C H A P T E R   1

The Logic of Sex

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."
>
> —Charles Darwin, *The Origin of Species*

SUMMARY

In the history of life on Earth, the first organisms reproduced asexually. Sexual reproduction then evolved and came to predominate. In some lineages, some species or some individuals of some species, have reverted to asexual reproduction. The history of changes from asexual to sexual reproduction, and in some cases back again, are outlined.

The predominant form of reproduction—sexual reproduction—involves, in most cases, the existence of two different forms of a species, the male and female sexes. The definer of sex is the size of the reproductive cell produced by an individual. In a species, by definition, males produce smaller reproductive cells than females.

Differences in the size and number of reproductive cells produced by males and females have given the sexes different interests. The differences in the roles of males and females have led to conflicts in relation to reproduction between the sexes. These sexual conflicts have led to various types of sexual selection. Members of one sex, usually males, compete for access to the other sex for fertilization opportunities. Members of the other sex, or in some cases both sexes, exercise careful choice as to which potential mates should be allowed fertilization opportunities. Sexual selection and the ways in which natural selection acts differently on the two sexes have led to a fascinating array of different reproductive strategies. Some of these operate prior to copulation; others after mating has occurred.

INTRODUCTION: FANTASY SEX RATIOS!

Consider, for a moment, Rincewind, the failed "Wizzard" of Terry Pratchet's Disc World—a world that has kept Pratchet as the top-selling fiction writer in

Britain for over a decade. After being attacked by dragons, tree nymphs, and sorcerers; falling off the world; and accidentally saving it on several occasions, despite his own best efforts just to run away, Rincewind finds his own Nirvana on a desert island. There, he encounters female, "abundantly female," representatives of a tribe who had lost all of their menfolk to a deadly plague, and were seeking a male to enable them to continue their line. I wonder what proportion of men have had a fantasy of this type, and what the female equivalent might be. As a student of evolutionary genetics, I long ago accepted the thesis that the biological roles of males and females are fundamentally different and, consequently, that the Darwinian selection pressures acting on the sexes will differ both in nature and intensity. That being so and being male, I freely admit to having little understanding of women, and so shy away from attempting to offer a female equivalent of Rincewind's male Nirvana.

A strongly female-biased sex ratio has been a feature of many science fiction stories, some of the best known perhaps being episodes of television series such as *Dr. Who*, *Star Trek*, and *Red Dwarf*. In perhaps the most extreme fictional stories, such as John Wyndham's (1965) *Consider Her Ways*, the human population has become solely female, males having been wiped out by a male specific pathogenic virus. As we shall see, this story, originally written in 1956, contains some interesting scientific insights. Not only does it involve a microbial male-killer, but the all-female society that evolves has a caste system, with strong similarities to social insects such as bees, ants, and termites, which are numerically dominated by females, only some of which reproduce. Furthermore, this reproduction is asexual, and involves the production of four offspring at a time, all offspring being female. Again, in this there are hints of some Hymenoptera, which reproduce parthenogenetically, that is, without sex.

Images of female-biased sex ratios are not only found in fantasy or fiction. In some human societies, both past and present, powerful males gather harems of females. Harems are a feature of many other mammals, with males fighting to gain and retain groups of females to mate with. Dominant males who are successful in collecting a harem are under regular attack by subordinate or younger males who try to usurp their position. In these species, the dominant males gain mating opportunities at the expense of other males who are denied them. The sex ratio at birth in such species is not biased; only the sex ratio among reproducing adults is female biased. Yet in some organisms, particularly among the invertebrates, female-biased populations are the norm, and the biases are not confined to reproducing adults.

REPRODUCTION — ASEXUAL, SEXUAL, AND SECONDARY ASEXUAL

The Ultimate Aim of Existence: The Passage of Genes

It is often assumed that the ultimate aim of an individual is to reproduce. However, there are exceptions. Damaraland mole rats live in large underground col-

onies, excavating vast networks of tunnels. A colony may consist of up to 40 individuals, all related. All work together to collect tubers and bulbs in the wet season to stock a larder that will sustain the colony through the dry season. Yet, only one pair in the colony breeds. Personal reproduction is put aside in favor of helping siblings. Having the same parents as the other mole rats in the colony, all the individuals share as many genes with all the other members of the colony as they would share with their own offspring.

Among the insects, several groups have evolved caste systems involving reproductive males and both reproductive and nonreproductive females. In these groups, which include the termites, ants, and social bees and wasps, the nonreproductive females have given up the opportunity of producing their own offspring in order to increase the reproductive output of the colony. Some bacteria kill their hosts, thereby committing suicide. In doing so, they make the resources in their host available to other hosts that carry identical copies of themselves. In all these cases, individual reproduction is sacrificed to aid kin that carry the same or a high proportion of the same genes. Examples of this type, in which individual reproduction is sacrificed specifically to increase the transmission of genes as a result of the reproduction of close relatives, which will carry many of the same genes, is termed *kin selection* (p. 144). These examples of kin selection suggest that it may be more accurate to say that the ultimate aim of an individual is to promote the passage of its genes through time whether this is by reproducing itself or by aiding the offspring of others that carry its genes.

Asexual Reproduction

The earliest life on Earth, dating back some 3.8 billion years, or maybe more, undoubtedly reproduced simply by making copies of itself. Many primitive organisms—viruses, bacteria, single-celled algae, and some animals—still reproduce in this way: amoebae, sponges, and sea anemones divide; hydra bud. Many plants, including higher plants have exclusive or partial asexual reproduction through the vegetative production of stolons, rhizomes, leaflets, and tillers. One major problem with asexual reproduction is that all individuals derived from one ancestor would be essentially the same. Only minor variations resulting from rare genetic mutations would exist. Populations of such genetically similar individuals—that by their very existence would have to be well adapted to the conditions in which they lived—would be in danger of extinction, due to the lack of genetic variation, should their environment change. Later, much later, perhaps about 1.5 billion years ago, an alternative form of reproduction arose, which allowed some exchange of genetic material between similar individuals. This involved the temporary fusion of two individuals in such a way that genetic material could reciprocally migrate from one to the other before reproduction. This was the start of sex.

SEXUAL REPRODUCTION

Initially, sex involved the fusion of whole individuals that were approximately the same size. The individuals in question were small, comprising just a single cell. Considering current single-celled organisms that reproduce in this way, such as the simple algae of the genus *Chlamydomonas*, it appears that at some stage in the early evolution of sexual reproduction, differences in the surface chemistry of individuals arose, whereby only individuals with different surface chemistries could fuse.

Genes with harmful effects are often recessive, which is to say they are only expressed when both copies of a gene in an individual are the same. When closely related individuals mate, the chance that both carry the same harmful version of a gene is increased. The offspring of reproduction between close relatives frequently show deleterious characteristics due to the expression of recessive genes. The reduction in fitness of such individuals compared to the norm is called *inbreeding depression*.

The evolution of differences in the surface chemistries in early sexual reproducers would have provided a mechanism that reduced the possibility of fusing with a genetically very similar or identical relative. The evolution of differences in surface chemistry would thus have been selectively favored because it would reduce the instances of rare, harmful, recessive mutations being inherited from both parental cells. In essence, fusing with unrelated cells avoids inbreeding depression.

In single-celled organisms that reproduce in this way, the cells that fuse are of the same size. In most species, only two types of individual occur with respect to their surface chemistry. These are called mating types, one being designated the + or recipient type, and the other the − or donor type.

But, if the reason for evolving different mating types is to avoid inbreeding, why are there just two mating types? With just two mating types, the potential mates available for each individual are reduced by half, assuming there are 50% of each type. This cut would be avoided if there were many mating types. The answer appears to involve the inheritance of organelles, the organs of cells, such as mitochondria and the photosynthesizing chloroplasts. These are inherited in the cytoplasm of cells, not in the nucleus. These organelles are normally inherited just from the female parent (although there are exceptions; e.g., the chloroplasts of conifers are paternally inherited).

The reason for the almost universal uniparental inheritance of organelles is that if they were inherited from both parents, there would be scope for intracellular warfare. Imagine that mitochondria, the energy-producing organelles of cells, were inherited from both parental cells. Mitochondria, of which there are many copies in each cell, pass randomly into daughter cells when the cell splits. There is no mechanism to ensure that the daughter cells each receive the same number of mitochondria. Therefore, if a strain of mitochondria evolved faster replication, it would spread through the population, even if this selfish behavior

were at the expense of its primary function, the production of adenosine triphosphate (ATP), a major carrier of energy in biological systems. The result would be the evolution of more and more selfish, but less efficient mitochondria, to the ultimate detriment of their host cells and the selfish mitochondria themselves.

Confirmation of this theoretical explanation of the limit to just two mating types in almost all species, was synthesized from some remarkable observations of ciliate protozoa, such as *Paramecium* (Hurst and Hamilton 1992). In these ciliates, cells do not fuse. Rather, when two cells lie together, each divides its nucleus. Thus, each forms two haploid nuclei, one of which is passed on to the other cell. Mitochondria are not transferred. Following this exchange of nuclear material, the two cells separate, and the two haploid nuclei that each contains fuse to form a diploid. By this mechanism, nuclear genes originate from two parents, while organelles come from just one. And these ciliates, in which there is no chance of warfare between organelles, have multiple mating types. However, one group of ciliates, the hypotrichs, employs both conjugation (cellular fusion) and gamete fusion. Amazingly, these have multiple mating types for conjugation, but just two for gamete fusion, elegantly confirming the theory.

Sexual reproduction appears to have been successful from the moment it arose. The evolutionary reasons why this novel type of reproduction was successful in competition with asexual reproduction need not concern us for the moment. This complex subject will be discussed in chapter 9.

Sex Cells of Different Sizes

The next major step in the evolution of reproduction came with the rise of multicellular organisms. Once an individual was composed of many cells, the different cells that comprised the whole could be specialized for particular functions. The cells that took the role of fusing together to give rise to new individuals are variously called sex cells, germ cells, gametes, spermatozoa, sperm, oocytes, or eggs. In early multicellular organisms that reproduced sexually, the cells that fused during sexual reproduction were of the same size and may be considered as donor and recipient types. However, in time, the sizes of the donor and recipient cells began to change, the donor mating-type germ cells becoming smaller and the recipient cells larger. Species in which the gametes produced are of the same size are called isogamous. When gametes produced are of different sizes, as occurs in all sexually reproducing higher animals and plants, species are said to be anisogamous.

