An Introduction to Behavioural Ecology

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THIRD EDITION

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Topics for discussion

1 How has game theory helped us to understand animal contests?
2 Why do territorial residents win?
3 Is assessment always based on reliable signals?

Chapter 8. Sexual Conflict and Sexual Selection

Ethologists used to view courtship rituals and mating as harmonious ventures in which male and female co-operated to propagate their respective genes. Admittedly some animals were obviously not co-operative, for example the praying mantis in which the female eats the male during mating, but on the whole courtship was seen as serving functions of common interest to male and female: to 'synchronize the sexual arousal of the sexes', to 'establish the pair bond' to 'allow species identification', and so on. However this view is no longer so widely held and more emphasis is placed on the idea that there are conflicts of interest between male and female in courtship and mating. The sexes are seen as forming an uneasy alliance in which each attempts to maximize its own success at propagating genes. They co-operate because both pass on their genes via the same progeny and therefore each has a 50 per cent stake in the survival of the offspring. But choice of mating partner, provisioning of the zygote with food, and caring for the eggs and young are all issues over which the sexes may disagree. The outcome of this sexual conflict is often more akin to exploitation by one sex of the other than to mutual co-operation.

In order to understand why sexual reproduction should be viewed in this way, we have to go right back to the beginning, to the fundamental difference between male and female.

Reproduction includes conflicts of interest between the sexes

Males and females

Sexual reproduction entails gamete formation by meiosis and the fusion of genetic material from two individuals. It almost always, but not invariably, involves two sexes called male and female. In higher animals the sexes are often most readily distinguished by external features such as genitalia, plumage, size, or colour, but these are not fundamental differences. In all plants and animals the basic difference between the sexes is the size of their gametes: females produce large, immobile, food-rich gametes called eggs, while male gametes or sperm are tiny, mobile, and consist of little more than a piece of self-propelled DNA. Sexual reproduction without males and females occurs in many protists such as *Paramecium* where the 'gametes' which fuse during sex are of the same size. This is referred to as *isogamous* sexual reproduction. The fusion of two gametes of unequal size, one large and one small is, however, much commoner and occurs in virtually all

females the sex that produces large gametes

sexually reproducing multicellular plants and animals. It is called *anisogamous* sex.

It is thought that anisogamy evolved from isogamy by an evolutionary process in which smaller than average gametes successfully parasitized those that were larger than average. This eventually led to the two distinct specializations we see today: small active sperm and large passive eggs (Parker *et al.* 1972).

As we shall show in the rest of this chapter, the fundamental asymmetry in gamete size and associated investment in offspring has far-reaching consequences for sexual behaviour. Because females put more resources than do males in each offspring, male courtship and mating behaviour is to a large extent directed towards competing for and exploiting female investment. Where the usual difference between the sexes in parental investment is reversed, males providing more care than females, so the roles in sexual competition are reversed and females compete for access to males.

FEMALES AS A SCARCE RESOURCE

Anisogamous sexual reproduction, then, involves parasitism of a large egg by a small sperm. Females produce relatively few large gametes and males produce many small ones. In addition, females often invest more than males in other forms of care. Because of this males can potentially fertilize eggs at a faster rate than they are produced (illustrated by the fact 5 ml of human semen contains enough sperm to fertilize in theory eggs amounting to twice the population of the USA), and females are therefore a *scarce resource* for which males compete. Even in species where males temporarily deplete their sperm supply when offered a surfeit of females, their potential for producing offspring is greater than that of females (Nakatsuru & Kramer 1982).

A male can increase its reproductive success by finding and fertilizing many different females, but a female can only increase her success by turning food into eggs or offspring at a faster rate (Fig. 8.1). This point is graphically demonstrated by mammals such as man, in which a female spends many months producing a single child, during which time a male could potentially fertilize hundreds of other mates. Only by speeding up her production of young can the female have more children in a lifetime. The same argument holds whenever females invest more than males in each offspring, whether the investment is in the form of food in the egg or care of the eggs and young later on.

This point was neatly summarized by Robert Trivers (1972), who was the first person to emphasize the relationship between
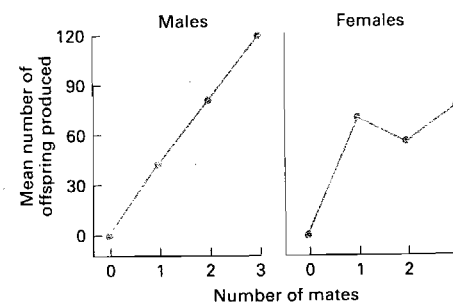

Fig. 8.1 A.J. Bateman (1948) put equal numbers of male and female fruit flies (*Drosophila melanogaster*) in bottles and scored the number of matings and offspring produced by each individual, using genetic markers to assign parentage. For males reproductive success goes up with number of matings, for females it does not, beyond the first mating. After Trivers (1985).

the investment of resources in gametes and other forms of care, and sexual competition. He wrote 'Where one sex invests considerably more than the other, members of the latter will compete among themselves to mate with members of the former'. The term 'investment' was used by Trivers to refer to the effort put into rearing an individual offspring from the parent's limited pool of resources. The sum of parental investment in all offspring during a parent's lifetime is referred to as 'parental effort'. Females generally put most of their reproductive effort into 'parental effort' while males put most of theirs into 'mating effort' (Fig. 8.2).

The consequence is that males usually have a much greater potential rate of reproduction than do females (Table 8.1) (Clutton-Brock & Vincent 1991) and are therefore under strong selection to be good at seeking out and competing for females: the pay-off for a successful male in terms of offspring fathered is enormous. Much of male reproductive behaviour can be understood with these ideas in mind.

THE SEX RATIO

If one male can fertilize the eggs of dozens of females why not produce a sex ratio of, say, one male for every 20 females? With this ratio the reproductive success of the population would be higher than with a 1:1 ratio since there would be more eggs around to fertilize. Yet in nature the ratio is usually very close to 1:1 even when males do nothing but fertilize the female. As we saw in Chapter 1, the adaptive value of traits should not be viewed as being 'for the good of the population', but 'for the good

[margin notes:]
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access to females

whilst females are
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Parental investment,
potential rate of
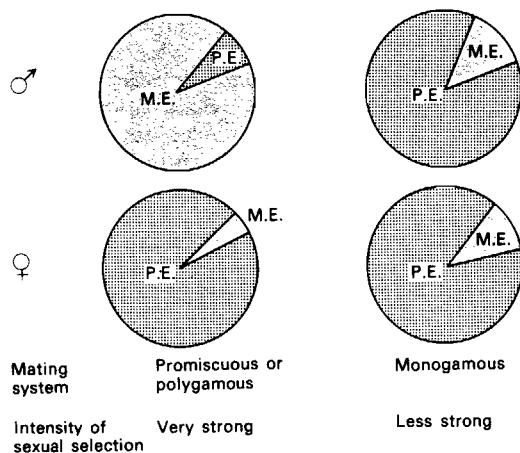reproduction and sexual
competition

Fig. 8.2 The total resources of time and energy used by an animal in reproduction is referred to as reproductive effort. This is represented by a circle. Reproductive effort can be partitioned into parental effort (provisioning and rearing offspring) and mating effort (acquiring mates). These are represented by the stippled and coloured areas of the circles respectively. In general, males put relatively more into mating effort than do females, but this varies between species. The intensity of sexual selection (see p. 183 for a definition) therefore also varies. The differences in relative parental effort of the sexes is often related to the mating system. In monogamous species male and female effort is more similar than in polygamous and promiscuous species (see Chapter 9). After Alexander and Borgia (1979).

Table 8.1 In polygamous or promiscuous species males have a much higher potential reproductive rate than females. The data for man came from the Guinness Book of Records: the male was Moulay Ismail the Bloodthirsty, Emperor of Morocco, the woman had her children in 27 pregnancies. The data for elephant seals are from Le Boeuf and Reiter (1988), for red deer from Clutton-Brock et al. (1982). In the monogamous kittiwake, where male and female invest similarly in each offspring, the difference in maximum reproductive output is negligible. From Clutton-Brock (1983)

Species	Maximum number of offspring produced during lifetime	
	Male	Female
Elephant seal	100	8
Red deer	24	14
Man	888	69
Kittiwake gull	26	28

of the individual', or more precisely 'for the good of the gene'. As R.A. Fisher (1930) first realized the 1:1 sex ratio can readily be explained in terms of selection acting on the individual; his argument is simple but subtle.

