1 The Theory of Sexual Selection

1.1 Sexual Selection

Among the many problematic animals that Linnaeus (1758) classified were two distinctive ducks. One species had mottled brown plumage and a blue wing patch; he named it *Anas platyrhynchos*. The other was pale gray except for a chestnut breast, a metallic green head and neck, and a blue wing patch; Linnaeus called it *A. boschas*. Later on, the two ducks became recognized as one species, *A. boschas* being nothing but the male mallard *A. platyrhynchos*. This is not the only time that a prominent taxonomist has mistaken the sexes for separate species (Darwin 1871; Mayr 1963). Why are males and females so different in appearance? What are the selective pressures behind sex differences in size, shape, coloration, and behavior? And, most puzzling, how do extravagant male traits evolve, such as bright colors, huge feather plumes or fins, and other conspicuous male attributes that can hardly improve survival? It was primarily to solve these problems that Darwin (1859, 1871) developed his theory of sexual selection.

This chapter introduces the main concepts in sexual selection theory, and describes the basic reasons why there will be sexual selection. The development of the theory has been rich in controversies and alternative explanations, briefly reviewed in sections 1.3–1.5, and discussed in much of the rest of the book (outlined in the Preface). A major issue concerns the mechanisms that favor conspicuous secondary sex ornaments and signals. The debate persists today; Maynard Smith (1991a) remarked that "no topic in evolutionary biology has presented greater difficulties for theorists."

According to Darwin (1871), sexual selection arises from differences in reproductive success caused by competition over mates. It therefore requires sexual reproduction: the combination of genetic material from two parents in the progeny. It does not necessarily require different sexes. Demonstrations of sexual selection in bacteria may not be soon to come, but competition over mates in principle can occur also in unisexual organisms that exchange genetic material. The most obvious results of sexual selection in animals and plants depend, however, on there being two different sexes with their defining gamete properties, with females making large,

From Andersson, M. (1994). Sexual selection (pp. 3-31).
Princeton University Press,

nutritious eggs and males small, mobile sperm. This anisogamy, with gametes of two different sizes, underlies the evolution of sex differences in behavior and morphology.

How and why sexual reproduction arose are questions outside of sexual selection theory, whose interest is the forms and consequences of competition over mates. The origin and maintenance of sexual reproduction is still a major debated problem in evolutionary biology.[1]

ANISOGAMY

Explaining anisogamy may be a more tractable problem than that of sex. It seems likely that sexual reproduction, with two different mating types, preceded anisogamy. Most models for the evolution of anisogamy assume two basic selection pressures: for increasing zygote size (which improves zygote survival), and for increasing gamete number (reviewed by Hoekstra 1987). As the resources available for reproduction are limited, these two pressures oppose each other. A compromise solution is the evolution of two different sexes, one of which produces few, large gametes, the other many small gametes.

Parker et al. (1972) suggested that once sexuality has arisen, anisogamy is likely to evolve from isogamy through disruptive selection. If there is variation in gamete size, and if zygote survival increases with size, selection should favor gametes that fuse with large partners. For certain relationships between zygote size and survival, the evolutionarily stable strategy (ESS) is anisogamy, with one large and one small type of gamete in the population (see, e.g., Maynard Smith 1982).

Knowlton (1974) made a start at testing these ideas, finding a correlation between degree of coloniality and anisogamy in Volvocidae. Anisogamy may be favored when zygote survival increases markedly with its size, and optimal zygote size is large. This seems likely in multicellular forms such as *Volvox* colonies, where the zygote must give rise to many cells. In a more extensive analysis, gamete dimorphism was correlated with the level of cellular organization among algae and protozoa, and anisogamy was correlated with large zygote size among seventeen orders of algae (Bell 1982; Madsen and Waller 1983). These comparative studies lend qualitative support to the ideas of Parker et al. (1972), but there are many exceptions, and more aspects need to be tested, especially the relationship between zygote size and survival (Hoekstra 1987).

Another set of ideas points to advantages of small sperm size in pre-

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[1] See, for example, Ghiselin 1974, Williams 1975, Maynard Smith 1978, Bell 1982, B. Charlesworth 1989, Hamilton et al. 1990, Hurst and Hamilton 1992. The volumes edited by Stearns 1987 and Michod and Levin 1988 treat in detail the ideas and evidence raised to explain sexual reproduction.

venting transmission of cytoplasmic organelles and parasites to the zygote. There is a possibility of harmful conflict among cytoplasmic organelles such as mitochondria and chloroplasts (Cosmides and Toby 1981). Whereas the nuclear genes from both parents are required for proper functioning of the diploid zygote, this is not necessary for genes in the organelles. Such a gene that codes for destruction of the organelles from the other gamete, for example through digestion by DNA restriction enzymes, might be favored by selection. This could lead to intracellular conflict with deleterious consequences for the zygote and its nuclear genome. The conflict may be prevented by stripping sperm from the cytoplasma and its attendant organelles (e.g., Cosmides and Toby 1981; Hurst 1992). In addition, small sperm size probably reduces the risk of transmitting cytoplasmic parasites. Compared to isogamous sex, this should reduce the diversity of parasites in the zygote (Hurst 1990). The possible roles of intragenomic conflict in the evolution of sexual reproduction and anisogamy are discussed by Cosmides and Toby (1981), Hoekstra (1987), Hurst (1992), and Hurst et al. (1992). There is evidence that such aspects may have been crucial in the evolution of two sexes (Hurst and Hamilton 1992).

Regardless of how sex and anisogamy evolved, once they exist the stage is set for sexual conflict, within and between the sexes. Females produce large macrogametes, rich in energy: eggs. Males make small, highly motile microgametes: sperm. Other things being equal, a male can make many more gametes than a female, and males will compete to mate with as many or as fecund females as possible. On the other hand, the greater investment in fewer gametes by females should make them more careful in their choice of mating partner (also see section 7.2). The nature and consequences of competition over mates is the subject matter of the theory of sexual selection.

COMPETITION OVER MATES

One of the greatest problems facing Darwin's (1859) theory of evolution by natural selection concerned conspicuous male traits, such as song and other display, bright colors, and horns and other weapons. These and other extravagant male characters would seem to reduce survival, and so should be opposed by ordinary natural selection (figure 1.1.1). How, then, can such traits be explained?

Darwin's solution to the problem was his perhaps most controversial idea. He made a distinction between sexual and other natural selection: "Sexual Selection . . . depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring" (Darwin 1859, p. 88). Male ornaments, according to Darwin, evolve through sexual