Geoff Parker and his colleagues (Parker et al. 1972) argued that the change from isogamy to anisogamy was the result of an arms race within a species. They envision a mutation in a population of isogamous individuals that caused one individual to produce slightly smaller germ cells or gametes. The reduction in the cost of production of these smaller gametes would allow this individual to produce greater numbers of gametes. As long as the majority of the rest of

the population were producing normal (i.e., larger) gametes, the mutant would be beneficial, as it would have greater reproductive success through the production of more gametes. Thus, it would start to spread through the population. However, as the smaller gamete–producing mutation increased in frequency in the population, the possibility of two of these smaller gametes fusing would increase. There would then be the possibility that the individual produced by the fusion of two small gametes had insufficient nutrient resources to develop successfully. In this case there would be selection in favor of small gametes that only fertilize large gametes. Furthermore, once there was competition between small gamete–producing individuals, there would be a pressure to produce even smaller gametes to increase the number produced. As the small gametes became ever smaller, selection would have imposed pressure on the individuals producing large gametes to produce still larger gametes with more nutrient resources to compensate.

Parker's theory of the evolution of anisogamy was widely accepted. However, other theories have also been proposed. For example, Laurence Hurst (1990) has suggested that inheriting cytoplasm from just one parent may have evolved to reduce the chance of inheriting parasitic organisms that live in the cytoplasm of host cells. The argument is simple, elegant, and self-evident because it is obviously more likely that progeny will inherit a parasite if this can come from both parents rather than just one.

A further idea, proposed by Laurence Hurst and Bill Hamilton (1992), suggests that the driving force behind the evolution of the uniparental inheritance of organelles in the cytoplasm that arises out of anisogamy is the minimization of the potential for conflict between the cytoplasmic genomes of fusing cells. In the same way that two individuals of a species may be in conflict with one another and compete over food, or mates, or some other limited resource, so the cytoplasms that come together at fertilization may compete. The conflict produced will certainly be to the detriment of the individual created. Should nuclear genes that suppress cytoplasmic mixing, by promoting inheritance of cytoplasm from just one parental cell, arise by mutation, such mutations would be favored.

As yet we have insufficient data on the interactions between intracellular parasites and their hosts, or on the conflict between cytoplasmic genomes, with which to judge the validity of these ideas. It may be noted, however, that these three theories for the evolution of anisogamy are not mutually exclusive, and all three may have had an influence.

We may perhaps combine the three to some extent in a summary of the evolution of anisogamy. Here we may consider the relative contributions of the two types of cell to the new individual. Reduction in the size of gametes produced may initially be beneficial, because more gametes can be produced for a set energetic cost. To avoid cytoplasmic conflict, the genes within the cytoplasm carried on some of the organelles in the cytoplasm should only be contributed by one parent. The gametes of this parent thus have to be large enough to contain sufficient organelles. This gamete will also contain the nutrients nec-

essary to fuel the zygote when it is formed. The other parent must then be stripped of its organelles, or the cytoplasm that carries them, so that it contributes just its nucleus and has no requirement to contribute nutrient resources to the zygote formed. The result is that one gamete will be larger than the other. It then makes energetic sense if the smaller gamete remains mobile while the larger gamete loses its mobility.

Males and Females: The Root of Sexual Conflict

Once gametes are of differing sizes, we can refer to them as different sexes, rather than mating types, for the fundamental distinction between males and females depends purely on gamete size. Females produce the larger and males the smaller gamete. No other difference between males and females is universally definitive. Usually, because the small gamete is mobile, the male gamete, or sperm, moves toward the more sedentary female gamete, or egg. However, there are exceptions to this course of action. For instance, in many seahorses and pipe-fish, the eggs are transferred from the female into the male through a penis-shaped organ, and it is the male that becomes pregnant, caring for the fertilized eggs in a specialized pouch.

Sexual Selection: Competing Males and Choosy Females

The evolution of different gamete sizes, the sexes, and the different roles played by the sexes allowed selection to act on the sexes in different ways. The differences in selection are based, at least in part, on the differences in the gametes that males and females produce. Thus, males produce huge numbers of energetically cheap sperm, while females produce far fewer, but much more costly eggs. Males thus have gametes to spare and have a much greater reproductive potential than females, as shown by the maximum number of offspring recorded to have been produced by males and females of a variety of species (Table 1.1). Males can gain by mating repeatedly, which in turn can lead to advantages in having weaponry to compete with other males for mating opportunities, or ornaments that are attractive to females. So males commonly will compete with each other for access to females. Females, on the other hand, should protect the large investment they have put into each of their eggs by doing all they can to ensure that this investment is not devalued through fertilization by sperm with poor genes. Thus, females should evolve mechanisms to assess the genetic quality of male suitors and opt to mate with the male with the best genes available. Females may obtain males of high genetic fitness by acceding sexually to the victors of male-male conflicts, or by selecting mates on the basis of specific traits indicative of high genetic quality. Any heritable character that enhances the probability of a male obtaining a mate, or which allows females to assess male quality, may become the subject of sexual selection.

These two mechanisms—male competition, which Darwin (1859) called the "Law of Battle," and female choice—involve selection that does not neces-

TABLE 1.1

The difference in the reproductive potential of males and females measured as the maximum number of offspring recorded to be produced by males and females of a number of animal species. Man, red deer, elephant seals, two-spot ladybirds, and angleshades moths are polygynous. Kittiwakes are monogamous. (Data from Krebs and Davies 1987; Majerus unpublished.)

	Maximum Number of Offspring Produced During Lifetime	
Species	*Male*	*Female*
Man	888	69
Red deer	24	14
Elephant seal	100	8
Kittiwake	26	28
Two-spot ladybird*	42,415	2,341
Angleshades moth*	17,549	487

*Measured in captivity.

sarily increase an individual's chance of survival, but increases an individual's chances of mating and producing fit offspring. Darwin termed this type of selection *sexual selection* and saw its existence as a prerequisite to explain some of the extreme differences seen between males and females within species.

Darwin cited many examples that are still often quoted in the context of male competition. These include the weapons, such as antlers, horns, and tusks used by male mammals in fights over females; the huge size of males compared to females in elephant seals and some primates; and the array of challenging songs used when rival male birds encounter one another in the breeding season. For female choice, he argued that male traits such as the extravagant plumage and displays of peacocks, male birds of paradise, and lyre birds could be of no direct survival advantage to the males themselves, but must serve to excite females so that they accept the most brightly adorned males.

Weaponry and elaborate adornments are not restricted to the vertebrates. Males and females of many species of insect are strikingly different. Male stag beetles and rhinoceros beetles sport impressive antlers or horns with which to fight other males. Male fig wasps have a variety of aggressive and defensive weapons, including body armor, femoral spikes, and large scythe-like jaws, all of which are used in often fatal battles with other males. Male butterflies are frequently far more brightly colored than their female counterparts, particularly in the ultraviolet spectrum. Some groups of flies have developed what are called stalk eyes, the eyes being set on long, protruding head appendages somewhat reminiscent of the heads of hammerhead sharks. In all these cases and many others, there is evidence that the traits have evolved through sexual selection.

Pre- and Postcopulatory Male Competition

Male competition, or what should more correctly be called *intrasexual selection*, because in a minority of species the roles of the sexes are reversed and females compete with each other while males choose (see p. 171), has had a fairly clear passage since it was first proposed by Darwin (1859) in *The Origin of Species*. It was rapidly accepted as a reasonable thesis and has changed little in emphasis. Perhaps the greatest difference between Darwin's and our contemporary views of male competition is that, rather than thinking purely of conflicts between males to gain mating opportunities with females, we now extend the competition to the point when sperm fertilizes the egg. Thus, male competition now encompasses sperm competition (defined as the competition between sperm from two or more males, within a single female, for fertilization of the eggs) and a range of other devices employed by males to secure paternity once they have copulated by preventing females from mating with other males.

The range of sperm competition strategies has been increasing steadily since Geoff Parker's pioneering paper on the subject (Parker 1970). Examples of elaborations of male genitalia, which allow males to scoop out or displace sperm from previous males, abound in many taxa, particularly insects. One species of crab has the ability to move sperm from previous males to a position within the female where it can be sealed off from the duct that leads to the eggs by a hard-setting gel secreted by the copulating male (Diesel 1990). Some fruit flies deposit into females, via the ejaculate, chemicals that kill or disable stored sperm from previous matings, but leave their own sperm unharmed (Harshman and Prout 1994)

In many species, sperm competition appears less sophisticated, involving little more than a numbers game. If the likelihood of each sperm within a female fertilizing an egg is the same, then just as buying more tickets for a lottery will increase your chance of winning, the male that puts most sperm into a female will father the most offspring from that female. Comparative analysis of levels of multiple mating by females (polygyny) and numbers of sperm in an ejaculate, in a variety of taxa, lend circumstantial weight to this lottery mechanism of sperm competition. For example, in primates, there is a strong correlation between degree of polygyny and male testis and ejaculate size. In male gorillas, where one single male, the silver back, mates with all the female members of his troop so that females only mate with a single male in a reproductive cycle, testis and ejaculate sizes are much smaller than in chimpanzees. In chimps, females may mate with several or, indeed, all of the mature males in their troop. Humans are intermediate between gorillas and chimps with respect to both the mean levels of polygyny and male ejaculate size.

More direct evidence comes from recent studies of an Australian dung beetle. The males are of two types. Most males have "horns" extending in front of them. The horns of these so-called "guard males" are used in competitive fights

with other males. Successful guard males pair with females, stay with them, help them to build burrows and resource these with a store of animal dung in which the female will lay an egg. Males of the second type are called "sneaks." These males are smaller, lack horns, and neither fight with other males nor form pair bonds with females, so they do not help females make or provision their egg-laying burrows. Rather, they find digging pairs of beetles and dig another burrow to intersect with the pair's burrow. Then, while the guard male is collecting dung, the sneak will move from his burrow into the main burrow and mate with the female. Analysis of testis size and sperm content of guard and sneak males has shown that the sneaks produce much larger ejaculates. This makes sense because, while many guards will not be sneaked upon and so will be involved in monogamous partnerships, all sneaks will be involved in polygamous pairings. Success for sneaks thus depends specifically on the ability of their sperm to outcompete sperm from the guard males of the females that they mate with. Here then, there is a tradeoff within a species between precopulatory male competition and postcopulatory male competition in the form of sperm competition. Guard males put resources into size, strength, and weaponry to help secure a partner and into parental care through burrow building and provisioning. They thus have fewer resources available for sperm production than do the sneaks who do not expend energy on body building or parental care.

