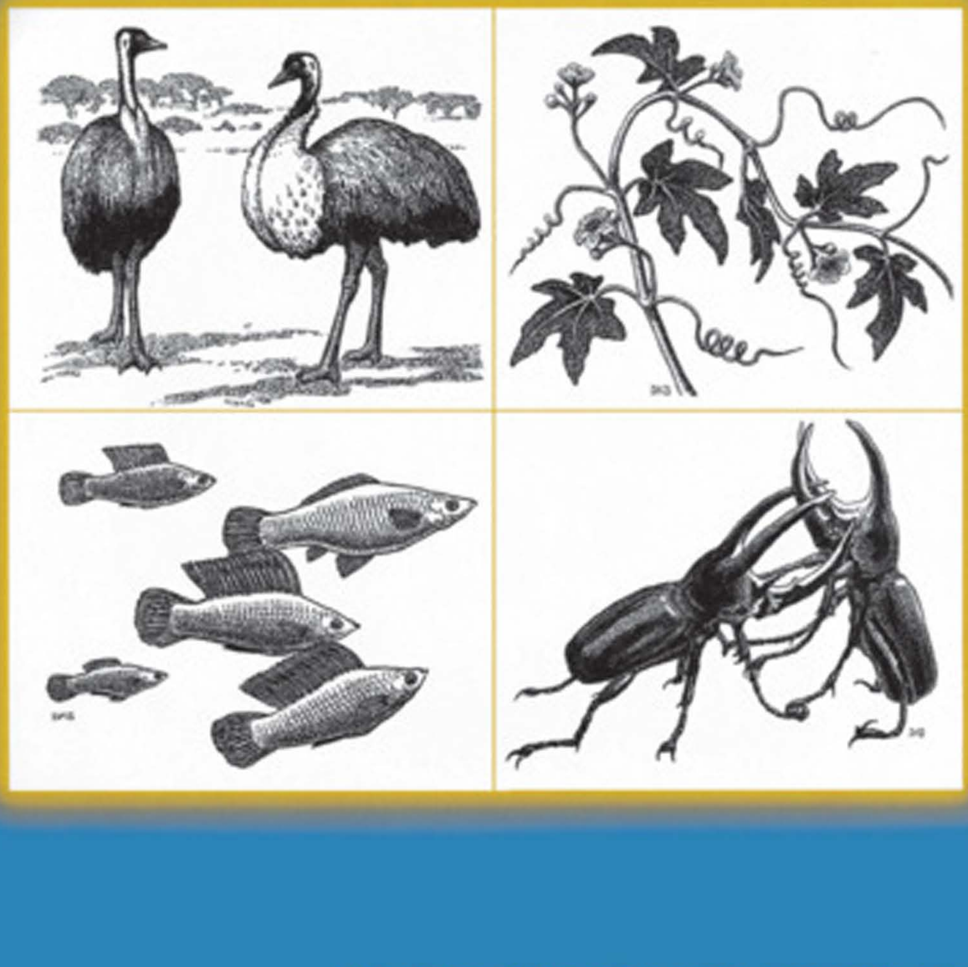
Mating Systems and Strategies

STEPHEN M. SHUSTER
& MICHAEL J. WADE



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Contents

Preface

We have written this book to provide a comparative, conceptual, and statistical framework for studying mating systems and alternative mating strategies in natural populations. When we began our discussions on these topics in 1988 over coffee and M&Ms, we were struck by the explosive growth of verbal, evolutionary models "explaining" male and female reproductive behavior, many unconstrained by the principles of evolutionary genetics. It seemed as though every human failing or inadequacy was being elevated by clever argument to the level of an adaptive strategy, and added to the repertoire of animal behavior by natural or, most often, sexual selection. We have attempted to make the fundamental relationships between the mean, variance, and covariance of male and female reproductive selection explicit and thereby establish a more solid theoretical foundation for future studies on mating systems and strategies.

In chapter 1, we explore the *Quantitative Paradox of Sexual Selection*, namely, the fact that the microevolutionary process of sexual selection and the macroevolutionary pattern it produces pose a paradox. On the one hand, the taxonomic pattern of extreme phenotypic diversity between males of closely related species suggests the action of a very strong and rapid evolutionary force. In contrast, selection restricted to one sex, to a single component of fitness within that sex, and opposed in the other sex, should be a very weak microevolutionary force, producing change slowly if at all.

Using a statistical approach for measuring the strength of selection developed by James F. Crow (Crow 1958, 1962), we show that the *sex difference in the opportunity for selection* is the key to resolving the quantitative paradox between microevolutionary process and macroevolutionary pattern. We illustrate how and why sexual selection, although restricted to one sex and opposed in the other, can be, as the taxonomic pattern indicates, one of the strongest and fastest of all evolutionary forces. Focusing on the sex difference in the opportunity for selection makes it clear that the spatial and temporal clustering of *female receptivity* as well as female reproductive life history are fundamental to understanding the more conspicuous male mating strategies now used for mating system classification. Our statistical framework encompasses the roles of both sexes in mating system evolution.

We apply our approach in chapters 2 and 3, respectively, to quantify the relationships between the *spatial* and *temporal* distributions of receptive females and the opportunity for sexual selection. We show how the spatial aggregation of female mating receptivity enhances the sex difference in the opportunity for sexual selection, while temporal aggregation of female receptivity (i.e., reproductive synchrony) diminishes it and, thereby, limits sexual selection. We show how the opportunity for sexual selection, caused by the spatial and temporal clustering of female receptivity, is related to the ecological concept of mean crowding (*sensu* Lloyd 1967) applied directly to the spatial and temporal aggregation of receptive females.

Sexual selection based on the spatial clustering of reproduction can lead to a runaway process that results in an overcrowding of females at resources. However, the trade-off between mate guarding and mate seeking by males can bring this runaway to a halt *without increased male mortality*. Similarly, we show that a temporal runaway process can favor reproductive asynchrony of females and that it can be halted by a trade-off between extremely early (and extremely late) receptivity and reduced fecundity. This is a runaway process that is halted by selection on females as opposed to the classic runaway Fisherian process, which is halted by male mortality. In fact, we identify more than ten possible runaway processes between male and female traits, most of which are limited by factors other than male mortality. In this context, we suggest that the high frequency of hidden or stolen copulations, now being revealed by molecular paternity analysis, is the expected equilibrium signature of both the spatial runaway process based on female aggregation and the temporal runaway process based on female reproductive asynchrony.

In chapter 4, we explain how female promiscuity (both mating-number and mate-number promiscuity) diminishes the sex difference in the opportunity for selection by limiting sexual selection on males. We combine male and female influences on the opportunity for sexual selection to predict overall patterns of male and female mating behavior.

In chapter 5, we explore the effects of female reproductive life history (multiple mating and multiple reproductive episodes) on the variance in offspring numbers among females. We show how the variance in apportionment of paternity by multiple mating in females affects sexual selection on males. We also show how female reproductive life history affects the sex difference in the opportunity for selection, ΔI, and how to measure ΔI in natural and experimental populations. We suggest that male genetic quality is *least* important to females in species with strong sexual selection and large values of ΔI, and *most* important to females in species in which sexual selection is negligible and ΔI is small. However, mating systems in which ΔI is small may be evolutionarily unstable.

In chapter 6 we propose a statistical framework for quantifying within- and between-species variation in the values of ΔI. We examine how the "ΔI surface" changes with changes in the spatial and temporal patchiness of receptive females. This approach is similar in concept to earlier methods for quantifying the opportunity for selection in nature (Wade and Arnold 1980; Arnold and Wade 1984a, b; Clutton-Brock 1991), and it provides us with a quantitative framework for classifying mating systems.

In chapter 7, we discuss what we consider to be difficulties with and contradictions in current theories of behavioral evolution, especially those applied to the evolution of mating behaviors. Much of existing mating system theory is based on parental investment theory (Trivers 1972), as well as on patterns of paternal care (Clutton-Brock 1994). We suggest that studies of mating systems that focus on mate numbers and factors affecting ΔI, rather than patterns of parental investment, can lead to greater insights into how and when sexual selection operates and the mating systems and strategies that develop as a result.