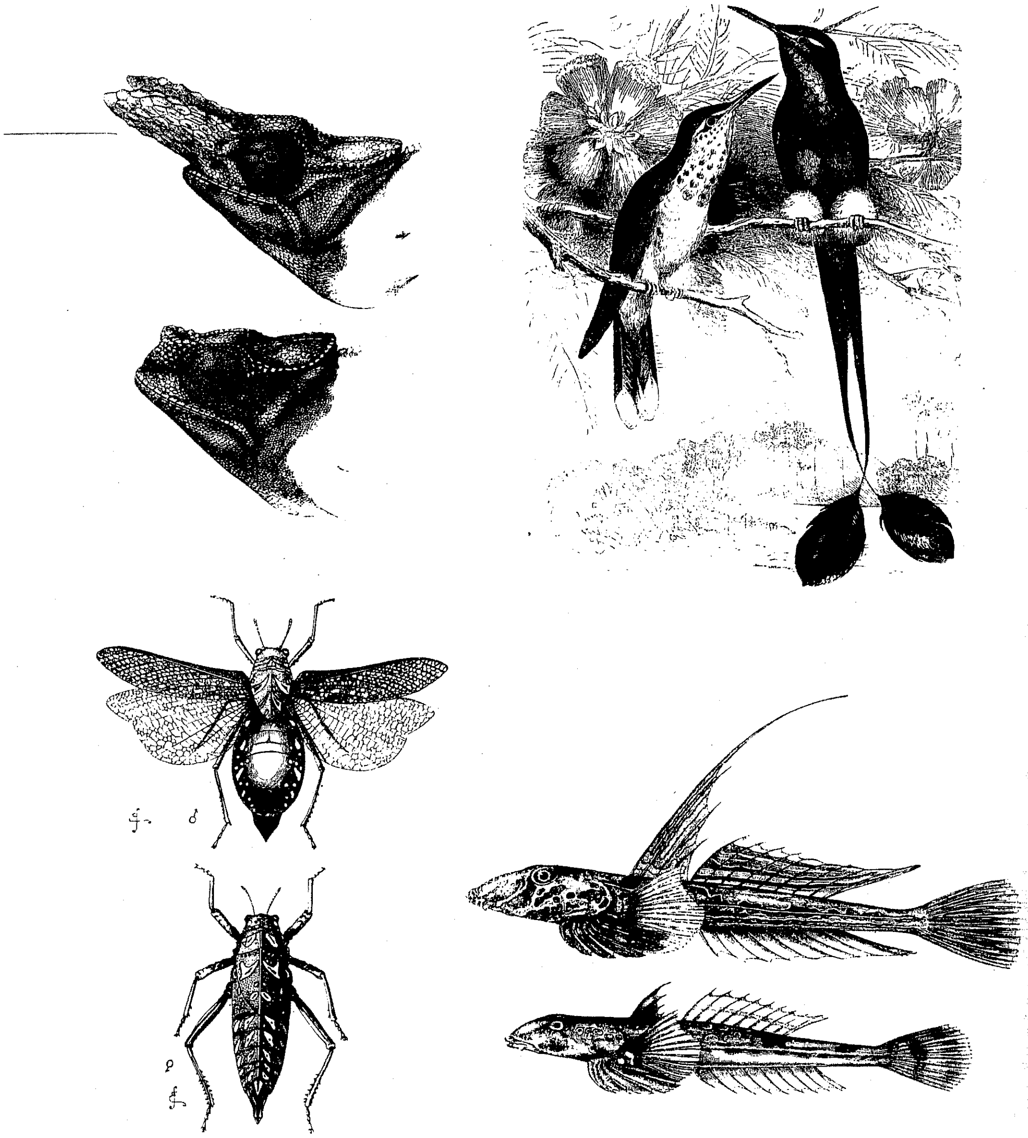

Figure 1.1.1 Some examples of the conspicuous dimorphism in secondary sex traits that provoked Darwin to develop his theory of sexual selection. In *Chamaeleon bifurcus*, only the male is horned. In the hummingbird *Spathura underwoodi*, the male is more brightly colored than the female, and has long ornamental tail feathers. The male gemmeous dragonet *Callionymus lyra*, with elongated dorsal fin, is also more brightly colored than the female. In the winged male of the *Pneumora* grasshopper, the air-filled abdomen is distended into a resonance chamber that probably amplifies his stridulation song. (From Darwin 1871)

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selection by female choice of mate, and male weapons evolve through sexual selection by contests over females.

From the previous and other passages, competition over mates emerges as the key aspect of Darwin's concept of sexual selection. (Competition is here taken in a broad sense, and includes not only contests, but also other mechanisms such as mate choice by the other sex; see below.) For instance, in *The Descent of Man, and Selection in Relation to Sex* (p. 257), Darwin talks about male organs "perfected through sexual selection, that is, by the advantage acquired by certain males over their rivals." More highly developed sensory or locomotory organs in males "serve only to give one male an advantage over another, for the less well-endowed males, if time were allowed them, would succeed in pairing with the females; and they would in all other respects, judging from the structure of the female, be equally well adapted for their ordinary habits of life. In such cases sexual selection must have come into action, for the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone. It was the importance of this distinction which led me to designate this form of selection as sexual selection."

SEXUAL SELECTION OF A TRAIT can therefore be viewed as a shorthand phrase for *differences in reproductive success, caused by competition over mates, and related to the expression of the trait*. Such differences can arise by many forms of direct or indirect mating competition. It may concern mate quality as well as numbers of mates, and can be brought about by mate choice, scrambles, contests, competition based on endurance, or any other form of rivalry over mates. Note that mate choice by one sex can suffice for there to be competition over mates in the other sex, even if there are no aggressive interactions (see below, this section).

Darwin did not define sexual selection in relation to reproductive success in general. Many traits that raise fertility and reproductive success have nothing to do with mating competition. For instance, the brood patch in birds improves incubation, and parental alarm calls help offspring avoid predators. Both traits increase the chances of successful reproduction, but probably neither improves success in competition over mates; they are therefore naturally but not sexually selected. Many aspects of courtship may also have functions other than improving success in competition over mates. For example, it may reduce escape responses or aggression in the mate, synchronize endocrine reproductive functions, or coordinate the behavior of mates in space and time for copulation (e.g., Bastock 1967).

Darwin (1871) noted that in borderline cases, such as sensory or locomotory organs that help a male find his way to a mate, it may not be possible in practice to distinguish between sexual and other natural selection. But such subtle exegetic problems do not concern the most puzzling traits mentioned above: advertising traits that are unlikely to improve survival. Such characters motivated the distinction between sexual and other natural selection.

A common cause of natural selection is the external environment, physical or biological; the agents of sexual selection are sexual rivals and mates (Ghiselin 1974). Contrasted with artificial selection, sexual selection in the wild is a subset of natural selection (J. L. Brown 1975). Yet Darwin's distinction between sexual and other natural selection is often useful; the evolutionary effects of competition over mates often differ in remarkable ways from those of other natural selection (see Endler 1986a for discussion and additional aspects of the relations between sexual and natural selection).

Conspicuous secondary sex traits may often be favored only or mainly by sexual selection and counteracted by other natural selection. Many other traits will be favored by both sexual and other natural selection, for example general metabolic efficiency, pathogen resistance, and any characteristic that improves both survival, mating, and reproductive success (figure 1.1.2). Although sexual selection is here viewed as a subset of natural se-

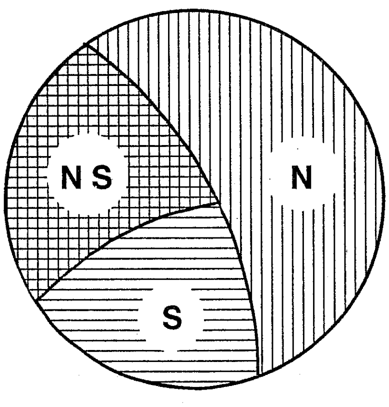

Figure 1.1.2 Relations between sexual and natural selection. The circle includes all traits favored by selection in the wild: natural selection. A subset of those traits is favored by competition over mates: sexual selection (horizontal hatching; areas NS and S). Some traits are favored by other natural selection (vertical hatching) as well as by sexual selection (area NS), or by other natural selection only (area N). Finally, some traits are favored only by sexual selection, but not by other natural selection (area S). This latter set of traits, favored only by competition over mates, contains secondary sex traits that reduce survival; they prompted Darwin to coin the term "sexual selection." Note, however, that many traits are probably favored by both sexual and other kinds of natural selection. (The relative sizes of the areas are arbitrary. The figure concerns only traits favored by selection in the wild, not those maintained by artificial selection or genetic drift.)

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lection, for brevity I will sometimes write of traits as being favored by sexual selection and disfavored by natural selection—that is, by natural selection other than that involving competition over mates. In spite of many suggestions to the contrary by leading biologists, from Wallace (1889) to Huxley (1938b) to Mayr (1982), the term sexual selection is here restricted to competition over mates. Darwin's concept still appears simpler and more useful than the alternatives.

Competition is here used in a similar sense as in ecology: competition occurs whenever the use of a resource (in this case, mates) by one individual makes the resource harder to come by for others. This is so whether or not the rivals meet in actual contests; the only requirement is that a user makes the resource less available to others. Mate choice by one sex therefore usually implies (indirect) competition over mates in the other sex, even if rivals never meet each other. When accepting and mating with a male that fertilizes her eggs, a female becomes unavailable to other males, at least temporarily. There is a similar distinction in evolutionary ecology between *interference competition*, often with direct aggressive struggles over some resource, with the competitors trying to exclude each other, and *exploitation competition*, where rivals consume the same resource, but do not necessarily meet each other (e.g., Pianka 1978; Futuyma 1986). For instance, they may be active at different parts of the day. Contest competition in sexual selection therefore corresponds to interference competition in ecology, whereas mate choice leads to exploitation competition over mates in the other sex. Among the mechanisms of mating competition, I therefore include not only contests, scrambles, endurance rivalry, and sperm competition, but also mate choice (table 1.1.1).

Competition over mates has been demonstrated in many studies. For example, if successful males are removed, their territories are often taken over by other males, and the mating success of previously less successful males rises (e.g., Watson 1967; Alatalo et al. 1991). Experimental increase of an ornament in some males often raises their success in attracting mates over that of other males, implying competition over mates (table 6.A).