The full extent of mechanisms of sperm competition are as yet unclear, but it is doubtful that we have yet discovered all the means by which males give their sperm a greater chance of achieving fertilization than the sperm of other males. Why, for instance are the spermatozoa of the fruit fly *Drosophila bifurcata* some 58mm long, or 20 times the length of the fly that produces them (Pitnick et al. 1995)? The reason is unknown, but it is difficult to believe that these giant sperm have evolved for reasons other than sperm competition.

Other mechanisms of postcopulatory male competition, which do not fall strictly within the definition of sperm competition, involve strategies that reduce the access of other males to the female a male has just mated with. Thus, males of the South American butterfly *Heliconius erato* inject an anti-aphrodisiac into their mates. This acts to repel other males for several weeks (Gilbert 1976). Tomcats have a less sophisticated method of reducing the likelihood that they will be cuckolded by a queenie soon after he has mated with her. The penis of a tomcat is armed with barbs that inflict considerable damage on the female's vagina as it is withdrawn, thus making further copulation extremely painful for some time afterwards. Many male insects, particularly among the butterflies, the grasshoppers, and the crickets, seal off the copulatory opening of their partners with a plug formed at the end of mating (see, e.g., Ehrlich and Ehrlich 1978). Perhaps the most common postcopulatory mechanism by which males attempt to protect their paternity is the least sophisticated: males just hang onto their females until they have laid eggs. This mate-guarding tactic occurs in many species of insect, some of the best-studied cases involving damsel flies and water striders.

Female Choice

Female choice of males (or again more correctly, *intersexual selection* because of male choice of competing females in sex role–reversed species) has had a much bumpier ride than male competition since it was first proposed by Darwin. Initial resistance probably owed something to chauvinistic attitudes of the Victorian scientific fraternity. More objectively, some critics of female choice, noting that Darwin used the mechanism to explain bright and elaborate adornments, argued that he was imbuing females with a highly developed aesthetic sense: females were choosing the most beautiful males. Furthermore, Darwin, in his writings on the subject, did not propose any explanation of how or why female preferences for particular types of male could have evolved. He simply took their existence to be necessary to explain certain secondary sexual characteristics of males.

Direct and Indirect Benefits to Choosy Females

During the twentieth century, a wide variety of mechanisms for the evolution of female mating preferences have been developed. Females that exercise a preference for particular males may, in so doing, increase their own fitness compared to females that mate randomly. For example, they may receive extra nutrients by choosing to mate with a male that brings them a particularly large piece of food as a nuptial gift, as seen in the hanging fly *Hylobittacus apicalis* (Thornhill 1976). In Clouded Yellow butterflies of the genus *Colias*, females mate preferentially with males sporting bright, immaculate color patterns. The brightness and perfection of the male color patterns is inversely correlated to adult age, which is in turn correlated to the probability of the male having previously mated. Spermatophores in these butterflies contain not only sperm, but also nutrients that are used by females in egg resourcing and maturation. The first spermatophore produced by a male has up to twice the nutrient content of subsequent spermatophores. Females, therefore, gain considerable benefit by choosing to mate with immaculately patterned males that have a high probability of being young and virgin.

Choosy females may make choices using a wide array of criteria. They may pick the males that hold the most resource-rich, or predator-free territories. Benefit may be gained by mating with a strong, fit-looking male rather than one that appears to be in poor health, as this may reduce the chance of contracting parasites from the male during copulation. In all these cases, females gain direct benefits from their mate selection because their own fitness is directly enhanced.

As an alternative to these direct benefits, a female may increase her fitness, not directly in the form of longer personal survival or the production of more progeny, but by increasing the fitness of her progeny. Different indirect benefits

theories include Fisher's "sexy sons" hypothesis, Zahavi's "handicap principle," and Hamilton and Zuk's "condition-dependent handicaps."

Sexy Sons

Fisher's sexy sons hypothesis proposes that if a female initially chooses a male because he bears some trait that is an indicator of good genetic quality, this preference will spread because her progeny will be more successful than the norm (Fisher 1930). Female progeny will gain because they are the offspring of a genetically fit father, while sons will gain this advantage plus the advantage of inheriting the trait by which females make their choice. In essence then, the preferred trait and the preference each helps select the other, leading to what has been termed *runaway sexual selection* (Box 1.1). There are several problems with this process. First, as Peter O'Donald (1980) has shown, the process is extremely slow in getting started. If a new preference gene arises in a population of reasonable size, it will initially only be expressed by a single female (we will assume that the gene is genetically dominant). This means that, initially, the only males that gain a reproductive advantage from the existence of this female mating preference are those that mate with this one female. The reproductive advantage arising out of this novel mate preference is thus exceedingly small at first. Fisher (1930) recognized that an evolutionary explanation of both the male trait and the female preference were required, and that the greatest difficulty was in getting the preference started. He solved this problem by proposing two selective influences on the evolution of the male trait:
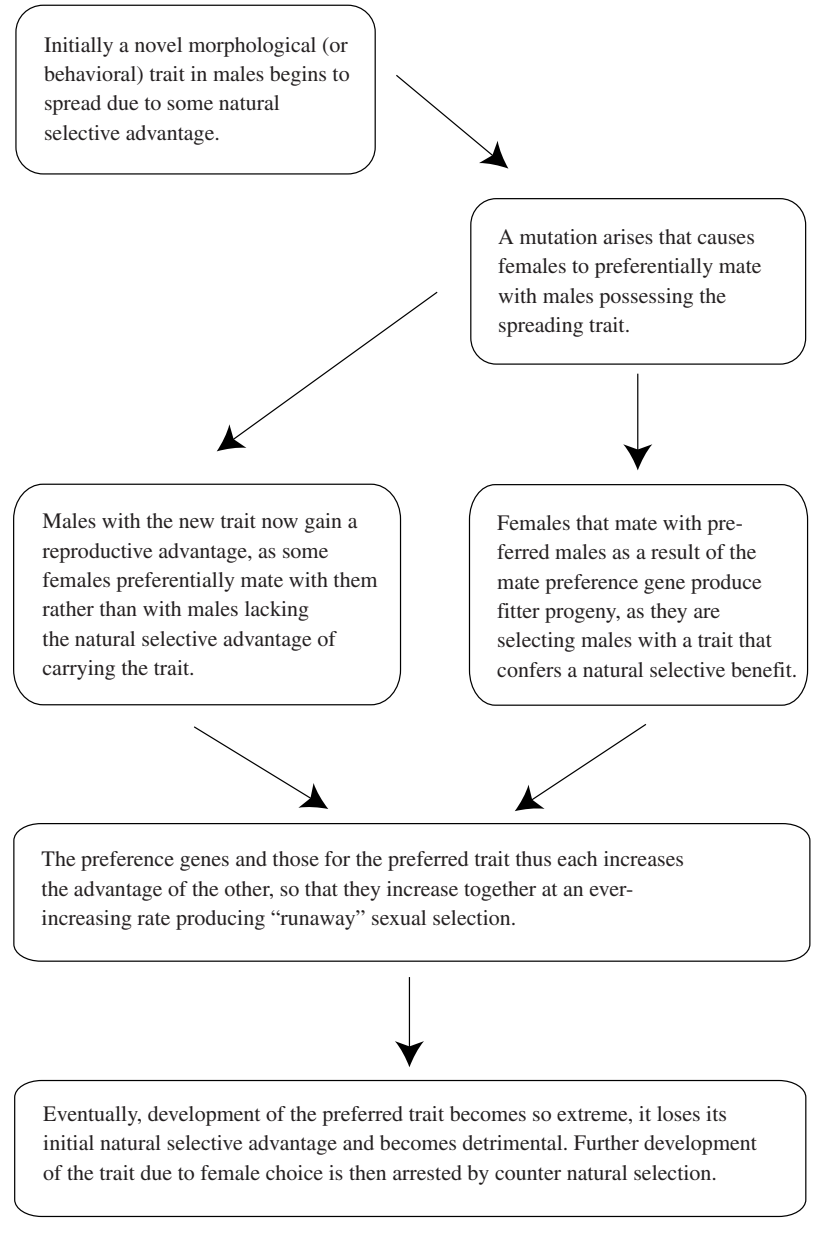
> i) an initial advantage not due to sexual preference, which advantage may be quite inconsiderable in magnitude, and ii) an additional advantage conferred by female preference, which will be proportional to the intensity of this preference. (p. 136)

Here Fisher is proposing that the initial evolution of female mate choice genes is aided by direct selection. Alternatively, the initial increase in the frequency of mate choice genes would be facilitated if the preference were based on traits associated with male dominance that had already evolved to an extent through male competition.

The second criticism of the Fisherian process is that the maintenance of mating preferences is problematic. Once the female mate preference has spread through the population so that many females are choosing males on the basis of a specific male trait, selection will favor the presence of this trait in all males. Eventually, once all males have the trait, all males will be equal. There will be no genetic variability between males with respect to this trait and so no reason why females should continue to base their choice on it. Only if mutations with respect to the genes controlling the preferred trait tended to cause a reduction in the trait would the preference be maintained (Isawa et al. 1991).

A third difficulty with the sexy sons idea is that it may be prone to invasion by cheats. Males, even if they do not possess good genes for overall fitness, need only produce the chosen trait to gain matings.

Box 1.1 Fisher's "sexy sons" hypothesis of the evolution of sexual selection by female choice.

Initially a novel morphological (or behavioral) trait in males begins to spread due to some natural selective advantage.

A mutation arises that causes females to preferentially mate with males possessing the spreading trait.

Males with the new trait now gain a reproductive advantage, as some females preferentially mate with them rather than with males lacking the natural selective advantage of carrying the trait.

Females that mate with preferred males as a result of the mate preference gene produce fitter progeny, as they are selecting males with a trait that confers a natural selective benefit.