Suppose a population contained 20 females for every male. Every male has 20 times the expected reproductive success of a female (because there are on average 20 mates per male) and therefore a parent whose children are exclusively sons can expect to have almost 20 times the number of grandchildren produced by a parent with mainly female offspring. A female-biased sex ratio is therefore not evolutionarily stable (p. 149) because a gene which causes parents to bias the sex ratio of their offspring towards males would rapidly spread, and the sex ratio will gradually shift towards a greater proportion of males than the initial 1 in 20. But now imagine the converse. If males are 20 times as common as females a parent producing only daughters will be at an advantage. Since one sperm fertilizes each egg, only one in every 20 males can contribute genes to any individual offspring

and females therefore have 20 times the average reproductive success of a male. So a male-biased sex ratio is not stable either. The conclusion is that the rarer sex always has an advantage, and parents which concentrate on producing offspring of the rare sex will therefore be favoured by selection. Only when the sex ratio is exactly 1:1 will the expected success of a male and a female be equal and the population stable. Even a tiny bias favours the rarer sex: in a population of 51 females and 49 males where each female has one child, an average male has 51/49 children. This average value is the same whether one male does most of the fathering or whether fatherhood is spread equally among the males.

The argument that the sex ratio should be 1:1 can be refined by re-phrasing it in terms of investment. Suppose sons are twice as costly as daughters to produce because, for example, they are twice as big and need twice as much food during development. When the sex ratio is 1:1 a son has the same average number of children as a daughter. But since sons are twice as costly to make they are a bad investment for a parent: each of its grandchildren produced by a son is twice as costly as one produced by a daughter. It would therefore pay the parents to concentrate on making daughters. As the sex ratio swings towards a female bias, the expected reproductive success of a son goes up until at a ratio of two females to every male an average son produces twice the number of children produced by an average daughter. At this point sons and daughters give exactly the same return per unit investment; a son costs twice as much to make but yields twice the return. This means that when sons and daughters cost different amounts to make, the stable strategy in evolution is for the

parent to *invest* equally in the two sexes and not to produce equal numbers. An example to illustrate this point is Bob Metcalf's (1980) study of the sex ratio of two species of wasp: *Polistes metricus* and *P. variatus*. In the former females are smaller than males, while in the latter they are similar in size. As predicted, the population sex ratio is biased in *P. metricus* and not in *P. variatus*. In both species the investment ratio is 1 : 1.

The prediction that parents should invest equally in sons and daughters does not always hold, and demonstrations of these deviations from 1 : 1 investment are among the most convincing pieces of evidence that the sex ratio has evolved in the way suggested by Fisher. We will pick out some examples in the following paragraphs.

(a) Local mate competition

Fisher's theory predicts a different outcome when brothers compete with each other for mates (so-called 'local mate competition'). Suppose, for example, that two sons have only one chance to mate and that they compete for the same female. Only one of them can be successful in mating, so from their mother's point of view one of them is 'wasted'. This is an extreme example, but it illustrates the general point that when sons compete for mates their value to their mother is reduced. The mother should therefore bias her ratio of investment towards daughters. The exact degree of bias predicted by Fisher's theory depends on the degree of local mate competition. Extreme competition is to be expected in species with limited powers of dispersal (because brothers will stay together in the same place) and therefore it tends to be associated with inbreeding. In the extreme case of inbreeding, a mother 'knows' that all her daughters will be fertilized by her sons. The best sex ratio in this instance is to produce just enough sons to fertilize the daughters, since any other males will be wasted. The crucial difference between this and the earlier argument for a 1 : 1 sex ratio is that here the ratio of males to females in the rest of the population does not matter. A female-biased ratio within a brood will not give other parents a chance to benefit by concentrating on sons. An example which supports this prediction is the viviparous mite, *Acarophenox*, which has a brood of one son and up to 20 daughters. The male mates with his sisters inside the mother and dies before he is born (Hamilton 1967).

Jack Werren (1980) has tested the prediction that the degree of bias depends on the extent of local mate competition. He studied

inside the pupae of flies such as *Sarcophaga bullata*. If one female parasitizes a pupa, her daughters are all fertilized by her sons and as predicted the sex ratio of her clutch of eggs is biased towards females. Only 8.7 per cent of the brood is male. If a second female lays her eggs in the same pupa, what should her sex ratio be? If she lays few eggs she should produce mainly sons, since the first female has laid predominantly female eggs. But as the proportion of the total number of eggs in the pupa that come from the second female increases, the chance that sons of the second female will compete for mates also increases. Therefore her brood should have a female-biased sex ratio. Werren found exactly this pattern: when the second female's clutch was 1/10 the size of the first female's it contained only males, but when it was twice as large as the first female's it contained only 10 per cent males, and the quantitative details of the change in sex ratio with relative brood size were much as predicted.

(b) Local resource competition or enhancement

Anne Clark (1978) found that the South African prosimian, *Galago crassicaudatus*, has a male-biased investment ratio among its offspring. She pointed out that this could be explained by the species' life history. As with most mammals, female *Galago* disperse less far than males, and often end up competing both with their mother and with each other for rich sources of food such as gum and fruit trees in the mother's home range. This local resource competition among females reduces their value as offspring: in the extreme case only one daughter might be able to survive on the food available near home, and so investment in other daughters would be wasted.

Exactly the opposite effect could arise if the sex that stays at home, rather than hindering one another or their parents, actually helps. As we shall see in Chapter 12, in some bird species, males but not females stay at home and help. The consequence of this is to make males slightly more valuable than females as an investment (since they help the parent in its future reproduction) and hence a male-biased investment ratio might be expected (Emlen *et al.* 1986).

(c) Maternal condition

We saw in Chapter 7 that male red deer compete for females by prolonged roaring and antler wrestling contests. In these contests it is an advantage for a male to be big, and size depends among

in turn depends on his mother's ability to compete for good sources of food and hence produce a plentiful supply of milk. In other words there is a direct link between a mother's competitive ability while lactating and her son's expected reproductive success. Now if a mother 'knew' that her sons would be highly successful harem holders it would pay her to invest heavily in sons rather than daughters: the pay-off in terms of grandchildren would be much greater. Similarly a mother who 'knew' that her sons would not grow up to be big and strong would do better to have daughters, since a daughter's future reproductive success does not depend so much on her mother's milk. Exactly this pattern has been found in red deer: dominant females who are able to gain access to good feeding sites while lactating and hence produce strapping sons, tend to have sons, while subordinate females have daughters (Clutton-Brock *et al.* 1984). It is not known how the sex ratio is adjusted by the mother in the red deer or the galagos studied by Clark, but the fact that they are adjusted is striking because agricultural geneticists have failed to select for adjustment of the sex ratio or to separate male and female sperm of domestic mammals (imagine the value of a female-biased sex ratio to the milk farmer!), and it has often been concluded that mammalian sex ratios are very inflexible (Williams 1979; Maynard Smith 1980). Adjustment of the sex ratio in Hymenoptera such as the wasps studied by Werren is not at all a problem because the mother can determine whether an egg becomes male or female by whether or not she fertilizes it (Chapter 13).

Female red deer in good condition tend to produce more male offspring

(d) Population sex ratio

When the population ratio of investment deviates from 1:1, a compensatory bias in favour of the rarer sex should occur. In Metcalf's study of *P. metricus* he found that some nests produced only male offspring. As explained in Chapter 13 these offspring are the product of unfertilized eggs and are produced by workers in nests where the queen has died. In the remainder of the nests in the population Metcalf found a female-biased sex ratio, so that the ratio of investment in the population as a whole is 1:1.

Biased sex ratios in paper wasp nests may be influenced by the population sex ratio

Finally it is worth pointing out that the theory of sex ratios discussed here is one example of a more general theory of sex *allocation* (Charnov 1982). Other examples of the problem of allocation of resources to male and female reproduction include the division of resources into eggs and sperms by simultaneous hermaphrodites and the timing of sex change in sequential hermaphrodites (see Chapter 10).