In polygynous species where some males mate with several females, others with none, success in competition over mates is crucial for the fitness of males, and their weapons and ornaments are often highly developed. Sexual selection can, however, work also in monogamous species if the sex ratio is skewed, or if mates differ in quality (Darwin 1871; Fisher 1958; section 7.3 below). For example, among female birds, those in best condition are ready to breed first in the season, and so will have most time for raising young, hence producing most offspring (reviewed by Price et al. 1988). The first males to mate are therefore likely to get the most productive females. In addition, variation in mate quality might also affect the

Table 1.1.1

Mechanisms of Competition over Mates, and Traits Likely to Be Selected in the Competing Sex

Mechanism	*Characters Favored in the Competing Sex*
I. Scrambles	Early search and swift location of mates; well-developed sensory and locomotory organs
II. Endurance Rivalry	Ability to remain reproductively active during a large part of the season
III. Contests	1. Traits that improve success in fights, such as large size, strength, weaponry, agility, or threat signals
	2. Alternative mating tactics of inferior competitors, avoiding contests with superior rivals
IV. Mate Choice	1. Behavioral and morphological traits that attract and stimulate mates
	2. Offering of nutrition, territories, nest sites, or other resources needed by the mate for breeding
	3. Alternative mating tactics, such as forced copulation
V. Sperm Competition	1. Mate guarding, sequestering, frequent copulation, production of mating plugs, or other means of preventing rivals from copulating with the mate
	2. Ability of displacing rival sperm; production of abundant sperm to outcompete those of rivals

partner's survival. The better a parent provides food and guards against predators, the better its family should fare, including its mate. Such effects should augment the advantage of having a high-quality mate in species with biparental care. Traits that improve the ability to compete over mates should therefore be favored in monogamous as well as polygynous species (O'Donald 1987; Price et al. 1988; Kirkpatrick et al. 1990). Owing to more similar parental roles in monogamous than polygynous species, female competition over mates should also often be stronger in monogamous forms.

In the minority of species with mainly paternal care, the sex differences in parental roles can override the effects of anisogamy and lead to a reversal of other aspects of sex roles and sexual dimorphism (chapter 7). Limits to the number of sperm (ejaculates) that a male can deliver may also favor male mate choice (Dewsbury 1982b). Depending on the mating system, parental roles, and reproductive ecology, there can be competition and mate choice in both sexes, but competition should usually be most pronounced in males, and mate choice in females (see chapter 7).

Although Darwin (1871) did not include plants in his review, they can also be sexually selected; this is presently one of the most active and exciting applications of sexual selection theory (reviewed in chapter 17).

Forms of Mating Competition

Competition over mates can take several forms and favor a wide range of attributes (table 1.1.1; also see Ghiselin 1974; Otte 1979). Scrambles to first find a mate are often important; such scrambles may partly explain why males in many arthropods have larger eyes, chemorecepting antennae, or locomotory organs than females (reviewed by Thornhill and Alcock 1983). In many animals and plants, scrambles to fertilize females may select for "protandry," for instance earlier male than female hatching, maturation, or appearance on the breeding ground (e.g., Ghiselin 1974; Wiklund and Fagerström 1977; Wang et al. 1990; Baughman 1991). Competition over fertilization in plants selects for conspicuous corollas and other pollinator attractants (chapter 17). Searching for females apparently favors better male than female spatial memory in some mammals, and is associated with larger male hippocampus, a part of the brain that plays an important role in spatial learning (Gaulin and FitzGerald 1986, 1989; Jacobs et al. 1990).

Sexual selection will often favor traits that improve the endurance of a male, enabling him to remain longer at a breeding site and mate with females that otherwise would mate with other males. Male mating success is then correlated with the length of time spent at such sites. Endurance should increase with foraging efficiency and several other factors that are also naturally selected (Koenig and Albano 1986). In some cases, however, selection for endurance in competition over mates may lead to consequences not favored by ordinary natural selection. For example, male insectivorous marsupials of the genus *Antechinus* remain at the mating site without feeding until they die from stomach ulcers, disease, or parasites. All males die at the end of the breeding season, whereas some females survive and reproduce a second year (A. Cockburn, in prep.).

Fights over mates select for strength, often achieved by large size, and for weapons such as antlers, horns, and spurs. This idea was accepted by many of Charles Darwin's colleagues; such a function of male weapons had been suggested already by his grandfather Erasmus Darwin (1794) and other zoologists (see Aiken 1982). Males fight over females in a variety of animals, including some intuitively unlikely cases such as a gastropod, the fighting conch *Strombus pugilis* (Bradshaw-Hawkins and Sander 1981).

In addition to large sensory or locomotory organs and weapons, males in many animals have conspicuous ornaments or behavioral signals. Being well aware of the amazing results from artificial selection of traits such as plumage in domestic pigeons, Darwin (1871) suggested that female choice of mate in the wild can have similar effects: "It appears that in a state of nature female birds, by having long selected the more attractive males, have added to their beauty." Female choice became the most controversial part of the theory of sexual selection, and the detailed mechanisms by which mate choice works still remains so (e.g., Ghiselin 1974; Heisler et al. 1987; Kirkpatrick 1987a; discussion of criteria for identifying female choice are found in, e.g., Searcy and Andersson 1986; Heisler et al. 1987; Ryan and Keddy-Hector 1992). It has been the subject of much modeling (chapters 2–3), whereas the "law of battle" between males is more easily observed and is probably therefore less controversial, and less attractive to theoreticians (but see section 11.1).

The main forms of competition over mates are here termed contests, mate choice, scrambles, and endurance rivalry. Since Huxley (1938b,c), contests and scrambles have often been called "intrasexual" selection; competition by mate choice in contrast is often called "intersexual" selection. Huxley also used "epigamic selection" and several other technical terms. They seem to offer little advantage over the simple everyday words of Darwin (1871), who seems to have liked playing with dogs but not engaging in ludic activity with canine companions (O'Donald 1980a; Bonner and May 1981; J. L. Brown 1983). Here, the term *contest* is used where rivals display to or fight each other in competition over mates (or resources needed to attract mates); *scramble* where rapid location of the mate is crucial for success; *endurance rivalry* where persistence, for example the length of stay at a breeding site, affects mating success; and *mate choice* where the mate at stake determines, or at least influences, which rival will win. This broad definition of mate choice includes behavior that would not be called choice in a human context; it refers to external events, not mental processes (see Halliday 1983; Maynard Smith 1987). Darwin (1882) discussed this aspect in his last defense of sexual selection, written a few months before he died and read at the Zoological Society of London only hours before his death (Bajema 1984): "It would, however, be more correct to speak of the females as being excited or attracted in an especial degree by the appearance, voice, &c. of certain males, rather than deliberately selecting them." Today, mate preference and choice are often defined broadly, for example as behavior patterns that make the female (or male) more likely to mate with some potential partners than with others (Halliday 1983; Pomiankowski 1988; Kirkpatrick and Ryan 1991).

Female choice has sometimes been put in contrast with male competition, but there is competition among males also when females choose their mate, even if rivals never meet. Competition for mates is the defining aspect of all forms of sexual selection, including that based on mate choice, because then "the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the most agreeable partners" (Darwin 1871, II, p. 398; also see Ghiselin 1974; J. L. Brown 1983).

In practice, all the mechanisms in table 1.1.1. may occur together; determining their relative importance is a challenging empirical task. For example, after males fight over dominance status or territories, females might choose among the winners. Contests and choice may favor the same or different attributes (table 1.1.1.).

Sexual competition does not always come to an end at mating. It can continue in several forms, one of which is sperm competition between males that mate with the same female (e.g., Parker 1970b; R. L. Smith 1984; Eberhard 1985, 1991; Birkhead and Møller 1992). Common male tactics of reducing the risk that a rival fertilizes the female is to guard or sequester and often mate with her during the receptive period (reviewed, e.g., by Birkhead and Møller 1992). Other tactics are blocking the genital opening of the female with a mating plug, applying "anti-aphrodisiac" substances that reduce her attractiveness (for example, by making her smell like a male), and reducing her pheromonal output (e.g., Happ 1969; Gilbert 1976; Frankie et al. 1980; McLain 1980; Sillén-Tullberg 1981; Thornhill and Alcock 1983). For instance, before proceeding further with the affair, a male spider *Linyphia litigiosa* that finds a virgin female will reduce the evaporation of attractive pheromones from her web by packing it into a tight mass (Watson 1986). Eberhard (1985) reviewed postcopulation competition over fertilization in animals.

Another form of sexual competition after copulation is induced abortion or infanticide that makes a female receptive to a new male.[2] Here, however, I will focus on the stages of mating competition up to copulation, that is, the realm of classical Darwinian sexual selection.