The preference genes and those for the preferred trait thus each increases the advantage of the other, so that they increase together at an ever-increasing rate producing "runaway" sexual selection.

Eventually, development of the preferred trait becomes so extreme, it loses its initial natural selective advantage and becomes detrimental. Further development of the trait due to female choice is then arrested by counter natural selection.

Handicaps and Condition-Dependent Handicaps

Amotz Zahavi (1975) considered this third problem. He argued that an indicator of good genes could only work (i.e., not be prone to cheats) if the preferred trait were costly to produce and could thus only be produced by males that really did have good genes. In consequence, females should only choose on the basis of expensive traits or "handicaps," which would thus be incorruptible indicators of high genetic quality. This hypothesis also has some difficulties because of a lack of a genetic correlation between the costly trait and the good genes. A female that mated with a male bearing the handicap and good genes, may, in addition to producing some progeny that had both the attractive trait (the handicap) and good genes, produce other progeny that lacked one or another of these components of the system. Such males would either have good genes but be rarely chosen by females, or be chosen by females but produce unfit progeny. In either case, they would contribute little to the choosing female's (i.e., their mother's) long-term fitness.

The handicap system only works properly if of those sons carrying the handicap trait genes, only those that are of sufficiently high quality are able to make the trait. Here the development of the preferred trait is dependent on the condition of the males. Sons in poor condition as a result of carrying poor genes do not bear the whole cost of the handicap because they cannot develop it fully. As Bill Hamilton and Marlene Zuk (1982) have suggested, this may occur when there are good genes for parasite resistance. Males with good genes would have fewer parasites, would be in better condition, and so would be able to develop the extravagant display trait.

Sensory Exploitation

A third hypothesis for the evolution of intersexual selection is that mating preferences have evolved as a by-product of pre-existing biases in the sensory abilities of a species. This is the *sensory exploitation hypothesis*. Here, members of the chosen sex take advantage of the likes and dislikes of the choosers. Thus, for example, males may evolve colors that are easily perceived by the visual system of the females, or songs that are in tune with female auditory ability, or scents that impact positively on the olfactory system of potential mates. The traits that males thus develop are the product of sexual selection because males gain a reproductive benefit, not a survival benefit. However, the female preferences are pre-evolved, having developed for some ecological or behavioral reason other than mate choice.

Making use of pre-existing sensory biases that have evolved for other unrelated reasons is easiest to explain by a couple of examples. First, in our own human context, we have a high sensory receptivity to certain colors, such as bright red and bright yellow. The reasons for this receptivity need not concern us, except to say that it was not evolved for use in shopping. Yet commercial

companies make use of our receptivity to these colors in the packaging of many of their products.

In a sexual context, recent work on sexual cannibalism in the fishing spider, *Dolomedes fimbriatus*, suggests that the habit of females eating males in this species is not adaptive, but has evolved as a by-product of female feeding behavior that has been selected to increase her fecundity. Arnqvist and Henriksson (1997) have shown that the number of eggs produced by females of this species depends on the female's size in her final immature instar. This, in turn, depends on her willingness to attack prey rapaciously. The more indiscriminate females are in their prey attacks, the more fecund they become. Many males of this species become food for the females that they mate with. Arnqvist and Henriksson showed that this sexual cannibalism benefits neither males nor females. Cannibalistic females do not increase their fecundity by eating their partner. Indeed, because sperm transfer may be interrupted as the male is devoured, fertility is reduced as a result of the cannibalism. Males also seem to gain no benefit. Certainly they show no signs of complicity in the process.

The nonadaptive explanation of sexual cannibalism in this spider is in stark contrast to findings in other spiders. In the garden spider, *Araneus diadematus*, female body mass increases significantly as a result of mate consumption (Elgar and Nash 1988). In the orb-weaving spider, female fecundity increases as well (Sasaki and Iwahashi 1995). In both these cases, it is argued that males gain benefit from their self-sacrifice by increasing the number of progeny produced by the females that they have mated with. In the case of the Australian redback spider, *Latrodectus hasselti*, the male's benefit is more direct. Here, males that are eaten by their mates fertilize more eggs than do those that are not eaten, simply because they stay *in copula* for about twice as long, this additional time being spent by the female in finishing her meal (Andrade 1996).

Mate Choice, Reinforcement, and Speciation

Finally, mating preferences may evolve as a consequence of speciation. Many pairs of species are thought to have evolved as a result of divergence during periods when a single, ancestral population was split by some environmental change or geographic barrier. If, while separated, two species have become sufficiently different genetically that, once they occur together again, hybrids between them are relatively unfit (hybrids have low viability, poor fertility, or are poorly adapted to environmental conditions), they are said to show some degree of postzygotic reproductive isolation. This simply means that the selection against the production of hybrids acts after fertilization between germ cells from two different species has produced a hybrid zygote. In such circumstances, individuals that choose to mate with males of their own species will be selected for, as these animals avoid the energy wastage incurred in producing unfit offspring from hybrid matings. The preference that evolves does not have to be for a trait that is an indicator of mate fitness: it simply has to indicate that the mate is from the same species. Both the preference genes and the genes

coding for the preferred trait are likely to spread through a species to fixation because hybrid matings will always be disadvantageous. The result will be the evolution of species-recognition systems that act prior to fertilization and usually prior to mating. Thus, such mating preferences lead to what are termed prezygotic reproductive isolation mechanisms.

This is a reinforcement system, the species-specific mating preference reinforcing the incomplete and wasteful postzygotic reproductive isolation. Such a system could account for the evolution of some differences between males and females of a species, as there is no reason why both males and females have to evolve the preferred trait, although both may do so. Let us assume that males exhibit a species recognition signal and females receive it. As all males should carry the preferred trait and all females in the population should exercise the same mating preference, there does not appear to be much scope here for mate choice within a species. However, there are two possible ways that such female choice could arise. First, at the start of the evolution of a species recognition system, selection will promote any system that allows the correct individuals (i.e., conspecifics) to be chosen, however this preference is expressed behaviorally. Thus, the preference could be for a specific trait, such as a bright color spot of specific dimensions, or for the most expressed trait, perhaps the biggest bright-colored spot. This means that, in some cases, a trait may become extremely exaggerated simply because the species recognition gene(s) that first arose, involved a "supernormal" stimulus. A stimulus is referred to as supernormal if the extent of the response to the stimulus is correlated to the size of the stimulus, even if the size of the stimulus is larger than that which the receiver normally encounters. If long tails, for instance, indicate to females of one of the two diverging species that males were from their own species, then the longer the tail of a male that one of these females mated with, the more positive she would be that she was making the right choice.

Alternatively, intraspecific mating preferences could evolve later as a consequence of the existence of species-recognition genes if the selective pressures that originally led to their evolution were relaxed. Should, for example, one of the two species become extinct or move away so the two species no longer came into contact, the selective constraints on the recognition system would be removed. The genes involved would then be free to evolve in new directions, one possible direction being that they would come to act as intraspecific mate fitness indicators.

There are pieces of evidence from a wide variety of examples to support all the preceding theories of the evolution of female choice. However, most of the evidence is circumstantial and much of it does not fully distinguish between alternative theories. In all probability, female mate choice has evolved as a result of each of these processes in some species. Indeed, as many of the theories are not mutually exclusive, two or more of the selection scenarios detailed above may have been involved in some cases.

Female choice has been a hot topic for research over the last thirty years. In particular, the development of molecular tools for the analysis of paternity in

the 1980s has allowed for studies of mate choice with much greater rigor and stringency than was previously possible. Few evolutionary geneticists would now argue that females are passive partners in mating. Females of many many species do choose their mates and their choices have a genetic basis. Much work is currently in progress in this field. However, as with male competition, it is now realized that female choice may operate not only prior to copulation, but also during and after copulation.

Cryptic Female Choice

In species in which females mate with more than one male and have the ability to store sperm, there is the opportunity not only for sperm competition, but also for females to have an influence over which sperm succeed in fertilization. This type of postcopulatory female choice has been termed *cryptic female choice*. William Eberhard (1996) argues that females have much greater postcopulatory potential to influence paternity than do males. He produces an impressive list of the ways that females may influence the success of a particular copulation. This list, split into those mechanisms for which cases are known, and those as yet unknown to occur in any species, is (with minor editorial changes) provided in Box 1.2.

Work investigating the role of cryptic female choice is already providing experimental and field data suggesting that females have a considerable degree of control and that in some cases the control is highly sophisticated. To give just a couple of recent examples, Tom Pizzari and Tim Birkhead (2000) have shown that feral female chickens eject sperm of subdominant males. Emma Cunningham and Andrew Russell (2000), working on mallard ducks, have shown that females alter the resources they put into eggs depending on the attractiveness of the drake that they mate with. Females that mate with attractive drakes in good condition produce heavier eggs. Similar results have also been found with zebra finches, *Taeniopygia guttata*, but here, in addition, females deposit into eggs more androgens, such as testosterone, if they have mated with attractive males. These androgens cause chicks in the nest to beg more and to grow faster and results in a higher social rank once fledged.

The yellow dung fly, *Scathophaga stercornaria*, has become a model species in which to study sperm competition and cryptic female choice. The female sperm storage organs of these flies consist of a bursa copulatrix and several spermathecae (Figure 1.1). Research, using radioactively labeled sperm, has shown that females have a considerable influence on the movement of sperm between the bursa copulatrix and the spermathecae (Simmons et al. 1996). Furthermore, it appears that females have control over which storage organ they release sperm from to fertilize their eggs. In an elegant field study, Paul Ward (1998) examined flies that developed from eggs collected from sunny or shaded portions of cow-pats. He found that the flies differed with respect to an enzyme, phosphoglucomustase, which affects larval growth at different temperatures. The different forms of this enzyme are controlled by different alleles of a gene.

Box 1.2 William Eberhard's listing of female behaviors that are known to or that may potentially influence the success of a particular copulation. (Based on Eberhard 1996, with minor editorial changes.) (See Eberhard 1996 for examples.)