In chapter 8 we describe the behaviors of males and females most likely to influence mating system evolution, and in chapter 9 we combine the methods and concepts introduced in the first seven chapters to generate a predictive scheme for classifying mating systems. We combine the spatial and temporal distributions of female receptivity with female reproductive life histories to examine their aggregate effects on the opportunity for sexual selection. We generate specific predictions about the occurrence of sperm competition, mate guarding, sexual dimorphism, sexual conflict, and alternative mating strategies. We illustrate our scheme using selected animal and plant taxa and we modify the nomenclature introduced by Emlen and Oring (1977) for mating system classification to address previously unrecognized mating systems.

In chapter 10, we discuss Darwin's perspective on alternative male mating strategies. Darwin clearly recognized male polymorphism as well as the necessary conditions for new male forms to invade and persist in populations. However, we show that he overlooked "female mimicry," one of the most common male mating strategies, in his emphasis on the timing of expression of sex-limited mutations.

In chapter 11, we discuss key conceptual developments in the study of alternative mating strategies since Darwin, as well as gaps and inconsistencies in existing hypotheses regarding alternative mating strategies. We identify the conditions under which genetic polymorphism in male mating behavior may persist and we argue that such polymorphism is probably more common than presently recognized.

In chapter 12, we describe patterns of alternative mating strategies in nature, including male polymorphisms, sequential hermaphroditism, and parental manipulation of family sex ratio. We also discuss gaps and inconsistencies in existing data, notably the apparent ubiquity of condition-dependent mating strategies. We describe factors likely to contribute to the evolution of alternative mating strategies, and we provide a statistical framework, based on parameters introduced in earlier chapters, for measuring selection on alternative mating strategies. We provide a new classification scheme for alternative mating strategies based, not on the relative degree to which phenotypes are condition dependent, but instead on the ecological conditions in which they are likely to arise. Lastly, we present our conclusions on alternative mating strategies operating within animal mating systems, and we propose directions for future research.

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Mating Systems and Strategies

1

The Opportunity for Selection

"When the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection."
—(Darwin 1859, p. 89)

Sexual Selection and the Sex Difference in Variance of Reproductive Success

Darwin recognized two patterns in nature and used them to frame the central questions of sexual selection (Darwin 1859):

1. Why do males and females of the same species differ from one another, with males exhibiting morphological and behavioral phenotypes more exaggerated than those of females?
2. Why do the males of closely related species exhibit much greater differences in morphology and behavior than the females of closely related species?

The first pattern is a microevolutionary one, seen commonly within species of almost all taxa with separate sexes, including plants. It indicates that some kind of selection is working to differentiate the sexes and it is affecting males to a much greater degree than females. The second pattern is a macroevolutionary one, observed across species within genera or families of almost all taxa (e.g., many avian taxa). These large differences in male phenotype among closely related taxa are the signature of a very strong and rapid evolutionary force. Darwin noted that, in many species, the phenotypic differences between the sexes are associated neither with essential reproductive physiology nor with development of the male and female gametes. The exaggerated plumage, coloration, behavior, and morphology of males are correlated with but not necessary to reproduction.

Both of Darwin's patterns are reflected in the language of natural history. In many species, the male is so conspicuously different from the female that the common name of a species describes only the male sex. Only male red-winged blackbirds (*Aegelaius phonecius phonecius*; Searcy 1979; Weatherhead and Robertson 1979), are black with red epaulets on their wings, whereas the females are inconspicuous and dull brown in color (fig. 1.1a). In the bullfrog, *Rana catesbania* (Howard 1984), it is only the male that makes the deep call for which the species gets its common name; female bullfrogs

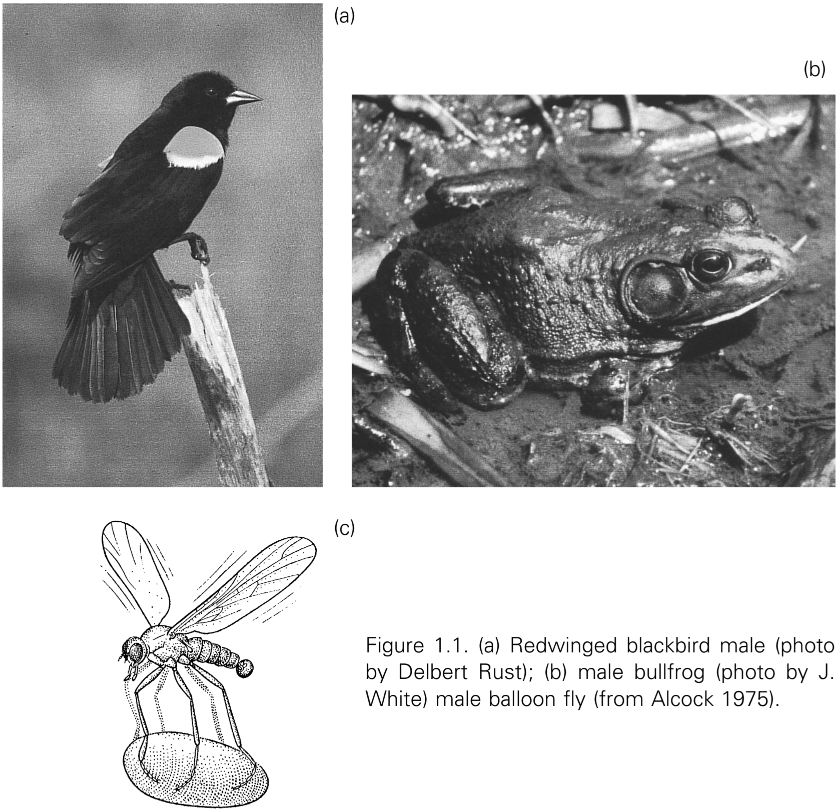


Figure 1.1. (a) Redwinged blackbird male (photo by Delbert Rust); (b) male bullfrog (photo by J. White) male balloon fly (from Alcock 1975).

are silent (fig. 1.1b). Only males carry balloons of silk as nuptial gifts for females in balloon flies, *Hilara santor* (fig. 1.1c; Kessel 1955). Neither the epaulets of the male blackbird, nor the call of the male bullfrog, nor the bower of the male bowerbird, nor the balloons of male balloon flies, are essential for sperm production or other physiological aspects of reproductive function. These males differ from the females of their own species in a rather arbitrary suite of phenotypic traits when considered across taxa.

Darwin used the term “trivial” to describe many of these exaggerated, male-limited characters because they appeared to have no clear relationship to viability or reproductive fitness. Despite very similar ways of life, closely related species could have males with very different phenotypes. Why should male tail length in one species be greatly elongated while, in another species of the same genus, males might possess a cape of expandable neck feathers and be rather ordinary in tail length (Gilliard 1962; Borgia 1986)? Why would longer tails be adaptive for males of one species but not the other? Furthermore, if these traits were adaptive for males, why were they not also adaptive for females? Darwin saw no obvious functional relationship between the exaggerated traits of males and the physical environment as he did for many other characters. Indeed, the "fit" between certain male phenotypes and the abiotic environment was exceptionally poor; exaggerated male characters might actually lower male viability.

The macroevolutionary pattern of large phenotypic differences between males of closely related species suggests that the selection responsible for these exaggerated male traits was *rapid and strong*. In contrast, we know from microevolutionary theory and empirical studies of artificial selection that selection acting on only one sex is considerably *slower and weaker* than selection acting in both sexes. In fact, selection on one sex but not on the other is only half as effective as selection acting on both, because half of the genes in any generation are derived from each sex in the previous generation (Falconer 1989). Selection restricted to one sex is tantamount to drawing half of the genes at random, and unselected. Selection that acts in *opposing* directions in the two sexes is slower still than selection absent in one sex.

To understand the microevolutionary perspective on single-sex selection, consider an experiment in which a laboratory or captive population is subjected to artificial selection to increase tail length in males. There are several different ways that we might impose artificial selection and these have different effects on the expected rate of response. Consider first artificial selection on both males and females. After measuring tail lengths of all males, those with long tails are chosen as parents and those with shorter tails are discarded and prevented from breeding. We can quantify the strength of this selection using the standardized selection differential experienced by males, S_{males} (fig. 1.2.a). The difference in average tail length between the selected males and the unselected males, divided by the standard deviation of male tail length, equals S_{males}. Similarly, we measure tail lengths of all females and choose those with the longest tails for parents and discard those with shorter tails (fig. 1.2.b). The strength of this selection, S_{females}, is defined just like S_{males}, but relative to the female trait distribution. Total selection on our hypothetical population is the average of these two selection differentials, S_{total} or $(S_{\mathrm{males}} + S_{\mathrm{females}})/2$. If our selection is as strong in males as it is in females, so that S_{males} equals S_{females}, which equals S, then S_{total} also equals S.