As they are likely to play major roles in the evolution of conspicuous secondary sex traits, mate choice and contests have received by far the most attention. The importance of endurance rivalry has only recently become clear. Scramble competition is important, for example, in many anurans and invertebrates where females are receptive for only brief periods (e.g., Wells 1977b; Thornhill and Alcock 1983). It has been clarified in detail by Schwagmeyer (e.g., 1988) in the thirteen-lined ground squirrel *Spermophilus tridecemlineatus*, where the most mobile males with largest ranges during the mating season are most successful (section 7.2).

1.2 Sex Traits and Sexual Dimorphism

Darwin (1871) distinguished three kinds of traits that differ between males and females: primary, secondary, and what might be termed "ecological" sex traits. Primary sex traits are "directly connected with the act of repro-

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[2] See, e.g., Trivers 1972, Mallory and Brooks 1978, Hrdy 1979, Schwagmeyer 1979, Labov

duction": gonads and copulatory organs. They are necessary for breeding and hence are favored by natural selection. But males and females also differ in secondary sex traits with no direct mechanical role in insemination; Darwin suggested that most such traits raise the success of the possessor in competition over mates. Examples are "the greater size, strength, and pugnacity of the male, his weapons of offence or means of defence against rivals, his gaudy colouring and various ornaments, his power of song, and other such characters." According to Darwin, these secondary sex traits evolve by sexual selection, often in opposition to natural selection. He noted that it is often not possible to separate clearly between primary and secondary sex traits. For example, prehensile organs such as the modified legs and antennae of males in oceanic crustaceans help ensure successful copulation, but they also make it harder for a rival to dislodge the male and take over the female. Such organs may be favored by sexual as well as other natural selection.

Also, copulatory organs and reproductive glands can be shaped in part by competition over mates or fertilizations. For example, the penis of the damselfly *Calopteryx maculata* carries stiff hairs and other structures that help remove sperm from males that have previously mated with the female (figure 1.2.1; Waage 1979; see Birkhead and Hunter 1990 for review). Testes size among primates provide other evidence of sperm competition (Harcourt et al. 1981; figure 4.3.2 below). Even within species, variation in testes size can reflect sexual selection. In the bluehead wrasse *Thalassoma bifasciatum*, large territorial males have smaller testes than small males that spawn in groups, where strong sperm competition puts a premium on massive sperm production (Warner and Robertson 1978).

In his review of animal genitalia, Eberhard (1985) suggested sexual selection by female choice has helped shape male copulatory organs among insects and other taxa. Animals with internal fertilization often show rapid and divergent evolution of male genitalia and other structures used in copulation. Patterns of variation suggest that earlier explanations may be inadequate. For example, the "lock and key" hypothesis states that complex, species-specific genitalia evolve because they reduce mismatings with other species. It fails, however, to explain for instance why male genitalia often vary much more than female genitalia among closely related species. Given the probably stronger selection of females to avoid mismatings, the opposite pattern is expected from the lock and key hypothesis. Eberhard (1985) instead proposed that male genitalia in part are "internal courtship

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1981, Sherman 1981, Freed 1987, Hoffman et al. 1987, Emlen et al. 1989, Wolff and Cicirello 1989, Veiga 1990. Reviews of postcopulatory competition are found in, e.g., Thornhill and Alcock 1983, Hausfater and Hrdy 1984, R. L. Smith 1984, Clutton-Brock 1991, Birkhead and Møller 1992.

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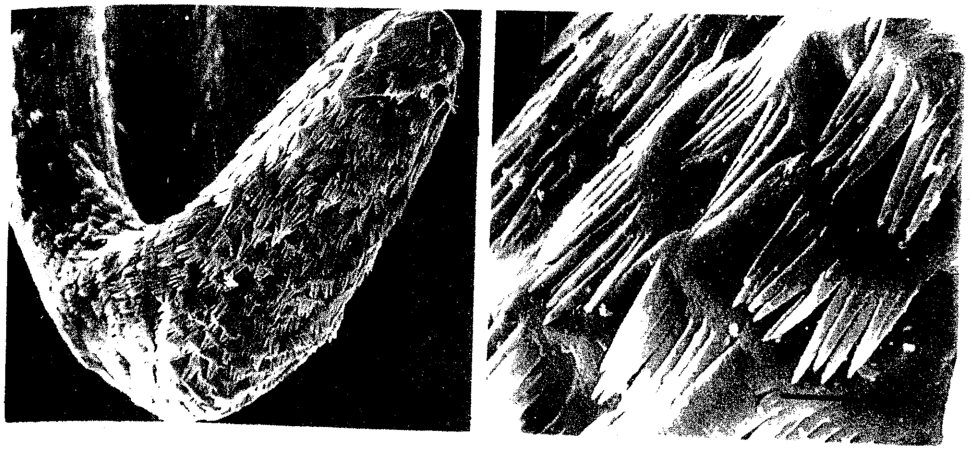

Figure 1.2.1 *Left*: Tip of the distal penis segment of the damselfly *Argia moesta*. *Right*: The segment carries spines used for scooping out sperm of previous males mated to the female. (From Waage 1986b)

devices" which increase the chances that the female will let the male's sperm fertilize her eggs. These new ideas render the distinction between primary and secondary sex traits less clear; perhaps it will eventually be abandoned.

A special, apparently less common kind of sex difference is "connected with different habits of life, and not at all, or only indirectly, related to the reproductive functions" (Darwin 1871, II, p. 254; see Shine 1989 for review). Such *ecological sex traits* are usually adapted to foraging differences between the sexes (which ultimately are probably related to anisogamy and sexual selection). Two examples are the mouth parts of mosquitos in which females suck blood and males live on flowers, and the bill of the extinct New Zealand huia (*Neomorpha acutirostris*; figure 1.2.2) and of certain woodpeckers in which the sexes use different foraging methods. In *Centurus striatus* on Hispaniola, and in several other island populations of woodpeckers with little or no competition from similar species, the sexes have evolved extreme dimorphism in bill morphology. Coupled with foraging differences, this should reduce food competition and expand the food niche of a pair (Selander 1966; Ligon 1968). Evidence that intraspecific foraging competition can create disruptive selection on the feeding apparatus comes from the African finch *Pyrenestes ostrinus*, in which two bill morphs (unrelated to sex) use partly different food resources (Smith 1990a,b, 1993). There is evidence that the morph difference may depend on a single gene locus (Smith 1993).

Slatkin (1984) concluded from quantitative genetic models that ecological sex differences may evolve under several conditions. For example,

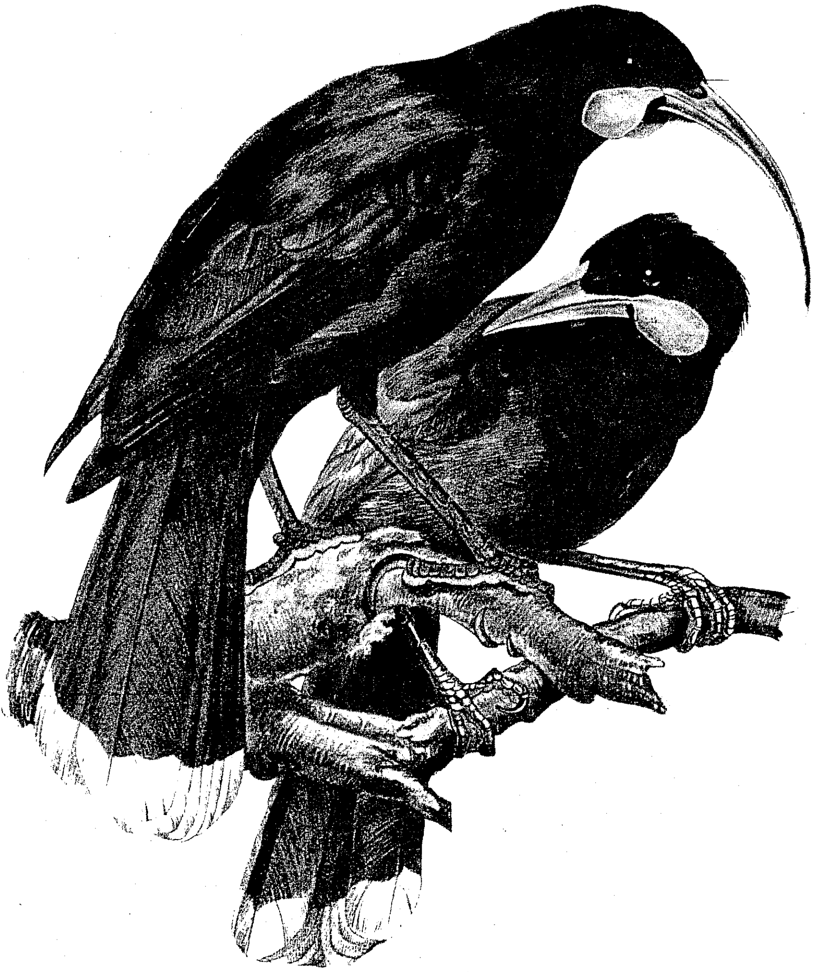

Figure 1.2.2 A pair of the extinct New Zealand huia *Neomorpha acutirostris*. The contrasting bill shapes probably allowed males (lower right bird) and females to take different kinds of prey, broadening the total food niche of the pair, which foraged together. (From Doflein 1914)