Mechanisms for Which Cases are Known

Premature interruption of copulation

Denial of deeper penetration of the male genitalia to internal sites where the male's sperm will have a better chance of being used

Lack of sperm transport to storage and/or fertilization sites within the female

Discharge or digestion of the current male's sperm or those of previous or subsequent males

Lack of ovulation

Lack of preparation of the uterus for implantation of embryos

Abortion

Lack of oviposition

Rejection or removal of mating plugs

Prevention of removal of mating plugs by subsequent males

Removal of sperm-injecting structures (spermatophores) before their contents have been transferred

Selective use of stored sperm

Failure to trigger sperm-injecting mechanisms of spermatophores

Failure to modify insemination ducts, making remating more difficult

Selective fusion with sperm that have reached the egg

Failure to fully resource a particular male's offspring

Lack of rejection of subsequent advances by other males

Potential Mechanisms, as yet Not Observed in any Species

Lack of sperm activation

Lack of sperm nourishment

Failure to seize and open spermatophores in the female's bursa copulatrix

Changes in sperm leakage

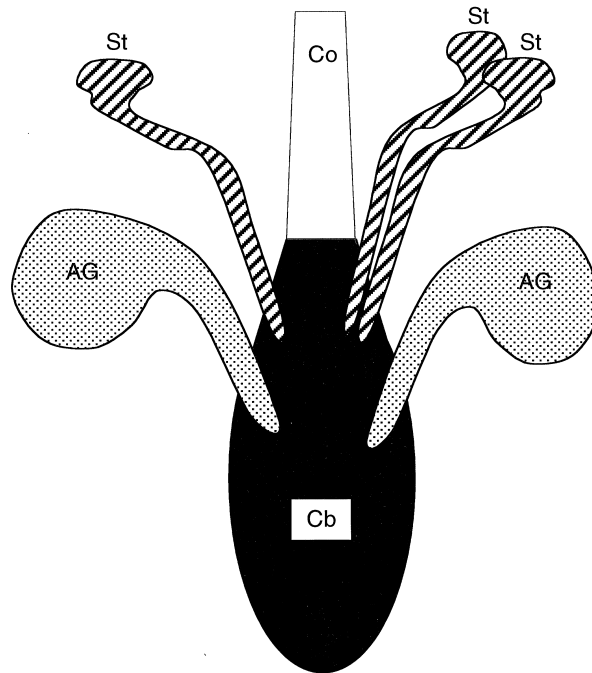Changes in the efficiency of sperm usage

Figure 1.1 Diagram of the reproductive tract of the yellow dung fly, *Scatho-phaga stercoraria.*
St = spermathecae,
Cb = bursa copulatrix,
AG = accessory glands,
Co = common oviduct.
(Redrawn from Hosken 1999.)

Ward's results suggest that, as fertilization occurs as eggs are laid, females selectively use sperm with particular alleles for this enzyme depending on their oviposition site on a cow-pat, that is, whether they were laying eggs in sunny or shaded positions.

Teasing out the intricacies involved in sexual selection in any species is not easy. Perhaps the greatest difficulty in the past has been in determining whether mating biases have been due to male competition or female choice. With the additional focuses of sperm competition and cryptic female choice, this task has not become simpler, although we now have powerful molecular genetic tools to help unravel the intricate interactions between males and females that may be involved in sexual selection.

Three final points are worth making in this context. First, with respect to female choice, almost all attention has been focused on the benefits that accrue to females that actively choose their mates or only accede to victorious males. Very little attention has been paid to the costs of female choice. However, there is a small but growing body of evidence to suggest that every time a female mates or rejects an unsuitable male, some cost is incurred. Just think of the wastage of time and energy employed in selecting or rejecting males, or the chances of contracting sexually transmitted diseases during each sexual encounter, or the possibility of injury to passive female bystanders as huge male elephant seals battle for their favors.

In an elegant experiment, Holland and Rice (1999) recently focused on the

costs to mating for females. They imposed monogamy on naturally promiscuous fruit flies, thereby all but eradicating sexual selection from their laboratory fly cultures. Their reasoning was that if sexual selection imposed a cost on females, the removal of such selection should result, after a number of generations, in male flies that caused less harm to females. This prediction was fulfilled. After 34 generations of imposed monogamy, both the reproductive rate and the longevity of female flies mated to males from the monogamous cultures were greater than for females mated to control promiscuous flies.

Here then is a further dimension to sexual selection that requires attention. If mating is costly for females, species in which females mate more often than necessary to maintain high fertility require explanation. Of course, it is possible that excess matings may act as an insurance policy against the chance that the first male is infertile. However, there is a growing body of evidence in invertebrates, such as spiders and grasshoppers (see Pardo et al. 1995; Schneider and Elgar 1998) that polyandry increases the genetic variability of progeny. In variable environments, this production of greater progenic variability may be a bet-hedging strategy, which is selectively beneficial because at least some of a female's offspring will have appropriate genes whatever the environment (Yasui 1998).

Second, although in the discussion above, and in most texts on sexual selection, male competition and female choice are treated separately, this does not mean that they are mutually exclusive. Both may operate together, as may sperm competition and cryptic female choice. An example often cited involves elephant seals. Here "beach masters," winners in violent battles with other males, collect, protect, and mate with harems of females. Males that have not secured a harem will attempt to sneak into a harem and mate with a female when the attention of the beach master is elsewhere. The very much smaller females have little chance of physically resisting the interloper. However, it is not in her interests to mate with a male whose genetic credentials have not been proven in the battle for the beach. Consequently, she exercises her choice in the only way she can: she protests loudly, screaming to attract the attention of her beach master, rousing him to attack and drive away the interloper.

The interaction between male competition and female choice is perhaps illustrated even more potently by the reproductive antics of a group of marine flatworms. These flatworms are hermaphrodite and their copulatory behavior shows not only that male competition and female choice go hand in hand, but also beautifully illustrates the difference in the energetic costs of male and female gamete production. These beautifully colored organisms, which come in a dazzling array of colors and patterns, compete with each other to be "male" when two of the same species meet. Both have the capacity to contribute either eggs or sperm to the partnership. However, there is no common agreement as to which partner is to contribute sperm and which eggs. Both jockey for position and form an intromittent organ so that they can inject sperm into the other. The first to succeed is effectively the male, as sperm are only transferred one way. The rationale behind this competition is that sperm are much cheaper to pro-

duce than eggs, so the sperm donor apparently gets the better end of the deal. The "female" in this copulation is not a complete loser, however, for although she has lost the battle to be "male," the victor has proved himself by "his" victory over "her," so she gains sperm carrying good genes from her mate.

Third, theoretical and experimental scientists have recently begun to turn their attention to the evolutionary causes of extravagant traits in females. Females of many species of both vertebrate and invertebrate possess showy traits. Many female birds, such as grebes, auks, and shags, have conspicuous crests, lappets, and bills. Bright plumage occurs in female hummingbirds, toucans, and parrots as well as in the males. Some mammals have horns or tusks or antlers in both sexes. Many fish and marine invertebrates are brightly colored in both sexes. In diurnal Lepidoptera, bright ultraviolet color patterns are not always confined to males. Some of these traits may result from the lack of genetic systems that completely limit to males the expression of secondary sexual characters that are beneficial to males for fighting or increasing allure to females. Others may be a consequence of accurate species recognition being beneficial to both sexes. However, there is increasing theoretical and empirical evidence suggesting that some of these traits are the result of either competition between females or male mate choice or both (see Johnstone et al. 1996, Amundsen 2000).

The complexities of reproductive systems and conflicts of interests between males and females, resulting, at least in part, from the disparity in size of male and female gametes, has resulted in a truly extraordinary array of variations on the theme of sexual reproduction. Almost every conceivable way of having sex (and many that, until they were observed, were probably beyond conception) occurs in some species or other. So it is perhaps not surprising that some species have reverted to an asexual lifestyle.

Secondary Asexual Reproduction: Parthenogenesis

One major hazard for sexually reproducing organisms is the need to find and secure a mate. For males, this need is at the root of male competition. Here securing a mate is often more problematic than finding a mate. This is taken to extremes in some spiders and a few insects, in which males not only have to compete with each other for access to females, but also have to give the right signals to females or they end up as the female's lunch rather than her mating partner. For females of most species, securing a mate once found is rarely a problem. However, finding a mate at the right time, that is, when the female is receptive, may be problematic, particularly in rare species scattered at low density. Many mechanisms for attracting males have evolved in females. Scent, in particular, plays a crucial role in many animals. In some silk moths, for example, males may by attracted across 10km or more by a "calling" virgin female. The attraction is very efficient, as evidenced when single female Emperor moth,

Saturnia pavonia (Plate 1a), attracted over 40 males to the cage she was hanging in, within half an hour of starting to call.

But what happens if a female fails to find a mate when she needs one? A female mammal that does not obtain sperm to fertilize her eggs will simply die without issue. But some invertebrates have another option, for in some species, eggs may develop without being fertilized. This type of reproduction is known as *parthenogenesis*. As these species have evolved from sexually reproducing ancestors, the phenomenon is sometimes also referred to as *secondary asexual reproduction*.

Several types of parthenogenesis are known and they have led to two different classifications of parthenogenetic organisms, one based on the genetic mechanism of parthenogenesis, the other on the sex that the unfertilized egg develops into. These two classifications are given in Box 1.3.

In the genetically based classification, the important difference between the classes is whether, as in the case of apomixis and endomitosis, the offspring are genetically identical to their parent (clones), or as in the case of automixis, different from it in that they have increased homozygosity. Given that increased homozygosity is generally considered disadvantageous because it allows the expression of more deleterious recessive genes (p. 32), it is perhaps not surprising that automixis is rather rare. However, there is no such problem with apomixis or endomitosis and we must ask why these forms of reproduction are not commoner, because not only is the need to find a mate avoided, but the cost of producing needless males is avoided.

The Twofold Cost of Sex

The evolutionary argument that leads to describing males as needless may require some explanation. If we imagine an organism that reproduces sexually, has no parental care further than provisioning the eggs, and produces equal numbers of males and females, we might think of a cockroach. Then let a mutation arise in a female cockroach. This mutation achieves two outcomes. First, it suppresses meiosis, the specialized cell division that gives rise to sex cells with a single set of chromosomes (haploid) from cells with two sets of chromosomes (diploid), so that diploid eggs are formed. Second, it causes these eggs to develop into females with the same genetic makeup as their parent. Theoretically, such a gene would be bound to spread. This is easy to see if the situation is considered from the gene's point of view. In the asexual female, all the offspring would get a copy of the meiosis-suppressing mutation and would be female. However, only half of the offspring of a normal female, that is, one that still produces sexually, would gain any particular gene she bore, say, a gene that caused meiosis, because her genes have to be combined equally with male genes in the offspring (Figure 1.2). The result is that when still rare, a mutation that suppresses meiosis and promotes apomixis (or endomitosis) should double in frequency each generation as a result of the so-called "twofold cost of sex": the production of males.