Now consider artificial selection *only* on males and not on females (fig. 1.3). As before, we measure tail length of males and select those with the longest tails as breeders (fig. 1.3a). However, we choose female parents at random with regard to tail length (fig. 1.3b). Thus, the selection differential in females, S_{females}, must be zero because the mean tail lengths of the breeding and nonbreeding females are the same. By using the *selected* males and *unselected* females as parents, fully half of the genes of each offspring, namely, those descending through the females, are not subject to any selection at all. Because half of the genetic material affecting tail length in the offspring generation has not been selectively screened but rather has been

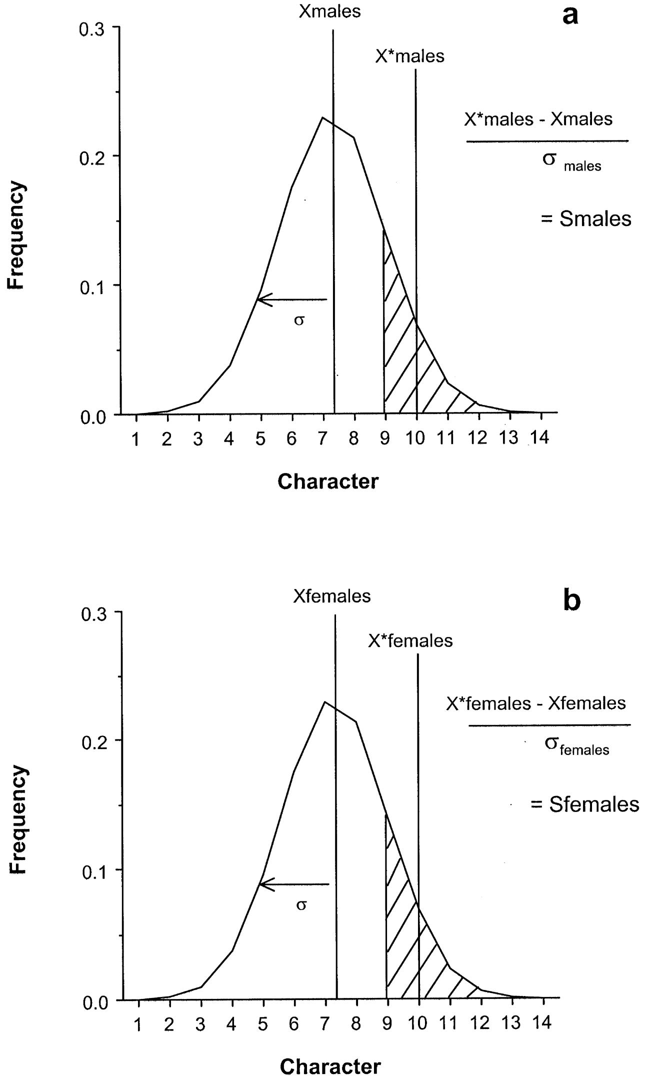


Figure 1.2. Selection on both sexes simultaneously; hatched areas represent breeding individuals; open areas represent nonbreeding individuals.

chosen at random, the total selection differential, averaged across the sexes, equals $S_{\text{males}}/2$ or, if we select on males as strongly as we did above, $S/2$. This makes single-sex selection weaker by half than selection on both sexes. Single-sex artificial selection experiments conducted on a number of species confirm this theoretical expectation (Robertson 1980).

The taxonomic observation of conspicuous male divergence between

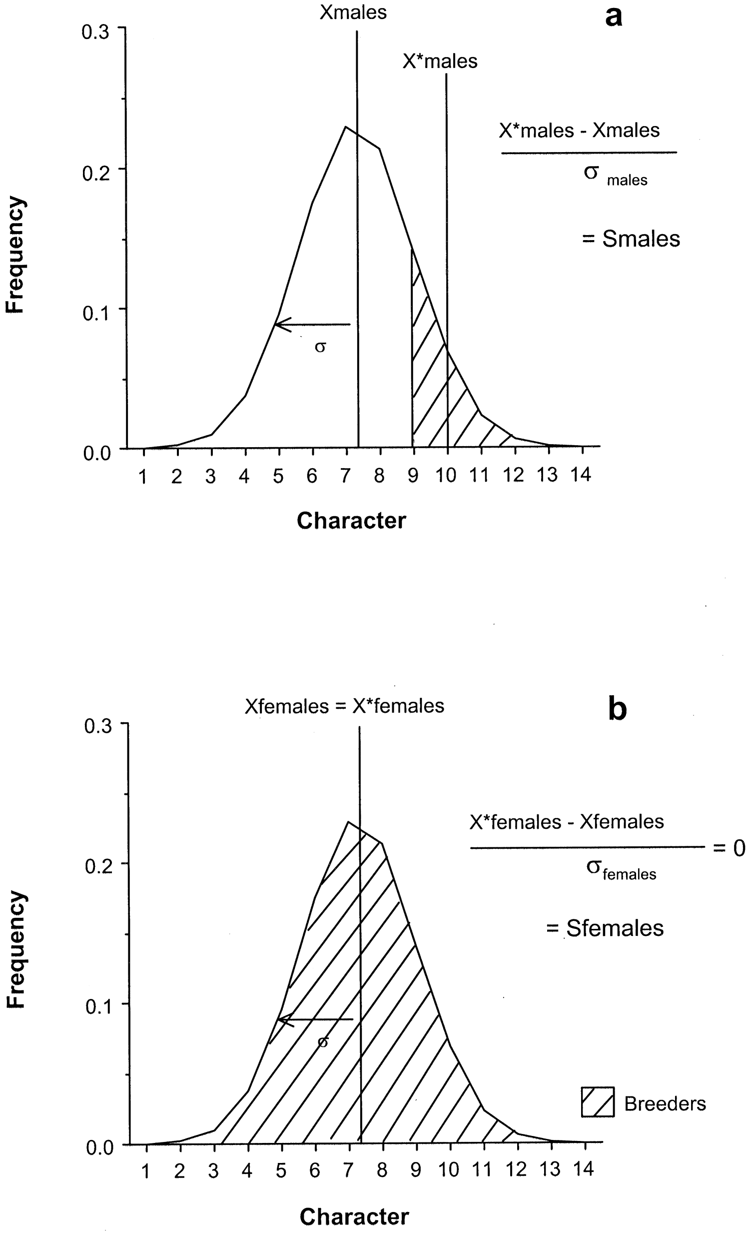


Figure 1.3. Single-sex selection, that is, selection on only one sex; hatched areas represent breeding individuals; open areas represent nonbreeding individuals.

closely related species stands in sharp contrast with the expectation from microevolutionary theory of a slower response to single-sex selection. This contrast between macroscopic pattern and microevolutionary process becomes even starker when we consider the evolution of sex-limited expression of male phenotypes. When genes are carried by both sexes but expressed in only one sex, we say that the expression of the gene is *sex-limited.* Most genes are expressed in both sexes; the limitation of a gene's expression to one sex is itself an evolved property of that gene or the developmental genetic system. Indeed, when artificial selection is practiced on only *one* sex, the focal character responds in *both* sexes, because selection in one sex does not limit the expression of the genes to that sex. For this reason, in our second artificial selection experiment (see above), we expect the tails of the unselected females to increase in length as a result of selection for increased male tail length. In the terminology of phenotypic selection models, the same trait (e.g., tail length) expressed in males and in females can be considered as two distinct but genetically correlated traits, one expressed in males and one in females. Because the genetic correlation across the sexes is positive, direct selection on one sex results in a correlated response in the homologous trait in the other owing to indirect selection.