ecological selection pressures can differ between the sexes, or they may compete over some resource (Darwin 1871; Lande 1980; Shine 1989). Ecological sex differences may first arise owing to sexual selection, later on being enlarged by natural selection for separation in diet or other aspects (Clutton-Brock and Harvey 1977; Clutton-Brock, Harvey, and Rudder 1977; Power 1980; Caro 1985). For example, in the isopod *Idothea baltica*, sex differences in coloration may in part be adaptations to different habitats and risks of predation in males and females (Jormalainen and Tuomi 1989).

For ecological sex differences to evolve, it may not be necessary that the initial difference in the trait arises through sexual selection. Even if the sexes are similar to start with, imperfect genetic correlations between them can permit natural selection to create sexual dimorphism (Slatkin 1984). For a particular type of sex dimorphism to have the same direction in many species that independently evolved the dimorphism, however, some initial sex-related bias in the trait seems necessary (Power 1980; also see Trivers 1972).

Probably most of the genes that influence secondary sex differences in higher animals are not sex linked, but sex limited in their expression. They are not located on sex chromosomes but on ordinary autosomes (for exceptions, see, e.g., Farr 1983). Both sexes therefore carry the genes. The difference in expression by males and females is usually brought about by sex-specific hormones produced by the gonads, whose sex differences do depend on genes in the sex chromosomes. In mammals, a newly identified Y-linked gene triggers the development of male rather than female gonads (Koopman et al. 1991; also see McLaren 1988). Testosterone is necessary for the development of the secondary sex traits of the adult male, and estrogen for those of the adult female. In birds, where females are the heterogametic sex, female gonadal hormones lead to the early development of female rather than male characters. It seems that the gonads of the heterogametic sex in vertebrates produce the signal substance that triggers sex differentiation of genitalia and other early sex traits (see, e.g., Daly and Wilson 1983; Renfree and Short 1988).

1.3 Criticism of Darwin's Theory of Sexual Selection

The idea that conspicuous male display, colors, feather plumes, and other secondary sex ornaments evolve through female choice met much early skepticism (reviewed, e.g., by Kellogg 1907; Ghiselin 1969b, 1974; Otte 1979; Ruse 1979; Kottler 1980, 1985; Aiken 1982; West-Eberhard 1983; Bajema 1984; Pomiankowski 1988; Cronin 1992). Darwin (1871, I, p. 259) seemed to assume a similar sense of beauty in other higher vertebrates as in man. But this assumption, right or wrong, is not necessary for female choice: discrimination among males in relation to size, shape, color, or other aspects should suffice. Yet the assumption was often held up against the entire idea of sexual selection by female choice (e.g., Morgan 1903; Dewar and Finn 1909; Huxley 1938b,c).

After first accepting female choice, Alfred Wallace (e.g. 1889) came to doubt its relevance, and a debate arose between him and Darwin over problems that are not yet fully resolved (also see section 13.6). Wallace objected against the entire concept of sexual selection: agreeing that male weapons might evolve through contests over mates, he argued that this is ordinary natural selection that increases the vigor, fighting power, and survival of males. Modern studies have shown, however, that sexual selection can lead to much higher mortality in males than in females (chapter 10).

Several influential biologists were even more negative to Darwin's ideas on sexual selection. One example is T. H. Morgan (1903), Nobel laureate and explorer of the Mendelian machinery with *Drosophila* as test organism. He concluded that "the theory meets with fatal objections at every turn," and he regarded it as definitely refuted. Morgan (1932) considered sexual dimorphism fully explained by a proximate mechanism—hormonal differences between males and females—and failed to see that it also requires an evolutionary explanation. A contributing reason for the strong early resistance to the idea of female choice was probably the rise of the mutation school of thought at the turn of the century, which largely dismissed the role of selection in evolution (Provine 1971).

Julian Huxley (e.g., 1923, 1938b,c) accepted several but criticized others of Darwin's ideas on sexual selection. Even Lack (1968) argued against the importance of female choice, referring to Huxley's views. Yet, as O'Donald (1980) points out, Huxley (1938b,c) confused sexual selection with natural selection, and natural selection with group selection; he also obscured the issue with a thicket of complicated terminology. Surprisingly, Huxley's confusing views for decades came to be regarded as superior to Darwin's (1871) clear insights.

Except for some important empirical or theoretical studies, for example by Huxley (1914), Fisher (1915, 1930), and Noble (e.g., 1934, 1936), almost a century passed before Darwin's ideas on sexual selection gained ground. Yet the stage seemed set for rapid growth of the field already in the 1930s, when it was seeded by exciting theoretical and empirical contributions. Fisher's (1930) important but difficult *Genetical Theory of Natural Selection* was, however, for long apparently not read or understood by many, and Noble's (1934, 1936; chapter 13 below) pioneering experimental approach in the field for some reason was not taken up in large scale by other workers. One reason why the study of sexual selection did not catch on from the 1930s was perhaps the disregard for, or neglect of, Darwin's and Fisher's ideas on the subject by the leaders of the "evolutionary synthesis," and their tendency to explain conspicuous secondary sex traits by species isolation (e.g., Dobzhansky 1937; Huxley 1942; Mayr 1942; see West-Eberhard 1983). In spite of early work by Sturtevant (1915), it also took many years for research on *Drosophila* mate choice to gain momentum (e.g., Bateman 1948; Merrell 1949; Reed and Reed 1950; Petit 1954; Maynard Smith 1956).

The publication in 1958 of the revised edition of Fisher's (1930) book roughly marks the birth of a new generation of work on sexual selection, two early examples being Maynard Smith (1958) and O'Donald (1962). If Darwin was the architect, Ronald Fisher clearly was his main assistant in the construction of sexual selection theory. Although his name is associated with self-reinforcing mate choice and the celebrated "runaway process" (section 1.5), Fisher also put forth two other major hypotheses for conspicuous secondary sex ornaments: contest competition and indicator processes (sections 7.4 and 1.5). Since Fisher (1958), interest in sexual selection has grown continuously, resulting in today's eruption of studies. This is part of a general move toward testing natural selection in the wild, reviewed by Endler (1986a). The development is also closely related to the shift of emphasis in ecology toward evolutionary problems, individual selection, and reproductive tactics, which began in the 1960s (e.g., Williams 1966; see Cronin 1992). But still, sexual selection is very incompletely understood, especially in species where females choose mates and males apparently contribute nothing but genes.

A main thesis of *The Descent of Man* was that sexual selection is important in *Homo sapiens*, and that mate choice has played a major role in the evolution of some conspicuous differences among human populations, differences that are not obviously related to survival. After a massive, but not necessarily correct, critique by the sociologist E. Westermarck (1891) in his *History of Human Marriage*, this idea of Darwin's has been largely neglected (Thornhill 1986b). On the other hand, speculations about sexual selection of various human traits are common but often difficult to test rigorously. Substantial indications are found in studies that put our own species in relation to the other primates in a quantitative, comparative framework, for example as regards sexual size dimorphism and testes size (sections 4.3 and 11.9). Human mate choice and the possible importance of sexual and natural selection in the morphological differentiation of human populations was reviewed by Diamond (1991b).

1.4 Selection of Secondary Sex Signals

A main goal of sexual selection theory is to explain the often conspicuous secondary sex traits. Studies during the last two decades have shown that sexual selection is common in nature (chapter 6), but the selective mechanisms behind conspicuous sex ornaments and behavioral signals are still debated. A host of alternative explanations has been suggested, summa-

Table 1.4.1

Explanations for Conspicuous Male Ornaments and Female Preferences

A. *Male ornaments* have evolved because of:
1. Pleiotropic gene effects
2. Selection ~~of ecological~~ sex differences
3. Males being unprofitable prey for predators
4. Male contests
5. Female choice and mating preferences

B. *Female preferences* for male ornaments (section 1.5) have evolved because of:
1. Fisherian self-reinforcing selection
2. Indicator mechanisms
3. Selection for species recognition
4. Direct phenotypic benefits to choosy females
5. Selection of the sensory system in other contexts (sensory bias)
6. Advantages in the timing of reproduction (mating sychronization)

rized in table 1.4.1. They form a heterogeneous set of ideas, some aiming to explain secondary sex signals, others also explaining mating preferences.