Sexual selection

The combination of females investing more than males and 1:1 population sex ratio means that males usually compete for females. The potential pay-off for male success is high, so selection for male ability to acquire matings is very strong. Selection for traits which are solely concerned with increasing mating success is usually referred to as *sexual selection*. It can work in two ways: by favouring the ability of one sex (usually males) to compete directly with one another for fertilizations, for example by fighting (*intra-sexual selection*), or by favouring traits in one sex which attract the other (*inter-sexual selection*). Often the two kinds of selection act at the same time.

Sexual selection: selection for traits that increase mating success

The intensity of sexual selection depends on the degree of competition for mates. This in turn depends on two factors: the difference in parental effort between the sexes (Fig. 8.2) and the ratio of males to females available for mating at any one time (referred to as the *operational sex ratio*). When parental effort is more or less equal, as for example in monogamous birds where both male and female feed the young, sexual selection is less intense than in species with very different levels of parental effort. This follows from the point made earlier that the sex making little investment has a higher potential rate of reproduction (p. 177). If equal numbers of the two sexes come into breeding condition at the same time, the degree of sexual selection is reduced because there is less chance for a few males to control access to very large numbers of females. In contrast, when females come into breeding condition asynchronously there is a chance for a small number of males to control many females one after the other. With such high potential pay-offs, sexual competition is very intense (see Chapter 9). The relationship between parental investment, operational sex ratio and sexual selection is discussed in more detail by Clutton-Brock & Vincent (1991).

Sex differences in parental investment and the operational sex ratio influence the strength of sexual selection

ARDENT MALES

The most dramatic and obvious way in which males compete for mates is by fighting and ritualized contests, and often males have evolved weapons for fighting. Males may dispute over direct access to females or over places where females are likely to go, as for example when male damselflies defend clumps of vegetation (Chapter 7). Fighting is often a risky business, as illustrated by the injuries sustained by red deer stags referred to in Chapter 7. The most intense fights in many species occur when females are
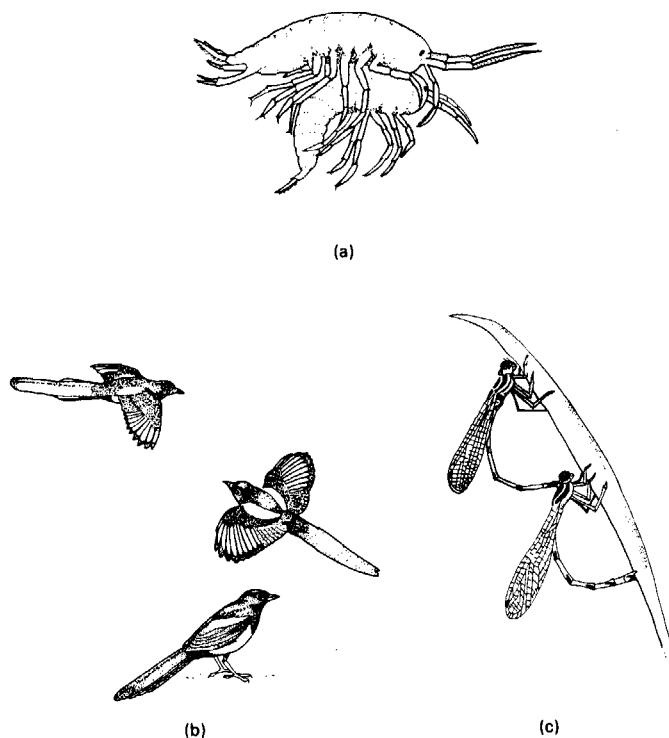
Males fight for access to females

Fig. 8.3 Mate guarding as a form of sexual competition. (a) Precopulatory mate guarding in the freshwater amphipod *Gammarus*. The mature female in this species is ready to be fertilized immediately after she moults. Males guard females in the few days preceding this moult. From Birkhead and Clarkson (1980). (b) Male European magpies (*Pica pica*) assiduously guard their mates against intruding males just before and during the period of egg laying. From Birkhead (1979). (c) After copulation the male damselfly guards the female while she lays her eggs, by clasping her thorax with the tip of his abdomen in the 'tandem' position. From Corbet (1962).

ready to be fertilized and once a male finds a female he often guards her (Fig. 8.3).

Males often compete in ways which are less conspicuous than fights, but are no less effective and often more bizarre. The invertebrates are a particularly rich seam of examples. Female dragonflies, as with many other insects, mate with a number of males and store the sperm in a special sac (the spermatheca) in the body for use at a later date. The males compete for fertilizations
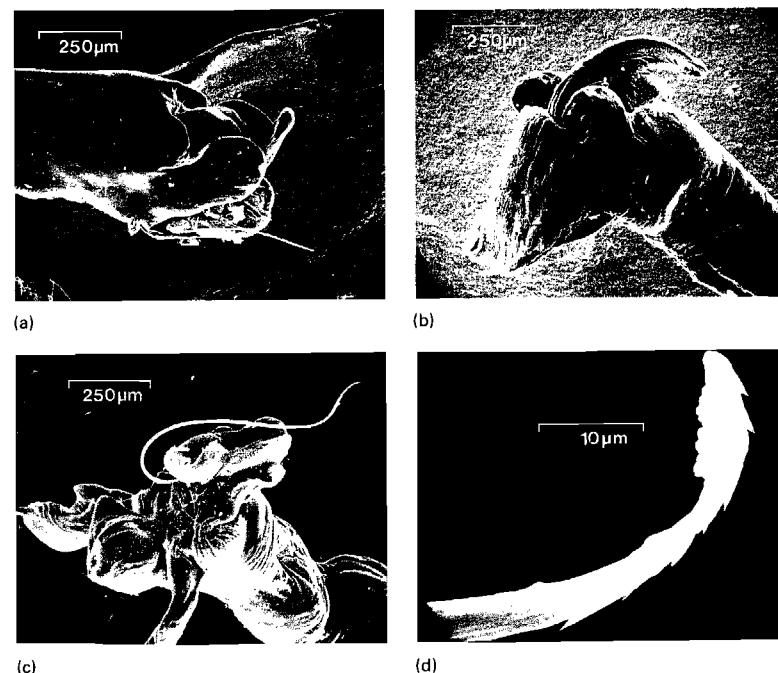
Fig. 8.4 Two sperm displacement mechanisms in Odonata. Photos by M. Siva-Jothy. *Crocethemis erythraea*: (a) Uninflated penis. (b) Inflated penis. The horn-like structure repositions sperm of previous males in the spermatheca. *Orthetrum cancellatum*: (c) The whip-like flagellum is everted during copula. (d) It carries barbs which remove sperm from the narrow ducts of the spermatheca (Siva-Jothy pers. comm.).

The penis of a male *Orthetrum cancellatum* is equipped with a barbed whip at the end which is used to scrape out of the female any sperm left by previous males before he injects new sperm into the sperm sac. *Crocethemis erythraea*, another dragonfly, uses an inflatable penis with a horn-like appendage to pack the sperm of previous males into corners of the spermetheca (Fig. 8.4; see also Waage 1979).

In some invertebrates (especially insects) the male cements up the female's genital opening after copulation to prevent other males from fertilizing her. The males of *Moniliformes dubius*, a parasitic acanthocephalan worm in the intestine of rats, produces a chastity belt of this kind but in addition to sealing up the

Copulatory plugs

them from mating again (Abele & Gilchrist 1977). No less remarkable are the habits of the hemipteran insect *Xylocoris maculipennis*. In normal copulation of the species the male simply pierces the body wall of the female and injects sperm, which then swim around inside the female until they encounter and fertilize her eggs. As with the acanthocephalan worms, males sometimes engage in homosexual 'copulation'. A male *Xylocoris* may inject his sperm into a rival male. The sperm then swim inside the body to the victim's testes, where they wait to be passed on to a female next time the victim mates (Carayon 1974).