With sexual selection, however, the selection differential in females is not zero, but actually less than zero (i.e., $S_{\text{females}} < 0$). Why is this so? Because, as Wallace (1868) argued, the exaggerated traits favored in males are *selected against* in females. Thus, the sex-specific selection differentials are of opposite sign, $S_{\text{females}} < 0 < S_{\text{males}}$. It is as though we divided a population's genetic composition into two separate pools of genes: one from females and one from males. In our hypothetical population, in the male gene pool, we select for those genes that increase tail length or body size ($0 < S_{\text{males}}$; fig. 1.4a). In the female pool, we select *against* these very same genes ($S_{\text{females}} < 0$; fig. 1.4b)! We then combine the two divergently selected pools by mating the selected males and females to create the offspring. The result is an evolutionary process that is even *weaker and slower* than single-sex selection (fig. 1.3) because the average selection differential on the trait $[(S_{\text{males}} - S_{\text{females}})/2]$ is *less than* that of single-sex selection, $S_{\text{males}}/2$. If the selection differentials were equal in the two sexes (but of opposite sign), then S_{total} would equal zero.

How does sex-limited gene expression arise? The evolution of gene expression that exists in one sex and not the other is believed to occur via the evolution of *modifiers*, genetic factors that modify the normal pattern of gene expression during development (Fisher 1928; Altenberg and Feldman 1987). The fitness advantage to the modifier, which is otherwise neutral, accrues when there is selection favoring the phenotype in one sex and opposing it in the opposite sex. That is, the evolution of sex-limited gene expression requires a sex difference in the direction of selection, as occurs with sexually selected traits. As modifier genes spread through the population, the expres-

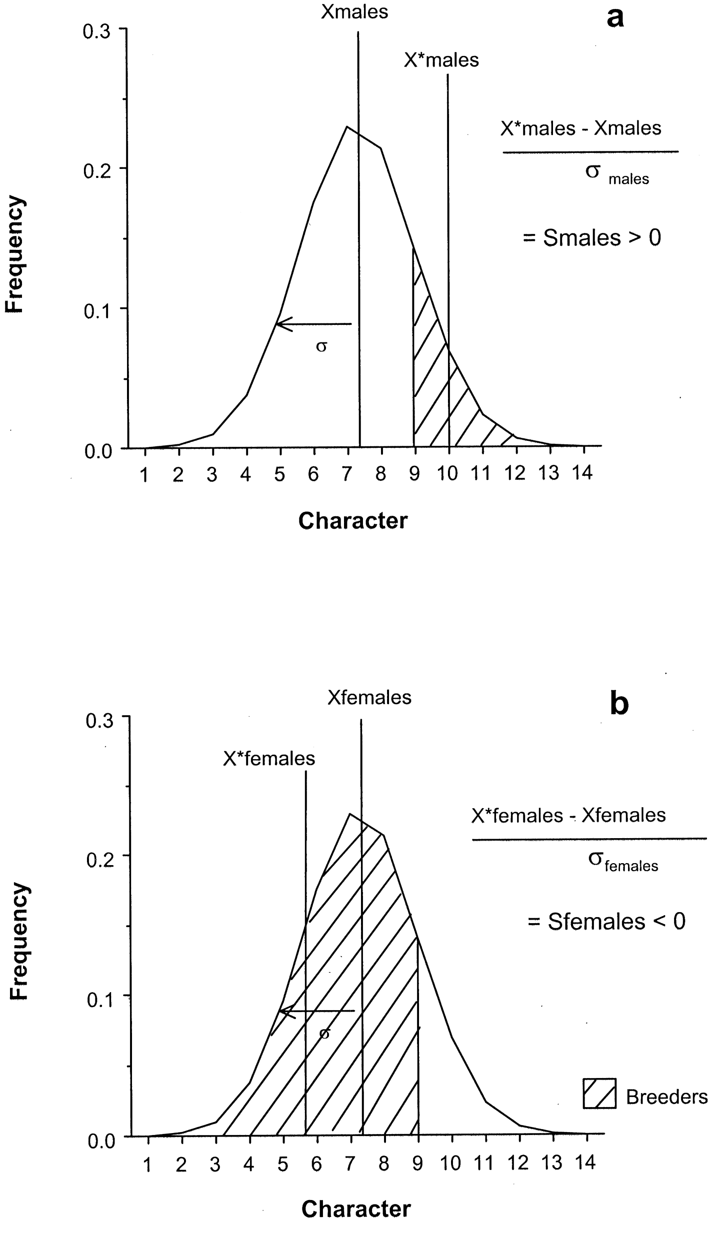


Figure 1.4. Directional selection in opposing directions between the sexes; hatched areas represent breeding individuals; open areas represent nonbreeding individuals.

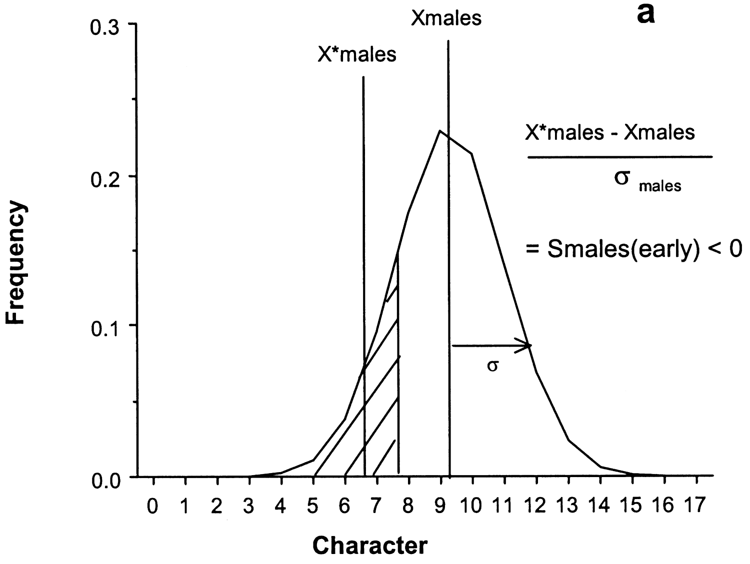
sion of the genes affecting tail length is diminished in the female sex and the trait can become sex-limited. Such modifiers can be viewed as genes that reduce the genetic correlation between a trait expressed in males and the same trait expressed in females. Reducing the genetic correlation reduces the limitation imposed by the sex difference in the direction of selection. However, the evolution of such modifier genes takes time, so the rate of evolutionary response for genes with initial phenotypic expression in both sexes is slowed.

There is an additional reason for sexual selection to be a slow evolutionary process. Exaggerated male traits do not appear to be adaptive at all life stages even in the male sex. Darwin (1859) reasoned that seasonal patterns in the expression of exaggerated male-limited traits indicate that these phenotypes may not be of selective advantage at other times during the life of males. Wallace (1868) went further, suggesting that such traits were selected against at these other times (see chapter 10). This conflict in the direction of selection at different life stages in the male sex makes total selection on these traits *weaker* and thus makes their evolution *slower*.

Consider again our population subject to artificial selection on males (fig. 1.5). In this population, suppose that selection is imposed on males at two different stages in the life cycle. When males are young and immature, selection may favor small tail size and act against males with larger tails, so that $S_{\mathrm{males}}(\mathrm{early}) < 0$ (fig. 1.5a). Only males with the smallest tails at this stage are permitted to mature. Later, at maturity, selection among the remaining males favors only those with the largest tails becoming parents, so that $S_{\mathrm{males}}(\mathrm{late}) > 0$ (fig. 1.5b). Genes that increase tail length at all ages will experience conflicting selection pressures, and, in particular, they will be culled and discarded at the first episode of selection. The total selection differential in males is the *combination* of these two opposing components, further weakening the overall strength of selection for these traits in the male sex.

Only those genes that fortuitously act later in male life to increase tail size will experience a coherent selection pressure and avoid the opposing juvenile selection. It is possible, and even likely, that there are “modifier” genes that could delay the timing of expression of tail size genes to late in male life. However, age-limited expression, like the sex-limited expression discussed above, represents another derived property of the genetic architecture and it further slows the expected rate of evolution under sexual selection.

