversity of sexual systems in nature is outlined entertainingly by Judson (2002) and the diversity of male and female mating strategies laid out by Birkhead (2000). A readable book-length treatment of the issue of the evolution of sex is Ridley (1993), whilst a recent review article is West *et al.* (1999). On current theory relating to mate choice and the evolution of ornamentation, see Kokko *et al.* (2002, 2003). Important contributions to the psychology of mating in humans include Buss (1989), Gangestad & Simpson (2000), and, with a focus on the way mate preferences vary according to ecology, Gangestad *et al.* (2006).