Box 1.3 Classifications of parthenogenetic organisms.

Classification Based on Genetic Mechanism of Parthenogenetic Reproduction

Haplo-diploidy: Meiosis in females is normal, the chromosomes doubling once, but dividing twice so that haploid oocytes result. Oocytes that are fertilized by sperm develop into females, while unfertilized oocytes remain haploid and develop into males. Haplo-diploidy is characteristic of the Hymenoptera and a number of smaller arthropod groups.

Apomixis: The reduction division of meiosis is suppressed with the result that all offspring have the same genetic constitution as their mother. Apomictic parthenogenesis is common in cockroaches (blattids), sawflies (tenthredinids), weevils (curculionids), and aphids.

Automixis: Normal meiosis leads to haploid products. Meiosis is followed by the fusion of two of the products of meiosis to restore diploidy. Alternatively, two genetically identical nuclei produced at the first mitotic division of the haploid egg division fuse to restore the diploid chromosome number. Exceptionally, in *Solenobia* (Lepidoptera) two pairs of nuclei fuse after the second mitotic division. Automixis produces offspring that are not identical to their parent, for it leads to an increase in homozygosity, some or all of the loci at which the parent was heterozygous becoming homozygous.

Endomitosis: Meiosis is preceded by chromosome doubling so that the cells that undergo meiosis are tetraploid. During meiosis, the newly replicated chromosomes pair with their identical copy and meiosis proceeds normally, giving rise to four diploid products. The resulting progeny are all identical to their parent. Endomitosis occurs in some species of lizard, stick insects (phasmids), scale insects (coccids), and psycids.

Classification Based on the Sex Produced from Unfertilized Eggs

Arrhenotoky: Unfertilized eggs produce only males.

Thelytoky: Unfertilized eggs produce only females.

Amphitoky: Unfertilized eggs may produce either males or females.

The Diversity of Parthenogens

Parthenogenetic species occur in most of the major plant and animal taxa, with the exception of gymnosperms and mammals (p. 189). Yet, most parthenogens are closely related to species that reproduce sexually. Indeed, some species comprise some parthenogenetic and some sexual individuals. For example, bugs of the genus *Lecanium* (Homoptera) have some populations that consist solely
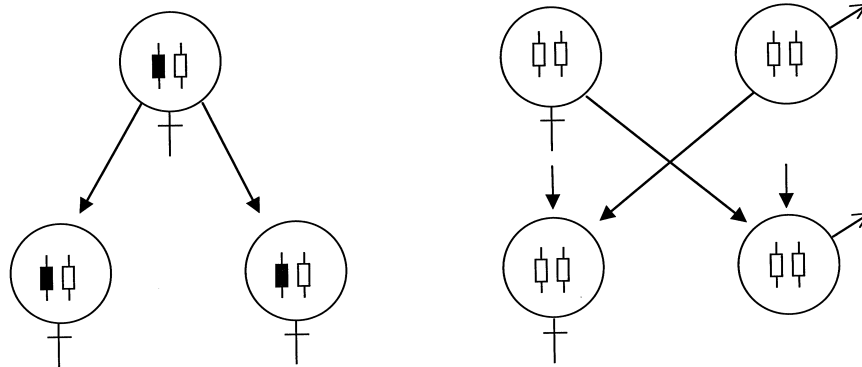
Figure 1.2 The twofold cost of sex. Here the blocked symbol represents a dominant
allele that suppresses meiosis, so that the female produces diploid offspring identical to
herself. The open allele represents an allele of the same gene that allows meiosis. If
females with or without the asexual allele are equally fecund, the frequency of the
asexual allele doubles each generation when this allele is rare. (After Maynard Smith
1989.)

of apomictically reproducing females; others consist of males and females with
females having the ability to produce female offspring either sexually or by
automictic parthenogenesis, with males only resulting from fertilized eggs. In
the weevil *Otiorrhynchus dubius*, parthenogenetic populations occur in the
north of Europe, while farther south sexual populations occur. This is a com-
mon pattern, with the frequency of parthenogenesis being greater at high lati-
tudes. So, for example, in this genus of weevils, 78% of species occurring in
Scandinavia reproduce parthenogenetically, while only 28% of those in the
Austrian Alps do so.

In the psychid moth, *Dahlica triquetrella*, females are wingless. Examination
of the chromosome complements of these females has shown that three types
exist in the wild. Some have two sets of 31 chromosomes giving a diploid
number of 62 (60 autosomes plus a Z and a W sex chromosome) (ZW). Others
have two sets but have only 61 chromosomes because they lacked the W sex
chromosome (ZO). The third type had four sets of chromosomes (tetraploid),
comprising four of each of the autosomes but just two sex chromosomes, both
Z sex chromosomes. Normally, tetraploid females reproduce by thelytokous
parthenogenesis. Of the diploids, ZW females reproduce sexually in the normal
way while ZO females, like the tetraploids, produce just daughters without mat-
ing. In fact, the situation is slightly more complicated than this, because ZO
females can reproduce either sexually or parthenogenetically, depending on
whether sperm is available for fertilization. In captivity, tetraploid females can
be induced to mate with diploid males. Such crosses produce offspring of two
types, parthenogenetic tetraploid females, and triploid intersexes with three sets
of chromosomes. This shows that the tetraploid females produce diploid ga-

metes that may either be fertilized to produce triploid offspring, or may effectively duplicate without fertilization to produce tetraploids (Seiler 1959, 1960).

An unusual type of parthenogenesis occurs in a "form" of the beetle *Ptinus clavipes*. Normal forms of the beetle are diploid and reproduce sexually. However, the form *nobilis* is triploid and exists only as females. These females produce eggs parthenogenetically, but embryo development is triggered by presence of healthy sperm from normal diploid *P. clavipes*.

Horses for Courses

It is already apparent from the above cases that some insects manage the neat trick of combining both sexual and asexual reproduction. This trick is of course employed by many species of plant that can reproduce sexually through pollen and seeds and can also reproduce vegetatively through stolons, rhizomes, corms, leaflets, and so on.

Perhaps the classic example of this ability in animals involves the aphids. Many species of aphid have an annual cycle that involves an alternation between sexual and asexual reproduction (Figure 1.3). Typically, sexual reproduction occurs in the autumn. Eggs are produced at this time. The eggs overwinter and give rise to asexually reproducing females. These reproduce thelytokously and several parthenogenetic generations follow. Rapid reproduction is achieved at this time because within a female females will be developing that already have developing embryos inside them and, of course, these have no need to spend time finding a mate. Late in the year, sexually reproducing males and females are again produced. The mechanisms by which this transition between sexual and asexual generations is achieved are explained in chapter 3.

Some parthenogenetic insects are also able to reproduce paedogenetically, which is to say that they can reproduce before they have reached the adult stage. This gives rise to some truly remarkable life histories. We have already encountered aphid species in which development of offspring begins in a female before she herself is born, but is still within the reproductive ducts of her mother. However, these young will not be born until the female has reached adulthood. However, in other cases no such requirement need be fulfilled. For example, in beetles of the genus *Micromalthus*, both adults and larvae can reproduce. Males and females are sexual in the normal way. Three types of larvae occur: those that give rise to males, those that give rise to females, and those that produce both male and female progeny. The life cycle is complex (Figure 1.4). Sexual females produce eggs that hatch into triungulin larvae that molt into legless larvae. These legless larvae may feed up and, via a pupal stage, may produce adult females. Alternatively, the legless larvae may produce triungulin larvae that, in turn, change into more legless larvae. A third option is that they may metamorphose into male-producing larvae. These larvae lay a single egg that sticks to the parent larva. When this egg hatches, the new larva eats the parental larva, subsequently pupating and eclosing to become a male. If the egg fails to hatch or becomes detached from its parent, so that the parental

Winter
Eggs on spindle tree. Eggs have to pass through a cold period before they begin to develop.

Late Autumn
Sexual females and males mate. Eggs are laid on the stems or buds of spindle trees.

Spring
Eggs hatch into females on spindle. These reproduce parthenogenetically. Colonies on spindle increase. In early summer winged females are produced.

Early Autumn
Winged females are produced. These fly to the primary host spindle tree where they produce sexual females. Winged males are produced on secondary host at the same time, and these migrate to spindle.

Late Spring/Early Summer
Winged parthenogenetic females migrate to secondary host (beans, sugarbeet, dock, poppy, etc.).