Competition between males to prevent each other's sperm from fertilizing eggs is sometimes referred to as 'sperm competition' (Birkhead & Møller 1992). Another insect example was described in Chapter 3: the sperm of a second male displaces that of the first male to mate with a female dungfly. Sperm competition also occurs in vertebrates. For example, during courtship male salamanders and newts deposit little sperm-capped rods of jelly (spermatophores) on the bottom of the pond and then try to manoeuvre the female onto the spermatophore to achieve fertilization. In the salamander *Ambystoma maculatum*, males compete by depositing their spermatophores on top of those of other males. The top spermatophore is the one that fertilizes the female's eggs (Arnold 1976).

A fourth example of the arcane methods of male–male competition found among invertebrates is the use of anti-aphrodisiac smells. Larry Gilbert (1976) noticed that female *Heliconius erato* butterflies always smell peculiar after they have mated. He was able to show experimentally that the scent does not come from the female herself, but is deposited by the male at the end of mating. Gilbert also found that the scent discourages other males from mating with the female, perhaps because it resembles a scent used by males to repel one another in other contexts.

RELUCTANT FEMALES

Since females in the great majority of species are the chief providers of resources for the zygote, they might be expected to choose their mates carefully in order to get something in return. To put it another way, each egg represents a relatively large proportion of a female's lifetime production of gametes when compared with a sperm, so the female has more to lose if something goes wrong. Mating with the wrong species could cost a female frog her whole year's supply of eggs, but would cost the male very little apart from lost time — he could still go on to mate success-

fully with a member of the correct species the next day. Not surprisingly therefore, females are on the whole choosier than males during courtship. Choosiness extends not only to discriminating between species, but also to discriminating between males within a species. Females often select males on the basis of material resources they can offer and perhaps sometimes to obtain genetic benefits for their offspring.

(a) Non-genetic benefits: good resources and parental ability

In many animal species males defend breeding territories containing resources which play a crucial role in the survival of a female's eggs or young (see also Chapter 9). For example male North American bullfrogs (*Rana catesbeiana*) defend territories in ponds and small lakes where females come to lay their eggs (Fig. 8.5). Some territories are much better for survival of eggs than others and these are the ones which females prefer. One factor which has an important influence on survival of eggs is predation by leeches (*Macrobdella decora*). Two environmental features of a territory influence leech predation: if the water is warm the eggs develop faster and are therefore exposed to predation for fewer days, and if the vegetation in the water is not too dense the eggs can form into a ball which the leeches find hard to attack. In territories with a dense mat of vegetation the eggs lie in a thin film on top of the plants and are more easily attacked. The bullfrogs also show that female choice and male–male

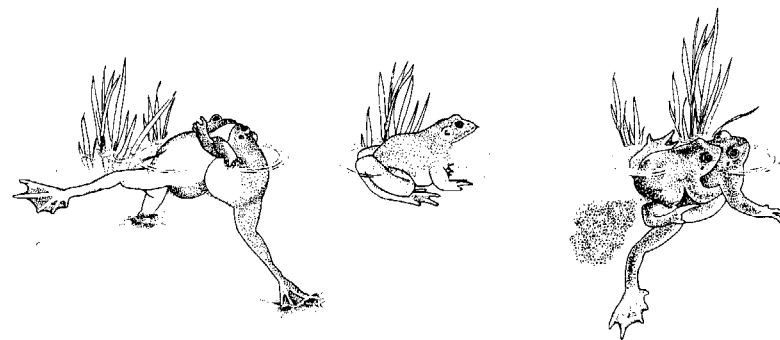Fig. 8.5 Sexual selection in male bullfrogs. Males compete by wrestling and calling (left and middle) for good territories, in which the females prefer to lay their eggs (right). The good territories have high survival of eggs because they are warm and because the vegetation is not too dense. From Howard (1978a,b).

Homosexual mating

anti-aphrodisiac scents

Female bullfrogs choose males with good territories

competition may go hand in hand. The preferred territories are hotly contested by males and the largest, strongest frogs end up in the best sites.

Food is a resource which often limits a female's capacity to make eggs and during courtship females may choose whether or not to mate with a male on the basis of his ability to provide food. In some birds and insects for example, males may provide food for the female during courtship ('courtship feeding') which makes a significant contribution to her eggs. Female hanging flies (*Hylobittacus apicalis*) will mate with a male only if he provides a large insect for her to eat during copulation. The larger the insect, the longer the male is allowed to copulate and the more eggs he fertilizes (Fig. 8.6). The female gains from a large insect by having more food to put into her eggs. Gifts provided by insects during courtship may help to protect, rather than nourish the eggs. In the moth *Utethesia ornatrix*, the male transfers protective alkaloids to the female during mating. Further, the same alkaloids are used by the male as a pheromonal attractant. The female is able to assess the quantity of poison she will receive by the concentration in the pheromone (Dussourd *et al.* 1991). In birds, the male usually helps to feed the young and courtship feeding may play the additional role of indicating to the female how good the male is at bringing food for the young. In the common tern (*Sterna fuscata*) there is a correlation between the ability of the male to bring food during courtship feeding and his ability to feed the chicks later in the season. Pairs often break up during the courtship feeding period and it is possible that females are assessing their mates and rejecting poor quality partners (Nisbet 1977).

(b) Genetic benefits

If some males have 'better' genes than others, could a female improve the success of her progeny by choosing males with good genes? Good genes are ones which increase the ability of her offspring to survive, compete and reproduce. One of the few studies attempting to test this experimentally by Linda Partridge (1980). She took groups of female fruit flies (*Drosophila*) and either allowed them to mate freely with a population of males or forced each female to mate with a randomly chosen partner. The offspring of the 'choice' and 'no choice' females were then tested for their competitive ability by rearing the larvae in bottles with a fixed number of standard competitors (these were distinguishable by a genetic marker). Partridge found that the offspring of the 'choice' group did slightly but consistently
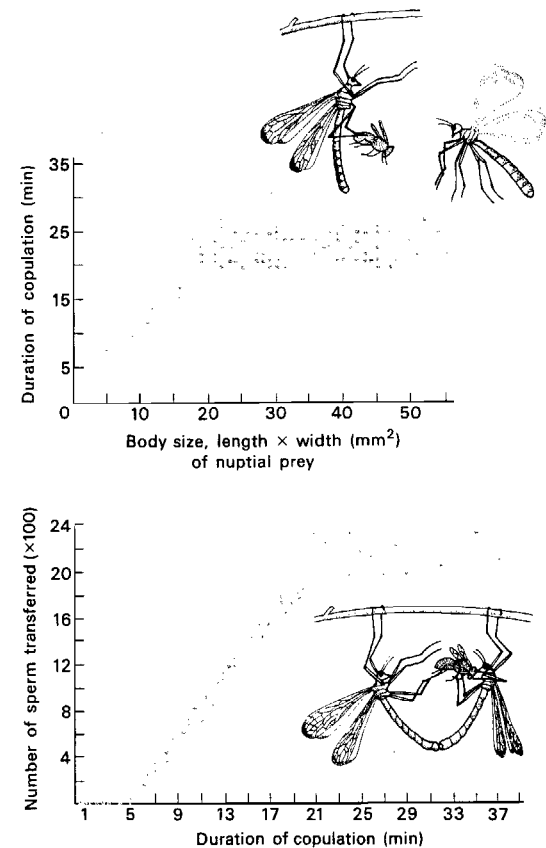
Fig. 8.6 Female choice for good resources. Female hanging flies (*Hylobittacus apicalis*) mate with males for longer if the male brings a larger prey item to eat during copulation. The male benefits from long copulation because he fertilizes more eggs. From Thornhill (1976).

better than those of 'no choice' females in the larval competition experiments. This experiment suggests that females are able to increase the survival of their offspring by choosing good genes in their mates, but it must be borne in mind that the results could also be in part explained by intra-sexual competition: in the 'choice' experiment, the males that mated may have been superior competitors against other males.

ELABORATE ORNAMENTS: FISHER'S HYPOTHESIS AND THE
HANDICAP HYPOTHESIS

The theory of sexual selection is most famous as an attempt to
explain the evolution of excessively elaborate adornments and
displays of male peacocks (Petrie *et al.* 1991), pheasants, birds of
paradise and so on (Plate 8.1, between pp. 212–213). Some
elaborate displays may have evolved for use in contests
between males, but some have almost certainly evolved as
a result of selection by females for genetic benefits. There are
two competing hypotheses to explain how selection for genetic
benefits might produce elaborate traits: *Fisher's hypothesis*
(sometimes called the 'runaway process' because it postulates
runaway positive feedback between female preference and male
displays), and the *handicap hypothesis*. In the following section
we will first describe two examples of studies in which females
have been shown to prefer elaborate male traits, then consider
how the two hypotheses might explain these results. Finally, we
consider whether there is any evidence for one or both hypotheses.