Such conflicts between the fitness components of male viability and male reproduction may exist for many exaggerated male traits. It is often hypothesized that exaggerated male traits lower male viability by making males more conspicuous to predators (e.g., bird territorial calls, plumage, and displays) or by imposing high energetic costs on males (e.g., male vocalizations in frogs and toads). In some species, these costs to males have been well documented. For example, only male frogs call, and calling has been shown by ecological physiologists to be extremely costly in energetic terms (Ryan



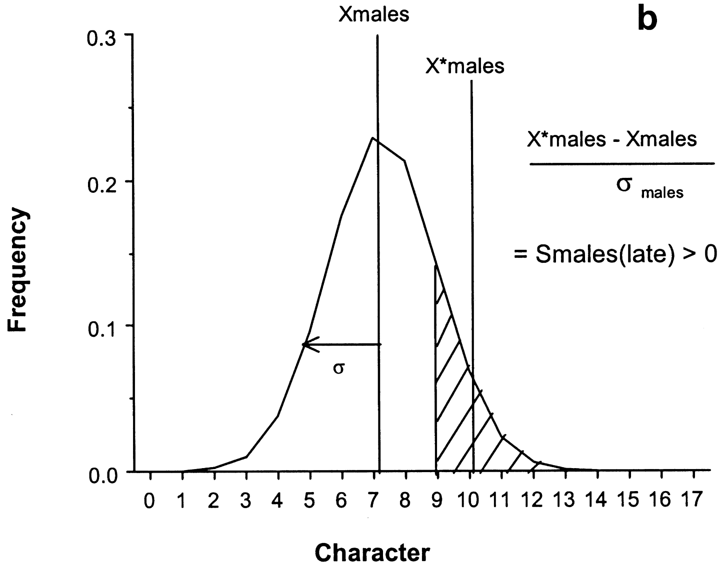


Figure 1.5. Directional selection in opposing directions within one sex over different life stages; hatched areas represent breeding individuals; open areas represent nonbreeding individuals.

and Tuttle 1981). Males of many anuran species expend large amounts of energy calling and, although more than 90% of matings will take place over three or four nights, the males might call every night for two or three months. Also, in at least one species, *Physalemus pustuluosus*, males are victims of frog-eating bats that use the sex-specific calls to locate their prey (Ryan and Tuttle 1981; Ryan 1983b).

There is a similar risk to males in some species of lampyrid beetles or "lightning bugs" (Lloyd 1966). In a typical species, the males fly around and emit a luminous, blinking signal. The males' visual calling elicits a response from females, which are flightless in many species. A signaling male finds a mate when a female responds to his signal with her own light. Not only is the energetic cost of flying borne solely by the males but also the more conspicuous males encounter a sex-specific risk of predation, sometimes from heterospecific females that mimic the response signal of another species and eat the responding males (fig. 1.6; Lloyd 1975). McCauley (1982) has shown that in mating pairs of milkweed beetles, *Tetraopes tetraophthalmous*, males in copula and guarding females succumb to wheel-bug predation more often than females. Male scorpion flies, genus *Panorpa*, forage in spider webs for insect prey that they then use as nuptual gifts to facilitate copulation with females (Thornhill 1981). In general, as a consequence of the expression of sexually selected traits, males suffer greater mortality than females. Indeed, many believe that lack of strong predation pressure probably facilitated the evolution of ground display habits by some birds of paradise as well as bower building by all bowerbirds (S. Pruett-Jones, pers. comm.).

In summary, there is an apparent conflict between the microevolutionary perspective on sexual selection and the macroevolutionary pattern. Whereas the comparative pattern indicates that sexual selection is one of the *fastest and strongest* evolutionary forces, microevolutionary analysis suggests that sexual selection should be *weak and slow* owing to single-sex selection, sex-limited expression, age-limited or stage-limited expression, and conflict between viability and fertility fitness within males.

The Quantitative Paradox of Sexual Selection

The Quantitative Paradox of sexual selection is this: *How can sexual selection be strong enough to counter the combined, opposing forces of male and female viability selection?* In studying the forces of evolution, we want to understand both the mechanisms by which they work, as well as the relative strength of each in relation to the others. Weak natural selection does not always override other evolutionary forces, like random genetic drift or mutation. Many equilibrium states in evolutionary genetics represent a balance between opposing evolutionary forces, such as mutation-selection balance

Figure 1.6. *Photurus* male being eaten by *Photinus* female (photo by J. Lloyd; see also Lloyd 1975).

(Hartl and Clark 1989; Lynch et al. 1998). The evolution of one trait can be limited by opposing natural selection on other genetically correlated traits. Although Darwin provided two mechanisms (see below) that permit us to understand *how* sexual selection operates, he did not address the *quantitative* issue of its *strength* relative to other evolutionary forces. How can sexual selection be such a strong and rapid evolutionary process that it can create large differences in morphology, physiology, and behavior among males of closely related species? How can Darwin's "less rigorous" process of sexual selection (see below) overpower the opposing forces of natural selection in both sexes?

We can address these questions by partitioning the effects of exaggerated male characters into separate components of male and female reproductive and viability fitness (table 1.1). When we do this, we find that only one component is positive and all the rest are negative. The paradox of sexual selection arises because the fitness decrements associated with exaggerated male traits appear to outweigh the fitness increments (see table 1.1). As explained below, Darwin proposed two compelling mechanisms of sexual selection, namely, female choice and male-male combat. However, he did not identify or even discuss this more quantitative issue. We will first discuss Darwin's mechanisms for sexual selection and then address the resolution of what we have called the Quantitative Paradox of sexual selection.

Table 1.1
The sex-specific selection differentials, partitioned into reproductive and viability components of fitness, for an exaggerated male trait.

	Viability	*Reproduction*	*Total Selection Differential*
Selection on Males	$S_{\text{early}} < 0$	$S_{\text{late}} > 0$	S_{males}
Selection on Females	$S_{\text{early}} < 0$	$S_{\text{late}} < 0$	$S_{\text{females}} < 0$

Note: A selection differential greater than zero indicates that the trait enhances this component of fitness and is favored by selection while a negative selection differential (< 0) indicates the opposite.

The Mechanisms of Sexual Selection

Darwin proposed sexual selection as a special mode of natural selection to explain the evolution of extreme male phenotypes. He defined sexual selection as that selection which occurs within one sex as a result of competition among members of that sex, for reproduction with members of the other sex. From the viewpoint of one sex, generally males, members of the other sex, generally females, are a scarce resource. Thus, males must compete among themselves for access to this scarce resource, that is, for females. Darwin argued that males who won this sexual competition for females obtained more mates (a higher mating success) than males who lost in this competition. He further postulated that the extreme or exaggerated phenotypes of males were beneficial to male fitness *solely in regard to this competition with other males for mates*. Wallace (1868) argued further that these same male phenotypes were selected against in females as well as in males at times other than during the courtship season (see above table 1.1 and chapter 10).

The evidence that these phenotypes were detrimental to viability and selected against in females came from several different lines of reasoning. First, because these “male” traits are lacking or expressed only mildly in females, Wallace reasoned that they could not enhance survival. If such traits were generally good for survival, they would be expressed by both sexes. Second, he observed that many male-limited phenotypes are displayed only during the breeding season. For example, the bright plumage of many male birds, the antlers of some deer and other ungulates, and the calls of male frogs are expressed only during a brief period of the year, the courtship and breeding season. If these traits were advantageous in ways other than competition for mates, Wallace reasoned that they would be displayed year round, especially considering the tremendous investment of energy expended during the growth and development of some male structures. If the antlers of male deer were generally useful for repelling predators, why were they shed after the mating season and not retained year round? Darwin inferred that exaggerated male traits *must* function in mate acquisition. He was not clear whether they were disadvantageous to males and females in other respects as Wallace argued (see Chapter 10). For these reasons, Darwin proposed two mechanisms whereby more ornamented males could achieve a greater mating success than less ornamented males: (1) male-male competition for mates, and (2) female choice of mates.

Male-Male Competition for Mates

By male-male competition for mates, Darwin meant those cases in which males contested directly with one another during the breeding season for access to females. In his own words, sexual selection ". . . depends, not on a struggle for existence, but on a struggle between males for possession of the females; the result is not death of the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection" (1859, p. 88). Winning males mate with more females than losing males, and as a result sire more offspring. This quotation from Darwin places the Quantitative Paradox of sexual selection in high relief. If it is less rigorous, how can sexual selection override opposing natural selection in both sexes?

Male-male competition is clearly the mechanism of sexual selection in organisms such as deer, elk, or horned beetles (Eberhard 1979; Clutton-Brock et al. 1982; Emlen 1996). In these species, males, but not females, develop a sexual ornament and intrasexual weapon, antlers, just prior to the breeding season. During the mating season, males establish territories and engage in prolonged head-to-head combat using these antlers. Vanquished males are excluded from access to females and the winning males mate successfully with many does. Antlers in most species are not only a male-specific phenotype but also play a central role in the male-male contests for mates, which are a pivotal component of male reproductive fitness. Clearly, as Darwin suggested, sexual selection has played a role in the evolution of this kind of male-specific trait because its adaptive function is mate acquisition.