These hypotheses aim to give ultimate, evolutionary explanations of male traits and female preferences (B.5 and B.6 in table 1.4.1 may not, however, suffice to do so). Few of the explanations are mutually incompatible, so they may not be open to "strong inference" testing (Platt 1964), where all the alternatives except for one can be refuted. Several mechanisms may work in concert, presenting the more difficult problem of assessing their relative roles.

Ghiselin (1974) discussed and refuted a number of additional, less plausible hypotheses, for instance some that require group selection (but see Seger and Trivers 1986).

PLEIOTROPIC GENE EFFECTS

In an otherwise excellent developmental study that helped clarify sex-limited and sex-linked inheritance, Morgan (1919) suggested that secondary sex traits are "only by-products of genes whose important function lies in some other direction." One way of testing this idea is to examine the consequences of secondary sex traits for mating success. If a trait enhances mating and reproductive success when other factors are controlled for, the trait is not a neutral by-product of pleiotropy. Many such cases have now been demonstrated (table 6.A). Even if pleiotropy may play a role in the origin of secondary sex traits, Morgan's hypothesis is refuted as a sufficient general explanation for their spread and maintenance, which requires some form of selection (also see Endler 1986a; Endler and MacLellan 1988).

Selection of Ecological Sex Differences

Ecological differences between the sexes seem to explain some sex dimorphic traits used for feeding, for instance the bill in some birds already discussed above (section 1.2). However, most ornamental or other sex traits used mainly for signaling do not seem explicable by ecological sex differences. Possibly, such differences will sometimes influence the traits selected and the direction taken by other mechanisms, such as Fisherian processes.

Males Are Unprofitable Prey

Baker and Parker (1979) proposed that some secondary sex traits evolve because the bearer is unsuitable as prey for predators. From their analysis of coloration in Western Palearctic birds, they concluded that bird coloration has evolved mainly in response to predation, not sexual selection. Evidence on this point is discussed in section 13.6. Even if this mechanism may sometimes contribute, it does not seem to be the main reason for conspicuous sex-dimorphic coloration, either in birds or in other animals.

Male Contest Competition

An important alternative to Darwin's idea of female choice was raised by several biologists in the 1930s. They suggested that male contests over mates select not only for horns, tusks, spurs, and other physical weapons, but also for conspicuous signals. Fisher (1930) proposed that ornament and display may be psychological weapons: "A sprightly bearing with fine feathers and triumphant song are quite as well adapted for war propaganda as for courtship." A similar idea, that bright plumage in male birds functions as a "gaudy uniform of battle" in contests over females, was put forth by R. Hingston (1933, p. 114). Noble (e.g., 1934) drew a similar conclusion from his work on the use of colors in display by lizards.

None of these authors explained how such badges of status might evolve. Huxley (1938a), Peek (1972), Smith (1972), and Borgia (1979) proposed that conspicuous male coloration and display in territorial species might be favored in part because it advertises occupancy and presence of the owner on the territory. Rohwer (e.g., 1975, 1982) suggested several other mechanisms, including the possibility that badges arise by natural selection, for instance in contests over winter food. Status-signaling badges that indicate strength could be selected for if they make good fighters recognizable and memorable, and spread in the population by mimicry. Under certain circumstances, this might give rise to sexual color dimorphism even without direct sexual selection of conspicuous colors (see Rohwer 1982; Butcher and Rohwer 1989; Rohwer and Røskaft 1989). Similar ideas were presented by West-Eberhard (1979, 1983, 1984), who emphasized that other forms of social competition than sexual selection can favor bright colors and other conspicuous signals (also see Ghiselin 1974; Weldon and Burghardt 1984). Members of a social group or population can limit each other's access to many kinds of resources, not only mates.

Social competition might sometimes lead to rapid open-ended evolution of signals. In contrast with traits adapted to ecological functions, such as the bill of a bird for which there may be a "best" shape depending on diet, a social competitive function in itself need not put a limit to the development of the trait (Darwin 1871). "Each successive improvement sets a new standard which the next can profitably surpass" (West-Eberhard 1979; also see Zahavi 1981). Sexual and other social selection can therefore lead to extreme traits, and some conspicuous signals may be socially selected through competition over resources other than mates. Social selection of signals used in contests might lead to rapid divergence in coloration between populations and species (Rohwer 1982; West-Eberhard 1983; W. S. Moore 1987). Mathematical models by Parker (1979, 1983a) and Maynard Smith and Brown (1986) suggest that contest competition can easily lead to evolutionary instability in favorable traits (section 11.1).

Zahavi (1977a), Borgia (1979), and Baker and Parker (1979) suggested a form of "indicator mechanism" (also see sections 1.5 and 13.6 below): "An evolutionary stable strategy (ESS) can exist in which only the opponent with the greater strength or fighting ability is prepared to fight, whereas the one with less ability withdraws. . . . A more brightly coloured male may have avoided predators under handicap and hence may also be stronger and more likely to win against a more cryptic rival" (Baker and Parker 1979). This situation could lead to a form of agonistic indicator process, if a male in good condition benefits from having larger ornaments than other males (Andersson 1982b; Parker 1982). The idea of condition-dependent badges is free from some of the problems of indicator mechanisms for female choice (see section 1.5); in particular, fitness need not be heritable.

Female Choice and Mating Preferences

There is now much evidence that females often choose their mate, and that such choice favors conspicuous male traits (e.g., table 6.A). The exact ways in which female choice selects for such traits are still debated, and so are the ways in which female preferences evolve, which remain a main controversial issue in the theory of sexual selection (e.g., Searcy 1982; Kirkpatrick and Ryan 1991; Maynard Smith 1991a; Williams 1992).

Some male traits may evolve simply because they make it easier for females to find the male. Natural selection will favor such traits if they reduce the time during which males and females are vulnerable to predation (Darwin 1871; Wallace 1889; Mayr 1972). A natural selection advantage is by no means inevitable, however: signals used for mate attraction can make the sender easier to locate for parasites or predators (chapter 10). In such cases, sexual selection has probably favored the signal in opposition to natural selection.

Mating usually contains an element of discrimination, at least as regards species identity. Otherwise, mismatings between members of different species should be much more common than they are. Among the acceptable signals, sexual selection should favor those which most effectively stimulate the recipients, that is, intense, persistent, or otherwise conspicuous signals (reviewed by Ryan 1990b). In Darwin's (1871, I, p. 418) words about acoustic insects, "individuals which were able to make the loudest or most continuous noise would gain partners before those which were less noisy."

Even though female choice based on visits to and comparison of several males does occur and is probably common (e.g., Robertson 1986a; Gibson et al. 1991), such "comparing" choice is not necessary to favor conspicuous signaling traits. A male with a strong or frequent signal might attract more mates simply because he is noticed more quickly or is noted farther away than other males (e.g., Otte 1974; Wells 1977b; Lloyd 1979; Parker 1982, 1983b). A game theory model by Parker (1982) suggests that such direct attraction can lead to conspicuous male traits even if there is no genetic variation in female preferences. In contrast with Fisherian self-reinforcing selection and indicator models (section 1.5 below), the female preference in this case may have evolved for reasons not related to fitness advantages for males with the most far-reaching signals. Other factors, for example an initial sensory bias, or selection for species recognition, might help explain such mate choice (Ryan 1990b). Direct attraction may be favored if, compared to other rules, it reduces female expenditure of energy or time, or exposure to predators (Wilson and Hedrick 1982; Searcy and Andersson 1986; Arak 1988c).

This kind of direct mechanism has sometimes been called "passive" attraction, in contrast with "active" choice based on examination of several potential mates and rejection of some of them. The terms active and passive choice may, however, confound proximate and ultimate causation, and passive attraction is no evolutionary explanation for the mating preference and its characteristics (see Pomiankowski 1988; Sullivan 1989; Ryan 1990b; Wiley 1991).

Direct attraction to the strongest signal might sometimes evolve into a more subtle, discriminating preference (Parker 1982). If males differ in their range of attraction, females that search for and compare several males and mate with the most effective signaler should also tend to bear sons with higher than average mating success; this could lead on to a Fisherian process (section 1.5).