*(a) Examples of female preference for elaborate
male displays*

There are many studies which have looked for correlations
between male mating success or female preference, and male
sexual displays. However studies based purely on observation or
correlations do not allow us to demonstrate a cause–effect
relationship. One of the classic experimental studies is that of
Malte Andersson (1982), who showed that females of the long-
tailed widow bird (*Euplectes progne*) in Kenya prefer males with
long tails. This highly polygynous species is an ideal candidate
for sexual selection; the male is a sparrow-sized bird with a tail
up to 50 cm long. The female's tail is about 7 cm long, presumably
close to the optimum for flight purposes. Andersson studied 36
males which he divided into four groups. In one group he docked
the tails to about 14 cm, while in another group he attached the
severed bits of group I tails with Superglue. This increased the
tail length of group II males by an average of 25 cm. The remaining
two groups were controls: one lot were left untouched and the
others had their tails cut and glued without altering the length.
By counting the number of nests in each territory, Andersson
showed that before his experimental manipulations there was no
difference in mating success of the different groups, while after-
wards the long-tailed males did significantly better than the
controls or the shorter tailed birds (Fig. 8.7).

Two hypotheses for
elaborate adornments

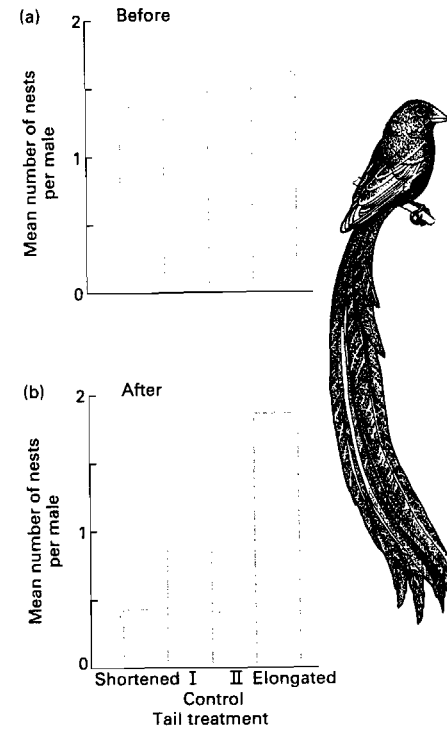Females prefer elaborate
traits

Fig. 8.7 Sexual selection for tail length in long-tailed widow birds. The top
line shows that there was no difference between the four groups before the
tails were altered. The bottom line shows that after the tails were cut and
lengthened the mating success went down and up respectively. The two
kinds of control birds were (I) unmanipulated, and (II) cut and glued back
without altering length. Mating success is measured as the number of active
nests in each male's territory. From Andersson (1982).

Another nice experimental study of a sexually selected elabor-
ate display is that of Clive Catchpole (1980; Catchpole *et al.*
1984) on the song of the European sedge warbler. The song consists
of a long stream of almost endlessly varying trills, whistles and
buzzes and is sung by the male after arriving back on the breeding
territory from the winter quarters: as soon as a male pairs, it
stops singing. Catchpole's measurements showed that the males
with the most elaborate songs are the first to acquire mates
(Fig. 8.9). Further, when female warblers were brought into the
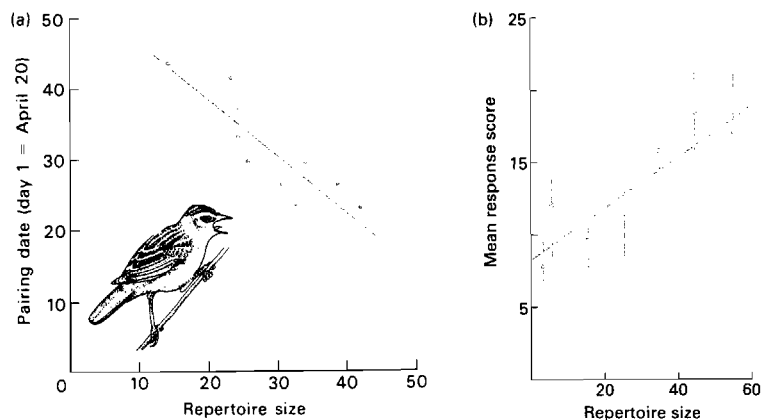laboratory and treated with oestradiol to make them sexually

Fig. 8.8 (a) Male sedge warblers with the largest song repertoires are the first to acquire females in the spring. The size of song repertoire is estimated from sample tape recordings of each male. The results were collected in such a way as to control for the possibilities that older males, or males in better territories, both mate first and have larger repertoires. From Catchpole (1980). (b) The mean ± s.e. response score of five females to repertoires of different sizes. The response score measures sexual behaviour. From Catchpole et al. (1984).

active, they were more responsive to large than to small repertoires. In contrast to the long tail of the widow bird it is not obvious what might be the counter-selection limiting the elaboration of song; one possibility is that elaborate songs are more readily detected by predators, as has been found in the leopard frog (Ryan et al. 1982).

(b) Fisher's hypothesis

R.A. Fisher (1930) was the first to clearly formulate the idea that elaborate male displays may be sexually selected simply because it makes males attractive to females. This may sound circular, and indeed it is, but that is the elegance of Fisher's argument. At the beginning, he supposed, females preferred a particular male trait (let us take long tails as an example) because it indicated something about male quality. Perhaps males with longer tails were better at flying and therefore collecting food or avoiding predators. An alternative starting point is to suppose that larger tails were simply easier to detect (Arak 1983) or that females had a pre-existing sensory bias to respond to certain stimuli (Ryan et al. 1990; see Chapter 14). If there is some genetic basis for differences between males in tail length the advantage will be

passed on to the female's sons. At the same time, a gene which causes females to prefer longer than average tails will also be favoured since these females will have sons better able to fly or more readily detected by potential mates. Now once the female preference for longer tails starts to spread, longer tailed males will gain a double advantage: they will be better at flying and be more likely to get a mate. The female similarly gets a double advantage from choosing: she will have sons that are both good fliers and attractive to females. As the positive feedback between female preference and longer tails develops, gradually the benefit of attractive sons will become the more important reason for female choice, and the favoured trait might eventually decrease the survival ability of males. When the decrease in survival counter-balances sexual attractiveness, selection for increasing tail length will grind to a halt. Box 8.1 describes some aspects of Fisher's hypothesis in more detail.

Box 8.1 *Sexual selection for nose length: the importance of genetic covariance for Fisher's hypothesis. After Lande (1981).*

1 Imagine that at the start there was a range of nose lengths and of female preferences in the population. Females with a preference for slightly longer than average noses would be mated to males with longer noses and vice versa. The crucial fact to note is that offspring of these matings would have *both* the nose and preference genes: either genes for long nose plus long preference or short nose and short preference. The preference is expressed only in females and the nose in males, but everyone carries both kinds of gene. In short, there will arise an association or *covariance* between nose and preference genes. You could look at a female's preference and predict what kind of nose genes she carries to give to her sons (Fig. a).

2 How will evolution proceed, given this covariance? If equal numbers of females have preference above and below the mean nose length (x), there will be no change. But if by chance there was a slight predominance of females on one side of the mean (it could be long or short but let us take long), then positive feedback will start. This is shown by the arrows on Fig. a. Females select for long noses (long-nosed males have a higher chance of mating) and thereby, *because of the covariance*, select for long preference. This

Box 8.1 *Continued*

(a)
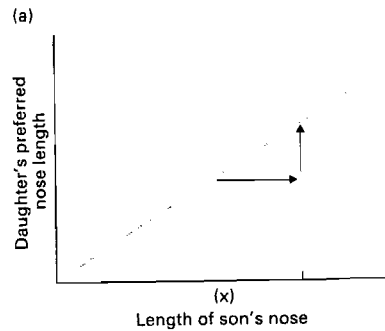
(a) Genes for long nose and long preference go together in the offspring. The slope of the line represents the degree of association or covariance.

in turn produces a further push to long noses and hence an increase in preference.