Similar male-male contests have been observed in many other species, including many beetles (Eberhard 1979; Emlen 1996). Male stag beetles (*Lucanus cervus*; Price 1996), for example, possess enlarged mandibles (fig. 1.7). Although carried by males throughout adult life, the horns are used only at the time of mating. When a male encounters another male copulating with a female, he uses the horns to pry his rival off the female and sometimes off the tree entirely. The winning male then mounts the female himself if she has remained in the vicinity. In many beetles, males will attack other

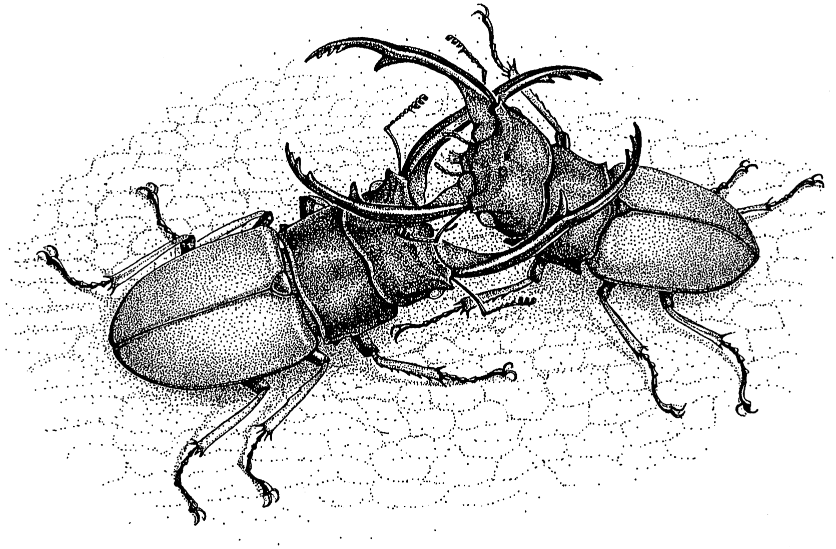


Figure 1.7. Stag beetles in combat, *Lucanus cervus* (from Price 1997).

mating males by biting the legs or antennae, and these attacking males often interrupt copulation. A similar evolutionary enlargement of protuberances on the pronotum of males has occurred in the forked fungus beetle, *Bolitotherus cornutus* (Conner 1988) and in the broad-horned flour beetle, *Gnathocerus cornutus* (fig. 1.8). The former species is found living on shelf fungus growing on dead trees. Females congregate on the bracts of fungi to lay eggs, and the larvae tunnel into and feed on the fungus. Males also aggregate where females oviposit and fight to exclude other males from the fungal bracts. These beetles are so sedentary in their habits that the same individuals can be found on the same bracts of fungus for up to six years! The male defending a bract can mate repeatedly with the females who lay eggs on that bract and sire many offspring.

In many primates, males sport enormously developed fangs, manelike ornamentation, and thick fur around the neck, as in hamadryas baboons (*Papio hamadryas*; fig. 1.9). Single dominant males may have reproductive access to a harem of several females. In this instance, the "fitness" stakes of a single male-male contest are not just the offspring of a single female but that of an entire group of females. With this kind of fitness reward attendant on male-male combat, it is obvious that successful males will have a much higher fitness than other, losing males. Indeed, in a species with a fifty-fifty Mendelian sex ratio at breeding, if one successful male has several mates, several males must necessarily have no mates at all. It is this consequence of sexual selection that establishes the fundamental relationship between the

Figure 1.8. Sexual dimorphism in *Gnathocerus cornutus*; male (right) with enlarged processes on the pronotum; female (left) unmodified (photo by M. J. Wade).

variance in male fitness and the variance in female fitness, which we will use to resolve the Quantitative Paradox of sexual selection (see below).

There are also male structures that function in reproductive combat but are less apparent than antlers, horns, manes, and fangs, because they are not used in face-to-face combat. Copulatory and seminal combat between males also occurs and appears to be commonplace in some taxonomic groups, especially insects (Smith 1984; Birkhead and Moller 1993a,b; Baker and Belis 1995; Eberhard 1996; Howard 1999). For example, males of some species of damselflies have a caudal structure employed at the time of mating whose function is to remove the sperm of other males from the reproductive tract of the female (Waage 1979). Males of some grasshoppers and katydids have an inflatable bulb on the end of the aedeagus, which also has a central groove. By inflating the bulb, a mating male mechanically forces the sperm of previously mating males out of the female reproductive tract back along the groove. Conversely, males of some species transfer not only sperm but also a

Figure 1.9. Male baboon with enlarged neck fur (photo by R. Willey).

"sperm plug" which may impede the copulatory efforts of subsequently mating males (Gwynne 1984).

In insects, the structure of sperm itself is often wildly elaborated and varied among closely related species (fig. 1.10) in much the same way that plumage and behaviors differ among males of related species of birds (Sivinski 1980; Eberhard 1996). It seems likely that postcopulatory but prezygotic

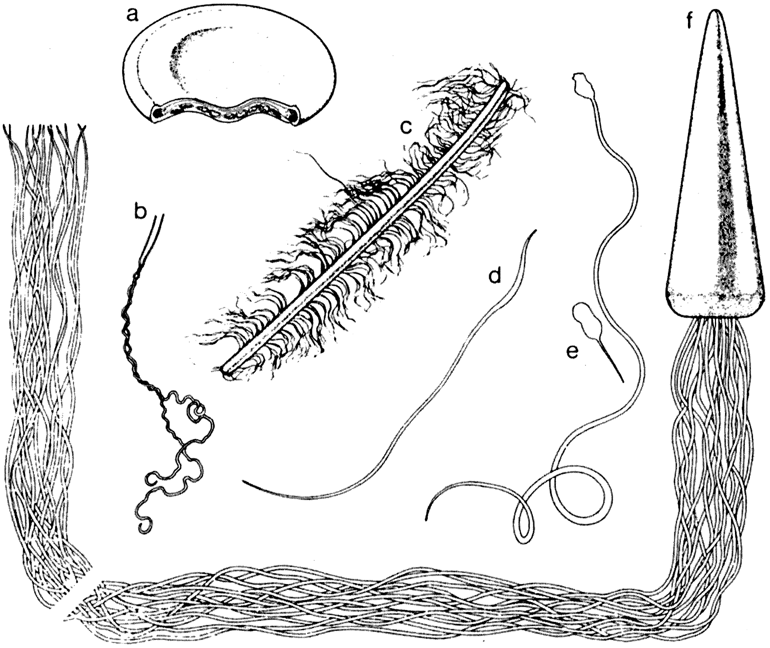


Figure 1.10. Elaborate insect sperm. (a) Proturan sperm, *Eosentonon transitorium*; (b) firebrat sperm, *Thermobia domestica*; (c) spermatostyle and spermatozoa from a gyrinid beetle, *Dineutus* sp.; (d) firefly sperm, *Pyractomena barberi*; (e) symphlan ssperm, *Symphylella vulgaris*; (f) termite sperm, *Mastotermes darwiniensis* (from Sivinski 1980).

competition between sperm of different males within the reproductive tract of multiply inseminated females results in sexual selection on sperm morphology (Pitnick 1996). This is a form of direct gametic competition between males with important ramifications for speciation (Robinson et al. 1994; Howard 1999).

Female Choice of Mates

All sex differences in phenotype cannot be explained by male-male competition alone. In many species, males differ from females in the extreme development of traits that appear to have no direct or plausible connection to male-male combat. Male peacocks do not fight one another with their tails nor do male bowerbirds fight one another directly with their bowers. Darwin believed that male-male combat was inadequate to account for the evolution of these other kinds of male-limited characters, and he postulated sexual selection via female choice of mates.

By female choice of mates, Darwin meant that females exhibited mating preferences for different kinds of males; i.e., they were more willing to accept certain males as mates than other males. Darwin reasoned, "if man can in a short time give elegant carriage and beauty to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect" (1859 p. 89). If female mating preferences were operating, then the traits of preferred males would become exaggerated by this mechanism of sexual selection in the same way and for the same reason that combat-related male traits evolved.