There are many possible tactics of female choice among males, based for instance on sequential comparisons or threshold decisions. What tactic is most favorable should depend on, among other things, the variation among males, and costs of choice in females (e.g., Janetos 1980; Parker 1983b; Wittenberger 1983; Real 1990, 1991).

1.5 Evolution of Female Preferences for Male Traits

THE FISHER PROCESS

Although much of the early criticism of Darwin's theory was mistaken, the theory had a large gap: it did not explain the origin of female choice. Darwin simply pointed to evidence that it exists (but in the second edition of *The Descent*, 1874, II, p. 495, he added a short section dealing with the evolution of preferences). This void was ridiculed by Morgan (1903), in words that suggested an explanation which he did not, however, take seriously: "Shall we assume that still another process of selection is going on, . . . that those females whose taste has soared a little higher than that of the average (a variation of this sort having appeared) select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of these ornaments on the other? No doubt an interesting fiction could be built up along these lines, but would anyone believe it, and, if he did, could he prove it?"

Morgan's (1903) sarcastic suggestion apparently came under the eyes of Ronald Fisher, who develped it into a coherent theoretical explanation for the evolution of female choice (see below). It is not fully certain that this is the source of Fisher's (1915, 1930) idea, as he did not refer to Morgan (1903). He knew Morgan's book, however, and cited it (Fisher and Stock 1915) in a paper published shortly before the article on mate choice (Fisher 1915). This, and the resemblance between their hypotheses, suggests that Morgan (1903) invented the idea of self-reinforcing evolution of female preferences and male traits ("the two continue heaping up the ornaments . . . and the appreciation of these ornaments"). Ironically, it therefore seems that a skeptical comment by Morgan (1903) became the seed of one of the most celebrated hypotheses for the evolution of female preferences and conspicuous male traits.

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Fisher (1930) suggested that "a sexual preference of a particular kind may confer a selective advantage, and therefore become established in the species." He envisaged a two-step process. Suppose there arises genetic variation in a male trait such as tail length, and that males with, say, a longer than average tail have a slight survival advantage, for example owing to improved agility. Assume also that females choose mates, and that there is genetic variation among females in their tendency to mate with males of different tail lengths. Females preferring males with long tails tend to bear sons with high survival. Hence alleles that code for longer tails in males will spread, and so will alleles that make females prefer long-tailed males, as the two types of alleles become associated in their offspring.

When this process continues, a new effect grows in importance: males with long tails are favored not only by better survival, but also by higher mating success as the preference for long tails spreads among females. The higher mating success of long-tailed males helps carry the associated alleles for the long tail and the female preference to yet higher frequency, and a feedback "runaway process" develops at accelerating pace. Although Fisher did not explain fully how this would happen, he suggested that females will prefer tails of ever-increasing length, until it finally becomes so long that higher mortality balances the mating advantage of long-tailed males. This brings the process to rest. (For further discussion, see O'Donald 1977, and Arnold 1983.)

Fisher (1930) provided the capstone for Darwin's theory of sexual selection and made it a coherent if untested explanation for the evolution of secondary sex ornaments by mate choice. He did not, however, clarify in detail how male traits evolve to extremes that apparently reduce survival. O'Donald (1977) suggested that male ornaments can become supernormal stimuli for females, which then prefer larger than natural ornaments (also see Halliday 1978; Lande 1981). This might explain how male traits evolve to extremes such as the tail of the peacock (section 2.2).

Eberhard (1985, 1991, 1993) proposed that not only ornamental traits, but also male copulation behavior, genitalia, and other contact organs used in copulation, have been affected by Fisherian runaway processes of female choice (section 1.2 above). Genital structures seem less likely than conspicuous ornaments or displays to incur costs such as increased risk of predation, perhaps leaving more freedom for runaway evolution of genitalia.

Fisher presented his idea on the evolution of female choice in words, even though it assumes changes in gene frequencies, which he treated mathematically in many other contexts. O'Donald (e.g., 1962, 1967) pioneered the mathematical modeling of sexual selection (chapter 2 below), verifying the logical consistency of the Darwin-Fisher theory (summarized in O'Donald 1980a). He showed that a preference allele can spread together with an allele for a preferred trait that improves survival. When the preference is sufficiently common, the allele for the trait can increase even if it reduces survivorship, as Fisher suggested. Sexual selection in few-locus systems was further clarified, for example, by Kirkpatrick (1982), who found that a strong and common female preference may even lead to fixation of a male trait that reduces survival (box 2.2.1 below).

Using quantitative genetics, Lande (1981) showed that male trait and female preference under certain conditions can evolve in runaway fashion, the outcome partly depending on chance events at the start (box 2.3.1 below). Such processes in small founder populations subject to genetic drift might help explain why related species often differ most in male secondary sex traits (Lande 1981; West-Eberhard 1983).

The previous genetic models of female choice assumed that mating preferences carry no cost. Mate choice often requires time and energy, or may increase the risk of predation, which can greatly affect the outcome of sexual selection (e.g., Parker 1983a; Kirkpatrick 1987b; Pomiankowski 1988; Iwasa et al. 1991). Most links in the chain of genetic events suggested by the Darwin-Fisher theory remain to be tested (chapter 2).

If females differ in fecundity or parental ability, and if mating reduces a male's chances of fertilizing other females, male preferences might evolve for the most fecund females, or for females that complement the male as regards size or other aspects. Male choice of mate is also likely to occur in role-reversed species, such as pipefish and certain waders, where females compete strongly over males (e.g., Williams 1975; Ridley 1983). There is increasing empirical evidence of female as well as male mate choice (chapters 6 and 8 and section 7.6).

INDICATOR MECHANISMS

Besides Fisherian self-reinforcing mating preferences, a much debated idea is that conspicuous, costly male traits become targets of female choice because such traits indicate high heritable viability. After mating with a highly ornamented male, a female might then bear offspring that survive well.

In some respects, already Wallace (1889, p. 295) foreshadowed this idea, proposing that female choice concerns male traits that indicate high general fitness: "This extremely rigid action of natural selection must render any attempt to select mere ornament utterly nugatory, unless the most ornamented always coincide with the 'fittest' in every other respect." Wallace did not, however, explain how females would come to have such preferences.

Although he is not usually associated with indicator models but with self-reinforcing "runaway selection," Fisher (1915) also gave the first outline of an indicator mechanism. "In every animal there are a few noticeable points or features which readily attract and arrest the attention; and of these it may be expected . . . that some will be more conspicuous among the healthy, active and biologically fit. . . . Consider, then, what happens when a clearly-marked pattern of bright feathers affords . . . a fairly good index of natural superiority. A tendency to select those suitors in which the feature is best developed is then a profitable instinct for the female bird, and the taste for this 'point' becomes firmly established among the female instincts. . . . Let us suppose that the feature in question is in itself valueless, and only derives its importance from being associated with the general vigour and fitness of which it affords a rough index."

Fisher's (1915) indicator idea received even less attention than his other work on sexual selection, and was largely forgotten. The same hypothesis was, however, redeveloped fifty years later by George Williams in his influential book, *Adaptation and Natural Selection*, a rich mine of ideas for evolutionary biologists: "It is to the female's advantage to be able to pick the most fit male available for fathering her brood. Unusually fit fathers tend to have unusually fit offspring. One of the functions of courtship would be the advertisement, by a male, of how fit he is. A male whose general health and nutrition enables him to indulge in full development of secondary sexual characters, especially courtship behavior, is likely to be reasonably fit genetically. . . . In submitting only to a male with such signs of fitness a female would probably be aiding the survival of her own genes" (Williams 1966, p. 184). Later, Williams (1975, 1992) came to doubt whether the heritability of fitness is high enough for such a process to work, but the passage cited probably helped inspire many versions of what has been termed "handicap," "indicator," or "good genes" models.

Williams' (1966) idea was taken up, for example, by Trivers (1972), Emlen (1973), and especially Zahavi (1975, 1977b), who presented his "handicap principle" as an exclusive alternative to Fisherian sexual selection by self-reinforcing mating advantages. Early genetic models indicated, however, that Zahavi's (1975) handicap principle is unlikely to work on its own. For this and other reasons, it was severely criticized, but later models that combine heritable viability differences with a mating advantage suggest that indicator mechanisms might contribute to the evolution of male ornaments. Many authors have put forth reasons why some form of indicator mechanism might be important (section 3.1). The idea of Hamilton and Zuk (1982) based on host-parasite cycles has received most attention. It suggests that genetic cycles of changing resistance in hosts, and virulence in parasites, maintain heritability of resistance in hosts. The degree of resistance is reflected in secondary sex traits such as bright colors, which might then be used as a cue in mate choice. Even if such coevolutionary cycles should turn out to be uncommon, parasites and pathogens may still make indicator mechanisms work; health is one of the aspects likely to be reflected by indicator traits (Fisher 1915; Williams 1966; Hamilton and Zuk 1982).