3 The final outcome of sexual selection in quantitative models of this hypothesis depends on the exact assumptions made in the model, for example whether or not there is a cost of female choice (Pomiankowski *et al.* 1991). However, the important general point is that covariance between the male trait and female preference underlies Fisher's hypothesis.

(c) The handicap hypothesis

Amotz Zahavi (1975, 1977) suggested an alternative view of elaborate male sexual displays. He pointed out that the peacock's long tail is a handicap in day-to-day survival, a view which few would dispute. He then went on to suggest that females prefer long tails (or other equivalent traits) precisely *because* they are handicaps and therefore act as a reliable signal of a male's genetic quality. The tail demonstrates a male's ability to survive in spite of the handicap, which means that he must be extra good in other respects. If any of this ability is heritable, then the tendency to be 'good' at surviving will be passed on to offspring. Thus females select for good genes by selecting to mate only with males whose displays honestly indicate their genetic quality. Note that in this hypothesis the 'good genes' are genes for the utilitarian aspects of survival and reproduction, rather than genes purely for attracting females, as assumed in Fisher's hypothesis. When it was first

published, Zahavi's idea was not accepted, but subsequent theoretical papers (Kodric Brown & Brown 1984; Nur & Hasson 1984; Grafen 1990a,b) have led to the view that the handicap hypothesis is a plausible explanation for the evolution of elaborate sexual displays, and perhaps of animal signals in general (Zahavi 1987; see Chapter 14). The most important feature of theoretical models of the handicap principle that 'work' (i.e. show that females could benefit from choosing males because of their handicaps) is that males only express the handicap, in other words develop the full sexual display, when they are in good condition. This gets around the difficulty some critics saw in Zahavi's original idea, that males were forced to carry the handicap whether or not they could afford it, because it was viewed as a fixed trait. There are different variants of the flexible handicap idea (some authors refer to 'revealing handicaps' that reveal a male's current vigour, others to 'condition-dependent handicaps' expressed in proportion to the male's condition), but the essential feature of all these models is that the degree of expression of the male sexual display tells the female about his genetic quality.

The best studied version of the handicap hypothesis is the one first proposed by Bill Hamilton and Marlene Zuk (1982), namely that sexual displays are reliable indicators of genetic resistance to disease. If males are able to show the full development of their secondary sexual characteristics only when they are free of diseases, females, by choosing for elaborate displays, might in effect be acting as diagnostic veterinarians. This particular version of the handicap hypothesis has two features which make it especially attractive. First of all, disease is a very widespread agent of selection, so the idea could have general application as a reason for selecting handicapped males. Second, diseases have the property of continually evolving new varieties, hence continually presenting new selective hurdles. The importance of this can be illustrated with a hypothetical example.

Suppose a farmer wants to select for larger body size in a population of pigs. He takes the heaviest males and females to start the next brood and repeats this procedure for several generations. What will happen? Assuming that there is some genetic variance for body weight, selection will at first be fairly effective, but soon the stock will become less variable with respect to genes for body weight, because only a few genotypes (the heaviest) have been allowed to breed. When the genetic variance is 'used up' selection will cease to be effective in changing body size. In the same way, females cannot improve the genetic quality of their offspring indefinitely by choosing males for good genes. Further, if choosing has a cost, for example time spent searching,

Selection for male quality may work if handicaps are flexible traits

Disease resistance and the handicap hypothesis

Exhausting genetic variation

females should stop choosing when genetic benefits no longer accrue. The fact that diseases continually evolve new forms might get around this problem: selection for disease resistance never continues for long enough in one direction for all the genetic variation to be used up.

(d) Evidence for the Fisher and handicap hypotheses

Both the Fisher and the handicap hypotheses are attempts to explain why females should prefer elaborate or extreme male displays. Therefore experiments and correlations such as those on long-tailed widow birds and sedge warblers described above, whilst consistent with both hypotheses, do not discriminate between them. In order to demonstrate that a trait had evolved by Fisher's process, it would be necessary to show that there is genetic variation for both female preference and the male trait, and that the genes tend to covary (Box 8.1). Because Fisher's hypothesis assumes that the only benefit of the selected trait is increased mating success, it would also be necessary to show that expression of the male trait did not correlate with any inherited 'utilitarian' aspect of fitness such as disease resistance or ability to gather scarce resources, as proposed by the handicap hypothesis. Two ways to examine this prediction would be (a) to see whether or not, within a population of males, more extreme expression of the trait was correlated with viability, and (b) to examine the offspring of males with extreme traits. According to Fisher's hypothesis they should have no enhanced viability, only enhanced male mating success. The difficulty with both of these tests is that in order to support Fisher's hypothesis one would need to see a negative result. Negative results could arise for many reasons, including not having a large enough sample or not measuring the appropriate variables.

Among the few studies to demonstrate a genetic correlation between male display and female preference is the work on guppies, *Poecilia reticulata*, by Anne Houde (Houde 1988; Houde & Endler 1990). Guppies occur in many different stream systems in Trinidad, and males from different populations differ greatly in the extent to which they develop bright orange and blue spots, which are a stimulus for females during courtship. These differences between streams are correlated with the presence or absence of predators, including other species of fish and prawns. In streams without predators males have large spots, in predator-rich streams the spots are smaller (Chapter 4). Females from streams with large-

small-spotted males. Furthermore, the differences between populations in both male sexual colour pattern and female preference are genetic: they persist in the laboratory for many generations when offspring are reared in standard conditions. Thus, in guppies, there is a genetic correlation between male display and female preference, which is essential for the Fisher process to operate. The fact that the differences persist under standard laboratory conditions suggests that the expression of the spot size does not depend on, for example, ability to gather food or on disease resistance, but as already pointed out, it would be difficult to prove that the trait is totally unrelated to viability. Therefore the guppy results, whilst consistent with Fisher's hypothesis, cannot rule out the handicap hypothesis. In contrast to the genetic differences between streams in spot size, the brightness of the orange pigment in the spots may be influenced by the environment (Kodric Brown 1989; Houde & Torio 1992).

Tests of the handicap hypothesis have mainly focused on the version proposed by Hamilton and Zuk, that male displays reveal their degree of resistance to parasites (Milinski & Bakker 1990; Clayton 1991). However, most of these studies are incomplete tests: they do not test the preference for the trait, the correlation between expression of the trait and disease resistance, and the heritability of resistance. The most detailed study to date to meet all these criteria is that of Møller on swallows (Box 8.2).

To summarize, there is now convincing evidence that females in a variety of species prefer extreme male displays. In some species, such as the guppy, we know that variation in the trait and the preference is heritable. In others, such as the swallow, we know that variation in the trait is also correlated with another aspect of fitness, as in the handicap hypothesis. We do not yet, however, have sufficient evidence to say which of the two hypotheses discussed in this section is more generally applicable. In fact, they are not necessarily incompatible with one another (Iwasa *et al.* 1991). Given a genetic correlation between preference and the trait, Fisher's process has the potential to operate even if the trait is also a handicap.

MALE INVESTMENT

We have so far assumed that females are investors (i.e. have low potential reproductive rate) and males are competitors. While this picture describes most animal species, there are exceptions. In many birds, some amphibians, and arthropods, both male and

Box 8.2 *A case study: the tail of the swallow.*

Testing the Hamilton–Zuk hypothesis is by no means straightforward. For example, it is not sufficient to show merely that females prefer males with lower parasite burdens. They may do this not because they are shopping for good genes for their offspring but simply because they want to avoid infection during the act of mating, or because they want a partner able to provide efficient parental care (heavily parasitized males may be debilitated). The four key assumptions that need testing are: (a) parasites reduce host fitness; (b) parasite resistance is genetic; (c) parasite resistance is signalled by the elaboration of sexual ornaments; (d) females prefer males with the most elaborate signals. All four factors have been demonstrated in a detailed field study of the barn swallow, *Hirundo rustica*, in Denmark by Anders Pape Møller (1988, 1989, 1990).