Questions about the existence of female choice, as well as how and why it operates on males, represent active areas of research today. It is only in the past ten years that strong female mating preferences for males with extreme ornamentation have been experimentally demonstrated in natural populations (review in Andersson 1994; Basolo 1990a,b). These studies show unequivocally that males with extreme values of preferred traits achieve more matings than males with less extreme values of these same traits. The number of mates that a male acquires in his lifetime indicates the degree to which he is preferred by females relative to other males. Here, differences among males in reproductive fitness result from the mating preferences exerted by females rather than from male-male combat. "Successful" males may have very high fitness, but the proximate reason for such differential mating success is female choice rather than male combat. Again, for every male who is accepted by and successfully mates with several females, there must be several males who *do not mate at all*. This simultaneous addition of winning males at one end of the mate number distribution and losing males at the other means that sexual selection always increases the *variance* in male mating success. It is this effect on the variance in male reproductive success that creates a sex difference in the variance in fitness. It is this sex difference in fitness variance that is fundamental to resolving the Quantitative Paradox of sexual selection.

The Strength of Sexual Selection Relative to Natural Selection: Resolving the Quantitative Paradox of Sexual Selection

Although the twin mechanisms of male-male combat and female choice explain why certain male traits have adaptive value in mate acquisition, we are still left with a critical quantitative issue (see table 1.1): *Why is the single positive component of male reproductive fitness sufficient to outweigh the totality of the several negative components in the evolution of these exaggerated male traits?* How can sexual selection be one of the strongest evolutionary forces when it affects only one sex, is opposed in the other sex, affects only one fitness component, and is exposed to selection only some of the time in the favored sex? It is not sufficient to say, as Darwin did, that the trait is favored in males by male-male competition for mates or by female choice of mates. Nor is it sufficient to measure the degree to which a particular character is modified within each sex and then attribute its greater modification in males to either of Darwin's mechanisms. Analyses that focus on the mechanisms of sexual selection are no substitute for measurements of the strength of selection. Identifying the mechanism of selection is different from quantifying its evolutionary effect.

We can resolve the Quantitative Paradox of sexual selection by considering, first, the *variance* in fitness and its relationship to the strength of selection and, second, the *sex difference* in variation of fitness between males and females. We are interested in this variation in fitness not only because fitness variance is required for selection, but also because the strength of selection is *proportional* to the variance in fitness: *the greater the variance in fitness, the stronger the force of selection.* Not only is fitness variation necessary for evolution, but also the variance in fitness sets an upper bound on the *rate* of evolution. Large differences in fitness between individuals mean strong natural selection. The absence of fitness differences between individuals (no fitness variance) means that natural selection, and, hence, adaptive evolution, are not possible.

Fitness variation determines the maximum rate (i.e., the upper limit) of evolution by natural selection because it limits the degree to which breeding parents differ from the average individual in the population before selection. The breeding parents are a subset of all individuals in the population and only they contribute genes to the next generation. The resemblance of offspring to their parents will be imperfect, to a degree that varies between zero and 1, a parameter better known as heritability. Because heritabilities are less than 1, the phenotypic mean of the offspring *must* differ from that of the breeding parents and be closer to that of the unselected population. If the average phenotype of the breeding parents is limited by the variation in fitness, the average phenotype of the selected offspring descended from those parents must also be limited. It is in this way that the total variation in fitness sets an upper limit to the rate of evolutionary change.

The Variance in Fitness and the Strength of Selection

These qualitative principles can be explained more precisely with simple mathematical terms and figures. Let the reproductive fitness of an individual with phenotypic value z be $W(z)$, and the frequency of such individuals in a population be $p(z)$ (fig. 1.11). The mean fitness of this population *before selection*, is, by definition,

$$W = \int W(z)p(z)dz. \qquad [1.1]$$

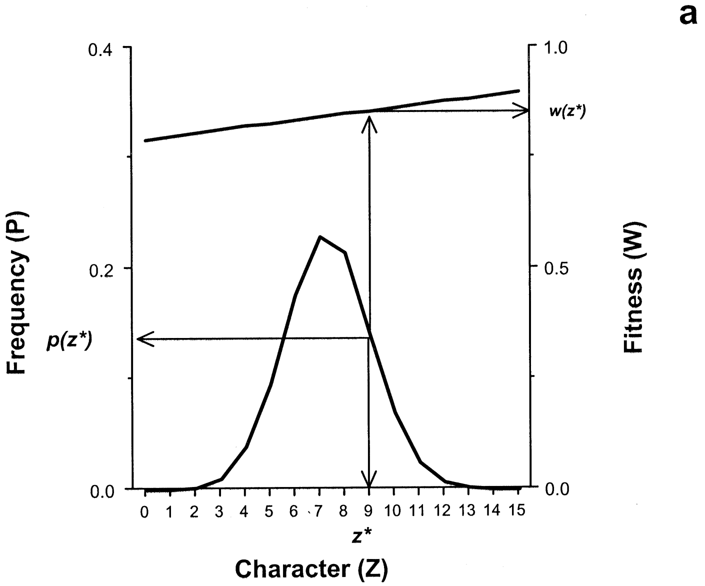


Figure 1.11. Figure showing the distribution of *p*(*z*) individuals in population with *W*(*z*) fitnesses.

That is, the fraction of the population exhibiting each phenotypic value, $p(z)$, is multiplied by its corresponding fitness $W(z)$, and the resulting products are summed, or integrated, over all values of z. The mean phenotype in the population before selection, Z, is

$$Z = \int zp(z)dz. \qquad [1.2]$$

That is, each value of z in the phenotypic distribution is multiplied by the proportion of the population, $p(z)$, exhibiting that phenotype, and then integrated over all z phenotypes. The relative fitness $w(z)$, for individuals with phenotype z is simply the ratio $W(z)/W$.

As a result of selection, the distribution of phenotypes changes from $p(z)$ in the population *before selection* to $p'(z)$ in the population *after selection*. These two distributions are related multiplicatively by relative fitness so that

$$p'(z) = w(z)p(z). \qquad [1.3]$$

The mean fitness W' of the parents selected to breed equals

$$W' = \int W(z)p'(z)dz = \int [W^2(z)/W]p(z)dz. \qquad [1.4]$$

Thus, the difference in fitness, ΔW, between breeding parents and the unselected parent population before selection is given by the difference between eqs. [1.4] and [1.1] or

$$\Delta W = (W' - W) = \int [W^2(z)/W]p(z)dz - \int W(z)p(z)dz. \qquad [1.5]$$

This expression can be rewritten as

$$\Delta W = [\textstyle\int W^2(z)p(z)dz - W^2]/[W] = V_W/W, \qquad [1.6]$$

where V_W is the variance in fitness of the parent population *before reproductive selection.*

The *relative* change in mean fitness by natural selection, $\Delta W/W$, is thus equal to

$$\Delta W/W = V_W/W^2 = V_w, \qquad [1.7]$$

where V_w is the variance in relative fitness. This is the increase in average fitness of the breeding parents *relative* to that of the parent population before selection. This entire change is not *transmitted* across generations to the offspring because not all of the variation in parental fitness is heritable. The offspring mean is given by the product of the parent mean (eq. [1.4]) and heritability. It is also given by adding the product of eq. [1.6] and heritability to the mean before selection. Offspring mean fitness is necessarily less than or equal to that of the breeding parents because heritability is a fraction always equal to or less than 1. Heritability is usually less than 1 because both genetic and environmental factors influence the expression of characters. The more the environment influences variation in phenotypic expression, the smaller heritability will be (Falconer and Mackay 1996).

Thus, the variance in relative fitness, V_w, places an upper bound on the change in mean fitness possible from one generation to the next. In fact, *the variance in relative fitness*, V_w, *places an upper bound on the change in the mean of any phenotypic trait* Z. The mean phenotype of the breeding parents, Z', is defined as

$$Z' = \int zp'(z)dz. \qquad [1.8]$$

We substitute $w(z)p(z)$ for $p'(z)$ to obtain

$$Z' = \int zw(z)p(z)dz. \qquad [1.9]$$

The variable Z', is equal to X^*_{males} in figs. 1.3a, 1.4a, and 1.5 or X^*_{females} in figs. 1.3b and 1.4b.