Models of genetic indicator mechanisms have been found to work most easily if ornament development depends on the phenotypic condition and overall genotype of the male, as implied by Fisher (1915) and Williams (1966) (chapter 3 below). Several empirical studies have provided support for indicator models, but the evidence can be interpreted in different ways. Indicator traits may be correlated with some direct (nongenetic) material benefit to female or offspring, such as food, protection, or parental care. It has not yet been convincingly shown that an indicator process based on genetic benefits for offspring is involved in the selection of any secondary sex trait, a similar situation as for Fisherian self-reinforcing selection.

SPECIES RECOGNITION

To increase in frequency, it is not necessary that an ornament initially reflects higher survival: improvement of species recognition is a plausible alternative (e.g., Fisher 1930; Mayr 1963, 1972; Trivers 1972; Halliday 1978; Maynard Smith 1978). Already Wallace (1889) discussed traits that enable "the sexes to recognize their kind and thus avoid the evils of infertile crosses." He suggested that this might explain "the wonderful diversity of colour and of marking that prevails, especially in birds and insects." Fisher (1930) pointed out that the "grossest blunder in sexual preference which we can conceive of an animal making would be to mate with a species different from its own."

The leaders of the evolutionary synthesis around the middle of this century often pointed to a species isolation function of secondary sex signals and mating preferences, that is, a form of natural selection. This emphasis on species isolation, and the neglect of choice among mates within the species, was apparently a consequence of the focus of the synthesis on speciation and related problems (e.g., Dobzhansky 1937; Huxley 1942; Mayr 1942).

Even if species recognition is involved, it appears unlikely to explain fully the most conspicuous secondary sex traits such as the peacock's tail, which are much more extreme than necessary for species recognition; some additional process seems likely to be involved. In several taxa, however, there is evidence that selection for species recognition has played a role in the evolution of secondary sex traits or mating preferences (chapter 9). Mating discrimination against members of another species can be viewed as a means of avoiding matings that lead to genetically inferior offspring.

Sex dimorphic traits may also function in sex recognition (e.g., Noble and Vogt 1935; Noble 1936; sections 13.5–13.6 below). This seems unlikely to be the main explanation for many conspicuous sex traits, however, which are developed far beyond what should be needed for sex recognition.

Direct Phenotypic Benefits

Fisherian and indicator models have been suggested to explain extreme ornamentation especially in cases where males provide females with nothing but genes, for example in lekking species (section 7.5). But males have conspicuous sex traits also in many species where females get direct material benefits from their mates. Heywood (1989) and Hoelzer (1989) concluded from genetic models that nonheritable variation in parental ability may lead to the evolution of male traits that advertise high parental quality (see also Grafen 1990a). The hypothesis does not require heritable variation in fitness among males. As a likely example, Hoelzer (1989) pointed to courtship feeding in birds (section 8.2 below). Male song rate is another trait that, owing to a correlation with food abundance in the territory, may give a clue to the male's future performance as a parent, and to the food situation for the female and her offspring (chapter 14). There are many other possibilities for direct selection of female preferences (e.g., Williams 1975; Kirkpatrick and Ryan 1991; chapter 8 below), for example asymmetrical fitness distribution of female choice in relation to a male trait that reflects his fertility. Williams (1992) suggested that such a mechanism might suffice for the evolution of extreme male traits and female preferences also in species where females obtain nothing but sperm from males.

Sensory Bias and the Origins of Preferences

Fisher (1930) suggested that new mating preferences can arise by mutations that change female responsiveness to aspects of male behavior or morphology. But the table can also be turned around: a new male trait might be favored because it happens to fit an already existing bias in the female sensory system.[3] If, say, the foraging ecology of a species has led to high sensitivity to certain colors, this bias might favor the evolution of male ornaments with such colors. The peacock's tail with its many "eyespots" might catch and hold the attention of females by exploiting a widespread responsiveness to eyes in animal cognition and communication (Ridley 1981). In some insects, males attract females by pheromones that

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[3] This idea has been suggested in one form or other by many authors, e.g., West-Eberhard 1979, 1984, Ridley 1981, Davison 1983b, Burley 1985, Ryan 1985, 1990b, Borgia 1987, Kirkpatrick 1987a,b, Endler and MacLellan 1988, Endler 1989, Enquist and Arak 1993; for review, see Endler 1992a,b, Ryan and Keddy-Hector 1992, Reeve and Sherman 1993, and chapter 10.7 below.

are also present in their fruit food (Baker and Cardé 1979; Löfstedt et al. 1989). Although there may be alternative explanations, in such cases it is possible that "by using responses strongly selected in other contexts, the signal in effect creates a sensory trap to manipulate behaviour in the signaller's own favour" (West-Eberhard 1984). This possibility was referred to as "sensory exploitation" by Ryan (1990) in the context of sexual selection (see section ~~10.7~~ below for examples).

Sensory bias may vary with aspects of the environment such as food, predation, and light conditions, influencing the direction of evolution of sexual signals, and sometimes leading to divergence in signals among populations. Such processes were termed "sensory drive" by Endler and MacLellan (1988) and Endler (1989, 1992a). He emphasized that it, together with runaway sexual selection, may lead to rapid divergence of mate recognition systems between species. The "preference" or bias may be common or even fixed when the male trait arises, which would permit rapid spread of the trait even if there is no self-reinforcing evolution of the female preference. The evolution of the male trait might occur without appreciable change in the female preference, for example if it lacks sufficient genetic variation (West-Eberhard 1984; Rowland 1989a; Ryan 1990b). Later on, trait and preference might coevolve further. Based on analysis of artificial neural networks, Enquist and Arak (1993) suggested that signal recognition mechanisms will have inevitable biases that impose selection of signal form, and that the two can coevolve to a state where extreme male traits are favored.

MATING SYNCHRONIZATION AND STIMULATION

Another idea from the era of the evolutionary synthesis is mating synchronization. Marshall (1936) suggested that "birds which have brighter colours, more elaborate ornamentation, and a greater power of display must be supposed to possess a superior capacity for effecting by pituitary stimulation a close degree of physiological adjustment between the two sexes so as to bring about ovulation and the related processes at the most appropriate time." Moreover, this is the "value of sexual display and of the adornment which in many species is taken advantage of to render the display more effective." According to Marshall, sex ornaments and courtship function after pair formation and are not involved in competition over mates, but are favored by natural selection (also see Morgan 1919; Huxley 1938b). Even if it has a long-term stimulatory function, however, male courtship behavior is also likely to be favored by sexual selection. It will be so, for example, if females leave males with poorly developed courtship signals for males that provide more effective stimulation. Examples of long-term priming effects of male signals are given in chapters 13–15 below.

Marshall's (1936) proximate hypothesis does not explain why females should be stimulated by conspicuous male traits. To provide an ultimate explanation, the idea must be supplemented with a mechanism for the evolution of female responsiveness. One possibility is that the development of male traits is correlated with reproductive condition, for example via testosterone levels. A well-developed male trait might indicate full gonadal development and high sperm numbers, with maximum probability that the female will have all her eggs fertilized (e.g., M. B. Williams 1978; G. C. Williams 1992). Other possible advantages to females were discussed above.

1.6 Summary

Sexual selection is the differences in reproduction that arise from variation among individuals in traits that affect success in competition over mates and fertilizations. Scrambles, contests, endurance rivalry, and mate choice are the main forms of premating sexual selection; sperm competition in many species also influences fertilization success. Anisogamy and greater female than male parental effort is the likely reason for stronger male than female competition over mates. In Darwin's theory of sexual selection, mating competition favors male secondary sex traits, such as weapons and conspicuous signal traits. His ideas on female choice have been much criticized, but they receive support from formal models and many recent empirical studies. Some male signals and ornaments may be favored by male contests rather than female choice, however, or by both mechanisms. The evolution of female preferences remains controversial. Some of the alternative explanations, which are all compatible and may apply in combinations, are Fisherian self-reinforcing selection, genetic indicator (handicap) mechanisms, avoidance of hybrid matings, direct material advantages for discriminating females, and male exploitation of female sensory bias.