Summer
Successive generations of parthenogenetic females. Most lack wings, but as a host plant deteriorates, winged females are produced. These migrate to new host plants, on which new parthenogenetic colonies form.
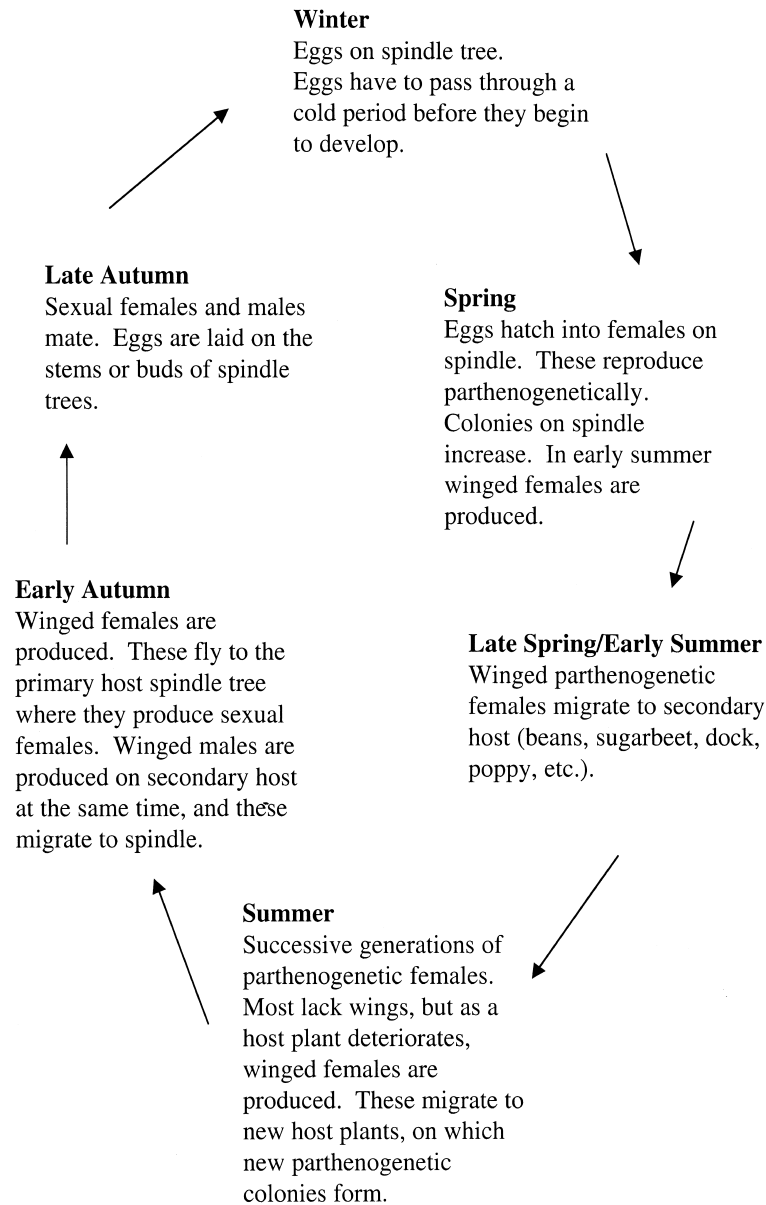
Figure 1.3 The annual cycle of the black bean aphid, *Aphis fabae*, showing alternation of sexual and parthenogenetic generations. The primary host of this species is the spindle tree, *Euonymus europaeus*. Secondary hosts are a range of herbaceous plants.
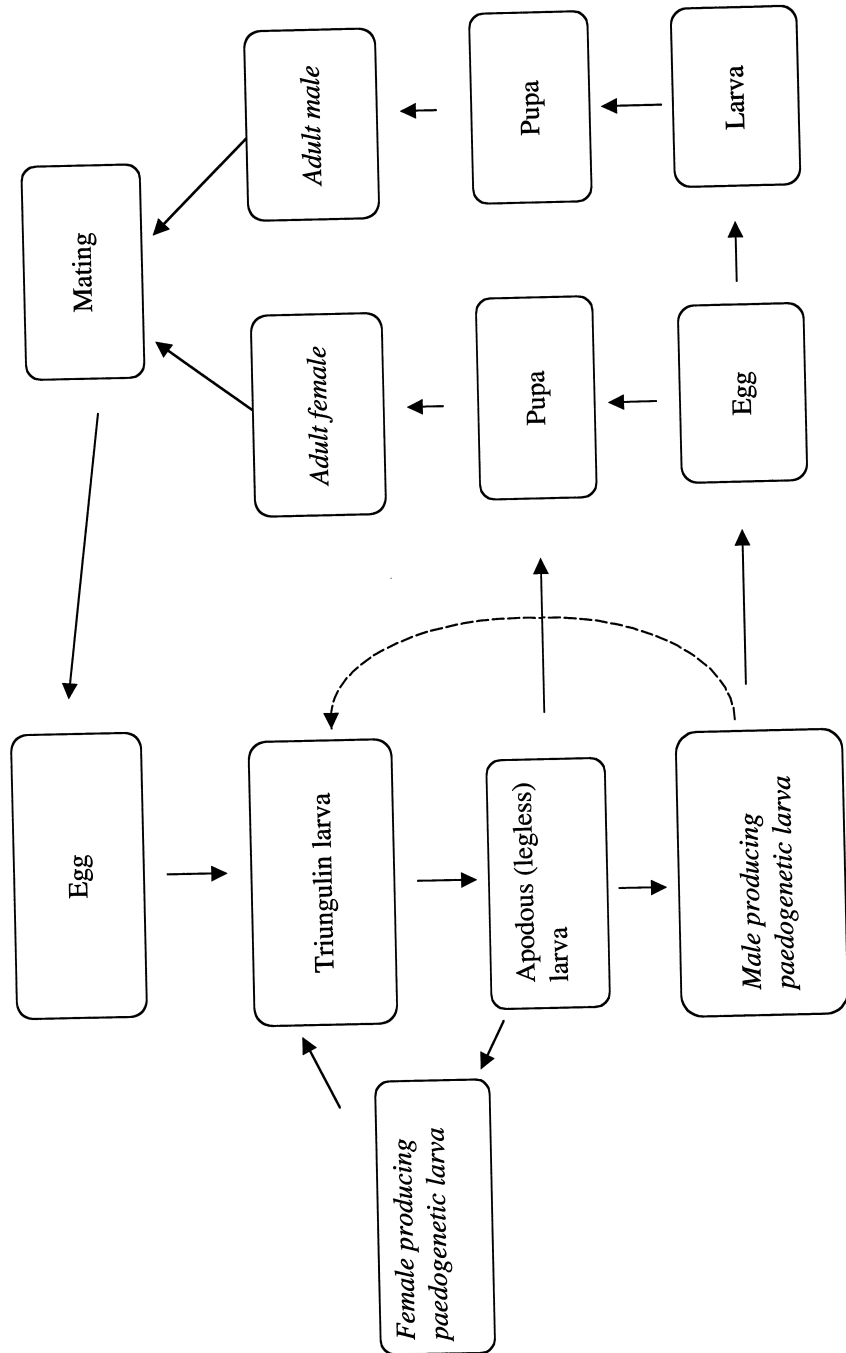
Figure 1.4 The complex life cycle of *Micromalthus*. Reproductive stages are given in italics. (Based on Pringle 1938.)

larva is not consumed, it will subsequently produce a small brood of triungulin larvae.

In the gall midges *Tekomyia* and *Henria* (Cecidomyridae), it is the pupae that give birth. Some larvae of these midges produce pupae and ultimately normal adults. Other larvae metamorphose into a rounded structure called a hemipupa. This hemipupa in turn ruptures to free 30–60 larvae that then develop into pupae.

Another gall midge, *Oligarces* (Cecidomyridae), has taken things a step further. Within the body of parent larvae, unfertilized eggs give rise to daughter larvae that consume and eat their way out of the parent larva. These daughter larvae usually repeat the process and, indeed, paedogenesis is the normal form of reproduction in this species. However, some larvae give rise to male and female adults, although it is not known whether these are capable of reproduction.

Although paedogenesis is usually associated with parthenogenesis, it is interesting to note that a few examples of sexual paedogenesis exist. The bug *Hesperoctenes* is a case in point. Here males mate with larvae by inserting their sipho through the body wall and depositing sperm into the main body cavity. These sperm then migrate to fertilize eggs in the ovaries of the larva and the eggs begin to develop.

Why Is Parthenogenesis Rare?

Despite these fascinating and surprising cases, it is still true that sexual reproduction holds sway in the animal kingdom, so we still have to address the question: why is parthenogenesis so rare, even though it has evolved many times in different evolutionary lineages? Two reasons are usually given and the two are not mutually exclusive. First, it can be shown that parthenogenetic forms evolve more slowly than sexual forms. Second, it has been suggested that parthenogenetic forms will be prone to the accumulation of harmful mutations. These two reasons have wider application because they relate to the general advantages of sexual over asexual reproduction.

Sex Accelerates Evolution

We can begin with a consideration of how sexual and asexual populations may be able to adapt to a changing environment. In an asexual species, rare mutations will give rise to rare individuals with new genotypes, so the population will consist of genetically different individuals, although the novel genotypes will be rare. But, if mutations are occurring at more than one locus, how likely is it that a single individual will carry multiple mutants? Box 1.4 considers the fate of two genes in a haploid, single-celled organism reproducing either asexually or sexually.

The calculation shows that the chance of two advantageous mutations occurring in the same individual is approximately 250 times greater in the sexual

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Box 1.4 Sex accelerates evolution.

Let mutations be from *A* to *a* and from *B* to *b*, each occurring at a rate of 1×10^{-5} (thus a single mutation will occur in 1 in 100,000 cells per cell generation). The chance of both mutations happening simultaneously in a single cell is therefore 1×10^{-10}. Mutations at different gene loci are thus likely to occur in separate cells. But these mutations are recurring and may, after some time, become established at low frequencies in the population. If each mutant has a frequency of 1%, the population will consist of:

Genotype	Frequency
AB	98%
Ab	1%
aB	1%

Given the existence of *Ab* and *aB*, the double mutant (*ab*) could arise in a single step. The rate of production would now be:

$$2[10^{-5} \times 10^{-2}] = 2 \times 10^{-7} \text{ (ignoring double mutations)}$$

This is the rate for a population reproducing by asexual means only. We can compare this with a sexually reproducing organism.

In a hypothetical single-cell organism that is haploid (i.e., fertilization is immediately followed by meiosis), with a population consisting of 98% *AB*, 1% *Ab*, and 1% *aB*, the chance of fertilization between *Ab* and *aB* individuals is $2 \times (10^{-2})^2 = 2 \times 10^{-4}$.

If such mating occurs, the diploid zygote will be heterozygous for both genes and a quarter of the progeny following meiosis will be *ab* (assuming no genetic linkage). Thus the probability of producing the *ab* genotype is:

$$0.25 \times 2 \times 10^{-4} = 5 \times 10^{-5}$$

This is 250 times the chance with asexual reproduction.

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population than if reproduction is asexual. Here, then, we have a situation in which, if a population is faced with a changing environment and needs to adapt if it is to survive, sexual reproduction is advantageous over asexual reproduction. This is simply because sex leads to more rapid generation of a wide array of variants, some of which may be able to cope with the new circumstances.

This idea leads to the feeling that when the environment for an individual is suitable and stable, asexual reproduction may be beneficial, but in a harsh or changing environment, sexual reproduction may pay. It is perhaps interesting to reflect that in aphids that show an alteration of generations, the sexual generation generally occurs as conditions deteriorate toward the end of the summer. It has also occurred to me that the advice given by many horticulturist experts with respect to persuading many potted plants to flower has a bearing on this idea of favorable and stressed conditions. For many types of houseplant, keeping the plant pot-bound will cause it to flower, whereas if the plants are regularly transplanted into larger pots, so they have plenty of room to grow vegetatively, this is exactly what they do. The result is a vibrant well-foliated plant with an absence of flowers and sex.