The barn swallow is a monogamous insectivorous bird which feeds on the wing and often nests in colonies in farm buildings. There is little difference between the sexes, except that males have more elongated outer tail feathers which they display, either in the air or while perched, in an attempt to attract a female (Fig. a). Although sexual selection is

expected to be less intense in monogamous species than in polygynous species like the widow birds (see above), there will still be competition between males for mates because there is an advantage to pair up early. This leads to greater reproductive success not only because there is often more food available early in the season but also because early breeding increases the chance of raising several broods in the year. Males compete, therefore, to pair up as early as possible.

First of all, Møller showed that females preferred males with longer tails. Males with experimentally elongated tails paired up more quickly and were also preferred by females seeking extra-pair matings (Fig. b). As a result of pairing early, males with elongated tails were more likely to have two broods in the season and so enjoyed greater reproductive success. Why then do males not grow such extra-long tails naturally? The answer is that there is a cost. Males with experimentally elongated tails were handicapped in their foraging; they caught smaller, less profitable, prey and grew poorer quality feathers and shorter tails at the next moult, probably as a result of food deficiency. As a result, they were slower to attract a mate the following year and suffered reduced reproductive success.

(a) Male barn swallow, in flight, showing elongated outer tail feathers.
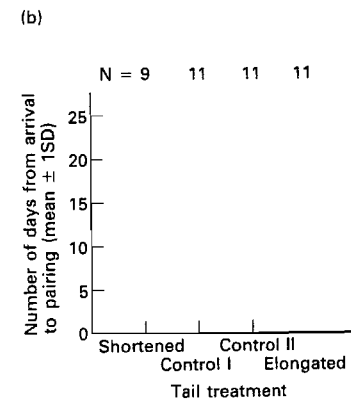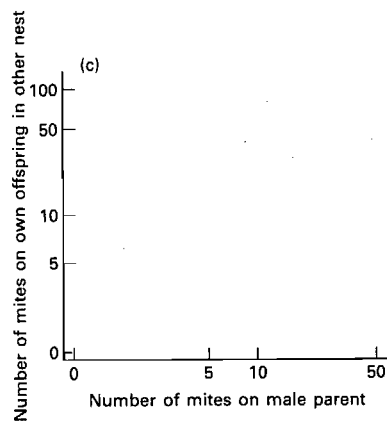
(b) Male barn swallows with experimentally elongated tails pair up sooner than controls (I, feathers cut and re-glued; II, unmanipulated), and males with shortened tails pair up last of all. From Møller (1988).

Box 8.2 *Continued*

Why do females prefer males with longer tails? Could the ornament signal a male's genetic quality in terms of his ability to resist parasites? The most obvious parasite on swallows is a blood-sucking mite, *Ornithonyssus bursa*, which infects both adults and nestlings. The life cycle of the mite, from egg to adult, lasts just 5–7 days so one reproductive cycle of the swallow provides time for 8–10 generations of mites. This means that numbers of mites in a nest can build up rapidly and the maximum recorded was 14 000! Møller showed that nestlings reared in nests with lots of mites were lighter and smaller and suffered increased mortality. Experiments in which mites were either added or removed (by spraying with pyrethrin solution) confirmed that mites were the cause of the reduced growth. The precise cause of the harm is not yet known; birds may have suffered simply from loss of blood or the mites could have been vectors of blood parasites such as haematozoa or viruses.

There was large variation in the population in the degree of parasite infection. To test whether parasite resistance was heritable, Møller exchanged half the nestlings between pairs of nests soon after hatching. He found that a nestling's parasite burden was correlated with that of its parents, even when the nestling was reared in another nest (Fig. c), but not with that of its foster parents. Thus the genetic origin

of an offspring was a predictor of its parasite levels, not the site of rearing. This suggests that parasite resistance is partly genetic.

And now finally to the link with the swallow's tail. In the cross-fostering experiments Møller found that parents with longer tail ornaments had offspring with smaller mite loads, even when their offspring were raised in another nest. This relationship was strongest for male parent tail length and offspring mite loads (Fig. d). This suggests that the length of a male's tail signals his degree of parasite resistance. In conclusion, the female's preference for the male ornament makes good sense under the Hamilton–Zuk hypothesis that they are choosing males able to pass on 'good genes' to the offspring.
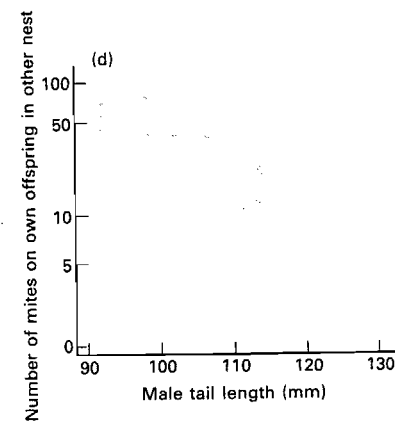
(d) Males with longer tails fathered offspring with lower parasite loads. From Møller (1990).

(c) Cross-fostering experiments showed that offspring parasite loads

Sometimes the usual sex roles are completely reversed so that males do the investing and females the competing (Chapter 9). The ideas about sexual conflict and sexual selection can still be applied in modified form to species with equal or primarily male investment. When both sexes care equally for the offspring, for example, courtship may involve assessment and choice by males as well as by females. Males of species with internal fertilization can never be absolutely sure that they have fathered the children of their mate, and one role of courtship may be as an insurance

allows males to assess whether or not females have previously mated with others. This was tested by Erickson and Zenone (1976). They found that male barbary doves (*Streptopelia risoria*) attack a female instead of courting her if she performs the 'bow posture' (an advanced stage of courtship) too quickly. Since the females which responded in this way had been pre-treated by allowing them to court with another male, the reaction of the test males in rejecting eager females is adaptive if courtship plays a role in assessing certainty of paternity, before investing in offspring. It would not have been predicted by the older view that male courtship serves to sexually arouse the female!

In species with high male investment, females tend to be the competitive sex and males may be choosy. In moorhens (*Gallinula chloropus*) males do almost three-quarters of the incubation and females play an active role in competing for the chance to mate with good incubators. These ideal husbands are small and fat: well equipped to survive on their reserves during long incubation stints (Petrie 1983). In other species, investing males may actually reject low quality females (Fig. 8.9).

Sexual conflict

Let us now return to the starting point of this chapter, sexual conflict. Recall the view of the origin of anisogamy as the primeval example of sexual conflict. The conflict was one about mating decisions. Macrogametes might have done better had they been able to discriminate against microgametes, but in the evolutionary race microgametes won. Similar, but more directly observable, conflicts of interest between the sexes are still apparent today, not only with respect to mating decisions but also in the contexts of parental investment, multiple matings and infanticide.

(a) Mating decisions

As we have emphasized earlier in the chapter, females have more to lose and therefore tend to be choosier than males. Thus for a given encounter it will often be the case that males are favoured if they do mate and females if they do not (Parker 1979). An extreme manifestation of this conflict is enforced copulation as exemplified by scorpionflies (*Panorpa* spp.). Male scorpionflies usually acquire a mate by presenting her with a nuptial gift in the form of a special salivary secretion or a dead insect (this is very similar to the *Hylobittacus* described earlier). The female feeds on the gift during copulation and turns the food into eggs
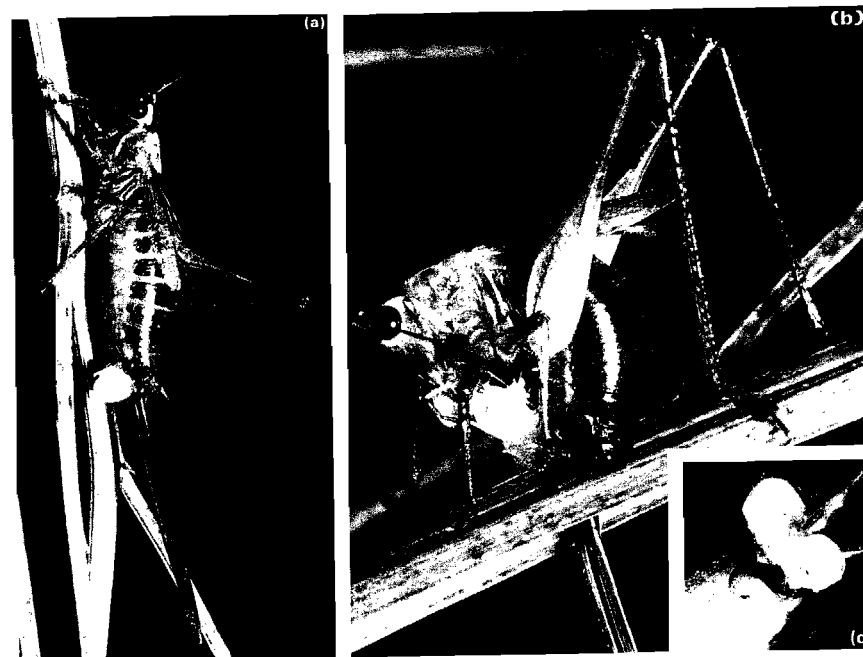