Muller's Ratchet

Several hypotheses have postulated that the advantage of sex lies in the removal of deleterious mutations. One suggests that sex may prevent harmful mutations from accumulating in populations. This theory is known as "Muller's ratchet" after the American geneticist Hermann J. Muller who first proposed it (Muller 1932). The idea is very simple. Most mutations, if they affect the fitness of their carriers at all, are detrimental because most beneficial mutations will already have been selected to fixation in the population. Although mutation in a particular gene is a relatively rare event, there are a lot of genes and so a lot of mutation. In an asexual population without recombination, each lineage will get its share of at least mildly deleterious mutations simply by chance. There will be a tendency, over time, for these slightly deleterious mutations to accumulate because there is no easy mechanism for purging a lineage of its harmful mutants. To see that this is so, we may classify a population according to the number of deleterious mutations carried by individuals: some will have none, some one, some two, and so on. Over time, the number will tend to increase rather than decrease. Now, consider an occasion when the number of individuals with no such mutations is small because population size happens to be at low ebb. There will then be a chance in each generation that, despite their highest fitness, all individuals with no harmful mutations will die without leaving offspring. If so, that optimal class is lost and can only be reconstituted by the rare event of back mutation. In Muller's view, the ratchet has clicked around one notch (Figure 1.5). The new optimal class will carry one deleterious mutation. In time this class may also be lost if the ratchet clicks again. Compare this scenario to that in a sexual population. Here, two individuals, each carrying a different harmful mutation, can, by breeding together, produce some progeny that are free of both mutations. The optimal class is thus continuously reconstituted.

A difficulty with Muller's theory is that while it may function well in small populations, in larger populations there will be little effect, at least in the short term. Kondrashov (1982, 1984) suggested an extension of this idea that would lead to the removal of deleterious mutations in both small and large popula-
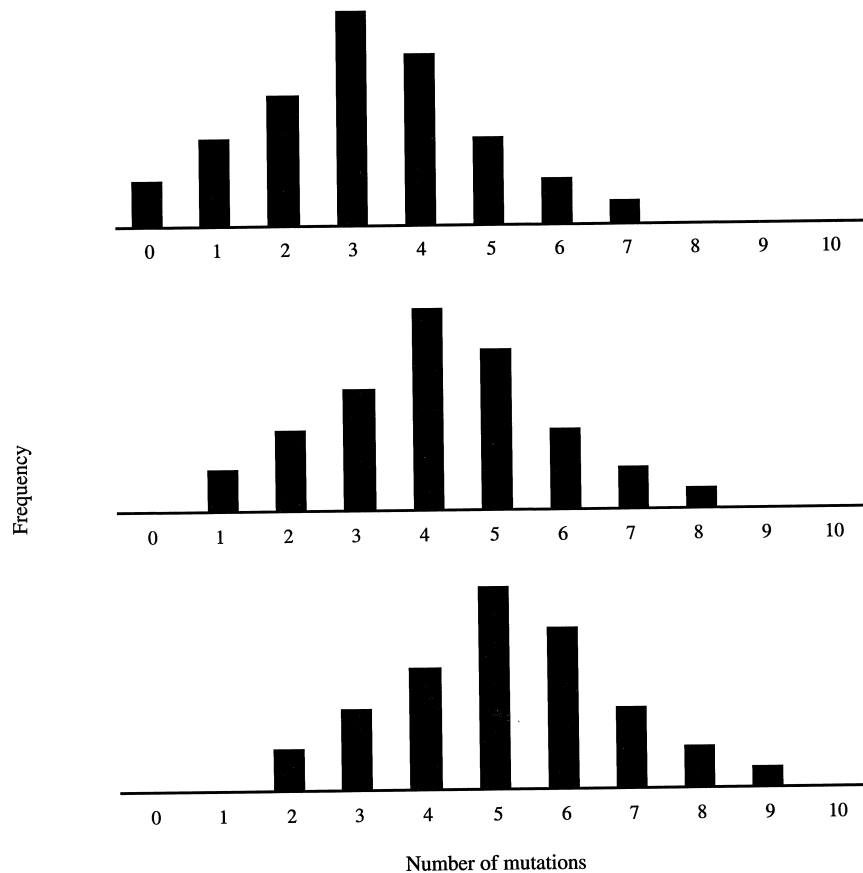
Figure 1.5 Muller's ratchet. The top histogram shows the distribution of individuals with different numbers of slightly deleterious mutations in an asexual population. The middle and bottom histograms show the same population, later in time, when the ratchet has clicked around once and twice, respectively.

tions. Kondrashov's model assumes that the effects of mutations are additive. Imagine two gene loci, with normal alleles *A* and *B* and deleterious mutant alleles *a* and *b*. Normal individuals will be *AB*. Individuals carrying one mutant allele (*Ab* or *aB*) will be less fit, and the double mutant *ab* is lethal. In asexual populations, genotypes such as *Ab* and *aB* may persist for some period in the short term because the lethal genotype *ab* will arise rarely. However, in a sexual population this genotype will regularly be produced if both *a* and *b* are present in the population, and these will thus quickly be purged. Over larger numbers of loci, the variance in the number of deleterious mutations is greater in sexual than in asexual populations. This allows selection to remove many deleterious mutations simultaneously when they occur together (Figure 1.6).
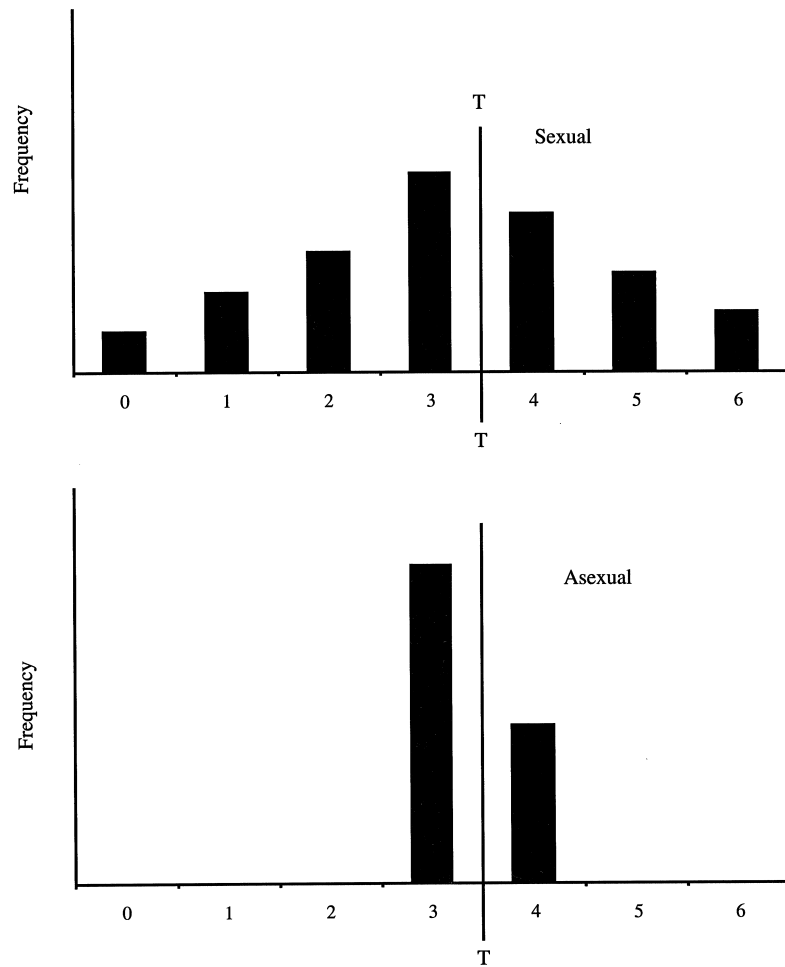
Figure 1.6 Kondrashov suggested that the variance in the number of deleterious
mutations per individual would be greater in sexual than in asexual populations.
Selective elimination of a fixed proportion of each population with the most deleterious
mutations would mean that more harmful mutations would be eliminated from sexual
than asexual populations.

The Maintenance of Sex

Both types of hypothesis outlined above involve the fitness of populations. In
the first, sex increases the adaptability of the population in a changing environ-
ment. In the second, sex prevents a gradual reduction in the fitness of the popu-
lation by providing a mechanism by which individuals free from harmful muta-
tions can be produced and, due to their high fitness, then be selectively favored.
The bottom line is that sexual populations are likely to be longer lived than

asexual populations. The advantage to sex here is thus a long-term one (although there may also be short-term benefits in some circumstances, see chapter 9). This is a problem if one is trying to explain the original evolution of sex, for the initial twofold cost of sex would surely mean that, in the short term, asexual individuals would be fitter than those that indulge in sex would be. In considering whether asexual reproduction can evolve from sexual lineages, however, we are looking at things the other way around. Now, the short-term advantage of asexual reproduction can allow for the evolution of asexual lineages from sexual ancestors. The long-term benefit of sex outlined above should mean that those species that do become parthenogenetic should be more prone to extinction than those that retain sex. And indeed, this appears to fit pretty well with the distribution pattern of parthenogenesis seen in the animal kingdom. Parthenogenesis is found in a very wide array of taxonomic groups and has certainly appeared independently many times, but there are very few taxa at the higher levels (from family up) that are exclusively parthenogenetic (the bdelloid rotifers are a notable exception). Furthermore, most parthenogenetic taxa have derived from sexual taxa fairly recently. So it seems that parthenogenesis does arise fairly frequently in evolutionary time and when it does arise, the short-term advantage through the nonproduction of needless males allows it to spread. But parthenogenetic populations thereafter are more prone to elimination because they cannot compete with sexual populations in the long term.

Here then we have a viable reason for the maintenance of sex and the rarity of secondarily parthenogenetic organisms. However, this long-term, group-selectionist argument cannot be invoked to explain the origins of sex, for when sex first evolved immediate advantages must have been required. I will consider these matters again in relation to the evolution of sexual reproduction in the final chapter of this book.