Fig. 8.9 A female katydid (bush cricket, *Conocephalus nigropleurum*). In some species of crickets the male produces a huge, protein-rich spermatophore (it may weigh up to 27 per cent of the male's body weight) which is eaten by the female and used to make eggs. With this large investment the male can afford to be choosy. Females prefer large males because they make large spermatophores while males reject small females because they are capable of laying fewer eggs than are large females. (a) Mated female with spermatophore. (b) Female eating spermatophore. (c) Close up of spermatophore. From Gwynne (1982).

with a special abdominal organ (the notal organ) without offering a gift (Thornhill 1980). Enforced copulation appears to be a case of sexual conflict. The female loses because she obtains no food for her eggs and has to search for food herself, while the male benefits because he avoids the risky business of finding a nuptial gift. Scorpion flies feed on insects in spiders' webs and quite often get caught up in the web themselves, so foraging is certainly risky (65 per cent of adults die this way). Why do not all males enforce copulations? The exact balance of costs and benefits is not known, but it appears that it results in a very low success

only when they cannot find prey or make enough saliva to attract a female.

(b) Parental investment

This is a topic to which we will return in the next chapter. Here it is sufficient to note that in species with investment beyond the gamete stage, each sex might be expected to exploit the other by reducing its own share in the investment. The outcome of this sexual conflict may depend on practical considerations such as which sex is the first to be in a position to desert the other. When fertilization is internal, for example, a male has the possibility of deserting the female immediately after fertilization and leaving her with the eggs or young to care for.

(c) Infanticide

Infanticide may benefit males and not females

As we saw in Chapter 1, male lions may slaughter the cubs in a pride shortly after they take over as group leaders. This behaviour (which is also seen in some primates) probably increases male reproductive success, as explained in Chapter 1, and clearly decreases female success. This seems to be a case of sexual conflict in which the males have won, but it is perhaps surprising that females have not evolved counter-adaptations. They could, for example, eat their own young once they have been killed in order to recoup as much as possible of their losses (Chapter 12).

(d) Multiple matings

As Bateman's experiments with *Drosophila* showed (p. 177) females may often gain little by mating with more than one male (but see p. 229). However, because of sperm competition males may gain by mating with already fertilized females. Multiple matings are likely to be costly to the female at the same time as being advantageous to the male. This is dramatically illustrated by the dungflies described in Chapter 7. When two males struggle for possession of a female, the female is sometimes drowned in cowdung by the fighting males on top of her!

Conflicts of interest between the sexes will lead to an evolutionary race of the sort envisaged by Parker *et al.* for sperms and eggs. There is no simple answer to the question 'Which sex is more likely to win the chase?' As we discussed earlier, factors such as the strength of selection and the amount of genetic variation will determine how fast the two sexes can evolve adaptation and counter-adaptation, but it is not possible to make any

more specific statements about the outcome of sexual conflict races.

The significance of courtship

As we have mentioned earlier in the chapter, some aspects of courtship behaviour can be interpreted in terms of sexual conflict and sexual selection. However this is not true of all courtship signals: many are designed for species identification, and here the interests of the two sexes are similar because both benefit by mating with a member of the same species. Some of the clearest examples of this role of courtship come from studies of frog calls. When several species of frogs live in the same pond, each has a characteristic and distinct mating call given by the male, and females are attracted only to calls of their own species. In some frogs (e.g. the cricket frog *Acris crepitans*) it has been shown that the female's selectivity of response results from the fact that the auditory system is tuned to the particular frequencies in the male call (Capranica *et al.* 1973).

Courtship displays may also play a role in competition between males within a species for mating opportunities. Often the same displays simultaneously serve to repel other males and attract females. An example for which this has been demonstrated experimentally is the mating call of the Pacific tree frog (*Hyla regilla*) (Whitney & Krebs 1975a,b). Males are repelled and females attracted by loudspeakers broadcasting the mating call and females select out of a group of loudspeakers the one which calls for the longest bouts. Females may choose between displays purely on the basis of sexual attractiveness, as explained by Fisher's theory of sexual selection, but there is also the possibility that differences in courtship between males may indicate habitat quality, for example males with territories containing a lot of food might be able to afford to spend more time displaying.

A third role of courtship to which we have referred is assessment. In a species with male parental care females may assess the ability of the male to look after young and males may assess whether a female has previously been fertilized. Early work by ethologists on birds and fish showed that at the beginning of courtship males are often aggressive and females are coy or reluctant. Courtship was seen, therefore, as serving to synchronize sexual arousal of the partners. A possible explanation of *why* it should be necessary to overcome aggression and reluctance is that the early phases involve assessment by both partners before investing in offspring.

Throughout this chapter we have emphasized the role of

Reproductive isolation

Intra-sexual competition

Assessment

females as investors in the zygote and offspring, but we have also mentioned that sometimes males invest as much as or more than females. Why should this happen in some species but not in others? In order to answer this question we will turn in the next chapter to the influence of ecological pressures.

Summary

Conflict lies at the heart of sexual reproduction. The fundamental difference between male and female is the size of gametes. Males produce tiny gametes and can be viewed as successful parasites of large female gametes. Because sperm is cheap, males can increase their reproductive success by mating with many females. Females can only increase their success by making eggs or young at a faster rate. Females are a scarce resource for which males compete and much of male courtship can be understood in terms of competition for matings. Females may be reluctant to mate unless they can choose partners with resources or genetic benefits. Sometimes the general rule of high female investment is reversed and males are the main investors: here females are competitive and males are choosy.

The two major hypotheses for how genetic benefits may be gained by sexual selection are (a) Fisher's hypothesis that the benefits are purely aesthetic (genetically attractive sons) and (b) the handicap hypothesis that the benefits are to do with general viability, for example disease resistance.

Further reading

Malte Andersson's (1993) book is the definitive account of sexual selection. Clayton (1991) reviews the evidence for Hamilton and Zuk's hypothesis and Gibson and Höglund (1992) discuss the idea that females in leks (Chapter 9) may copy each other's choice of mate. Charnov's (1982) book is the definitive work on sex allocation, including sex ratio theory.

The papers by Burley et al. (1982) and Burley (1986a,b) present a remarkable set of data on mate choice in a monogamous species of bird, the zebra finch. Burley discovered that the coloured leg rings placed on the birds for individual identification in her captive colony influenced mating success. Males with red rings and females with black ones had a higher reproductive success than those with some other colours, green and blue being especially unattractive rings on males and females respectively. It appears that individuals with attractive rings get partners who are willing to do more parental work in return for mating with a desirable member of the opposite sex.

A study of a species with male investment is that of Smith (1979) on a giant water bug, in which the male carries the eggs on his back. To ensure paternity of the eggs he carries, the male repeatedly inseminates the female during egg laying, the record being 100 copulations in 36 hours.

McKinney et al. (1983) give an excellent review of forced copulation in waterfowl.

Topics for discussion

1 How might sexual selection have given rise to (a) antlers and (b) the peacock's tail?
2 What hypotheses might account for bright coloration in birds (see also Baker & Parker 1979; Lyon & Montgomery 1985 and references therein).
3 Why do males usually compete for females rather than vice versa? (Include in your discussion the concepts of parental investment, operational sex ratio and potential rate of reproduction.)
4 Is it possible to discriminate with empirical data between Fisher's hypothesis and the handicap hypothesis?