The change in mean phenotype *before* and *after* selection is equal to

$$\Delta Z = (Z' - Z) = \int zw(z)p(z)dz - \int zp(z)dz. \qquad [1.10]$$

It is important to note that ΔZ is the numerator of S, the selection differential (cf. figs. 1.3–1.5). Or, differently put, S is ΔZ, divided by the standard deviation of the phenotypic distribution $p(z)$. This conversion of ΔZ into units of standard deviation is important for comparing selection intensities across different populations, different experiments, and different traits, where both the mean and variance vary.

We note that $\int w(z)p(z)dz = 1$, and we can rewrite eq. [1.10] as

$$\Delta Z = \int zw(z)p(z)dz - [\textstyle\int zp(z)dz]\,[\textstyle\int w(z)p(z)dz]. \qquad [1.11]$$

We can recognize this expression as the covariance between z and $w(z)$, i.e., the covariance between phenotype and relative fitness. Thus, the change in mean phenotype resulting from selection is

$$\Delta Z = \mathrm{Cov}(z,w[z]). \qquad [1.12]$$

As with W, the fraction of ΔZ transmitted across generations depends on the heritability of the phenotype, which is always less than or equal to 1.

It is important to understand that the average fitness as well as the average phenotype may change as a result of selection. However, it is more important to understand that there is a *relationship* between the variance in fitness, V_W and the covariance between phenotype and fitness, $\mathrm{Cov}(z,w[z])$. To understand this relationship, we first must recognize that the ratio $\mathrm{Cov}(z,w[z])/(V_Z\ V_w)^{1/2}$ is the product moment correlation between a phenotype z and its relative fitness $w[z]$. Unless a perfect correlation exists between phenotype and relative fitness, this expression will always be less than 1. Next, note that the ratio $\mathrm{Cov}(w[z],w[z])/V_w$ is the product moment correlation between relative fitness and itself; thus its value is equal to 1. We can use these relationships to establish that

$$\mathrm{Cov}(z,w[z])/(V_z\ V_w)^{1/2} < 1 = \mathrm{Cov}(w[z],w[z])/\ V_w. \qquad [1.13]$$

We can further transform our phenotypic values of z and $w(z)$ to the unit normal scale x, where x equals $(z - Z)/\sigma_z$ and $w(x) = \dfrac{w(z) - 1}{\sigma_w}$. Thus, eq. [1.13] becomes

$$\mathrm{Cov}(x,w[x]) < V_w. \qquad [1.14]$$

Hence, the variance in relative fitness places an *upper bound* not only on the change in mean fitness itself, but also on the standardized change in the mean of *every other* phenotypic trait. It was for this reason, that Crow (1958, 1962) defined I, the "opportunity for selection," as

$$I = V_W/W^2 = V_w. \qquad [1.15]$$

It is this "opportunity for selection" that sets an upper bound on the rate of evolutionary change in the mean of *all* phenotypes.

The Sex Difference in the Variance in Fitness

We will now examine the opportunity for selection in the male and the female sex. We will see that there is a fundamental algebraic relationship between the opportunity for selection in males, I_{males}, and that in females, I_{females}. Based on the derivation above, note that the opportunity for selection for each sex is equal to the variance in fitness among members of that sex, V_i, divided by the squared average in fitness among members of that sex, X_i^2. Thus, $I_{\text{males}} = V_{\text{males}}/X^2_{\text{males}}$ and $I_{\text{females}} = V_{\text{females}}/X^2_{\text{females}}$. These expressions are linked together through the sex ratio and mean fitness. Furthermore, we will show that the variation among males in the numbers of mates caused by either male-male competition or female choice has two consequences:

1. the opportunity for selection in males exceeds the opportunity for selection in females, i.e., $I_{\text{males}} - I_{\text{females}} > 0$; and
2. given certain assumptions, the sex difference in the opportunity for selection equals I_{mates}, where I_{mates} is defined as the ratio of $V_{\text{mates}}/X^2_{\text{mates}}$, and where X_{mates} is the average number of mates per male. Thus, $I_{\text{males}} - I_{\text{females}} = I_{\text{mates}}$.

Hence, the opportunity for selection that results from the competition among males for mates, I_{mates}, is responsible, in large part, for the sex difference in the strength of selection.

We can now rewrite table 1.1 in terms of the strength of each component of selection (table 1.2). This notation will allow us to show why I_{mates} is often greater than the weighted sum of the other three terms in table 1.2 and thus resolves the Quantitative Paradox of sexual selection. However, to fully understand why this is so, we must first quantify the strength of sexual selection in males relative to the strength of natural selection on males and females to resolve the Quantitative Paradox concerning the evolution of extreme male traits (tables 1.1 and 1.2). Let us begin by considering the variation in male fitness associated with mating success.

The Average and Variance in Mating Success

In most breeding populations, males can be divided into a series of mating classes, k_i. The number of mates males obtain defines each mating class. Thus, k_0 males do not mate, k_1 males mate once, k_2 males mate twice, and so on. The number of males in each mating class, m_i, depends on how variable male are in their mating success. For example, in fig. 1.12a, all of the males

Table 1.2
The opportunities for selection represented by the components of reproductive and viability fitness as they affect the evolution of an exaggerated male trait.

	Reproduction	*Viability*
Male Fitness	I_{mates}	$I_{\text{viability}}$
Female Fitness	$I_{\text{fecundity}}$	$I_{\text{viability}}$

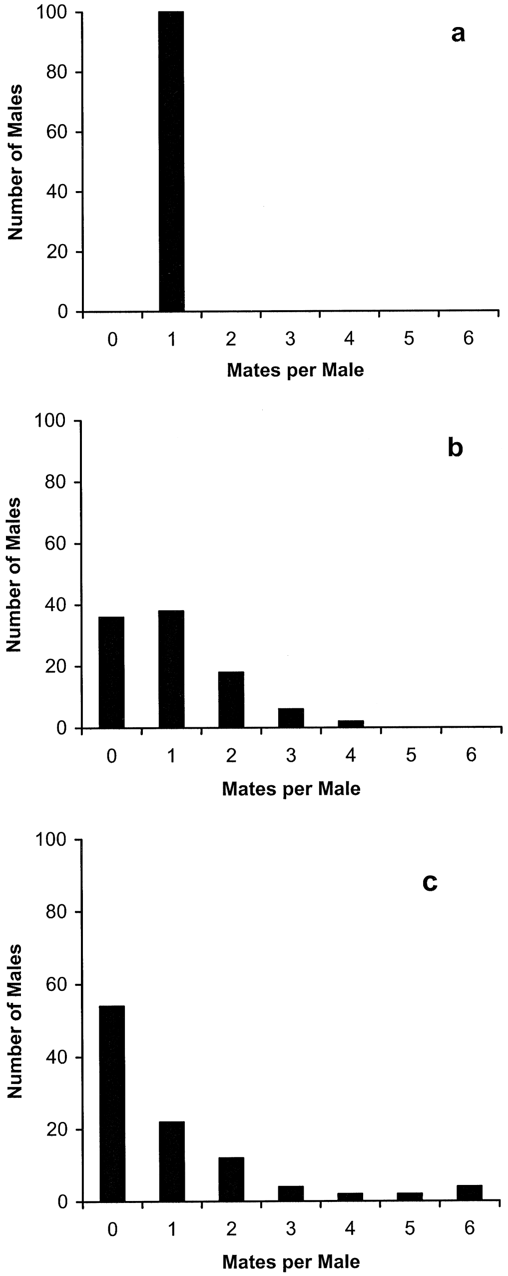


Figure 1.12. The distribution of male mating success in a population consisting of 100 males and 100 females (a) who each mate only once; all males secure a single mate; (b) mating occurs approximately at random; (c) certain males mate with more than one female.

mate once. Thus, all m_i categories equal zero except $m_1 = 100$. The sex ratio R in this or any population can be expressed as the ratio of the number of females to the number of males. In this case, $R = N_{\text{females}}/N_{\text{males}} = 1$ (Wade 1995).

The average mating success per male, M, equals the number of females in the k_ith mating class, multiplied by the number of males in the m_ith class, added up over all i classes, and then divided by the total number of males. Thus, $M = (\Sigma\ k_i\ m_i)/\Sigma\ m_i$, or in fig. 1.12a, $M_a = [(0)(0) + (1)(100) + (2)(0) + (3)(0) + (4)(0) + (5)(0) + (6)(0)]/100 = 1$. Clearly, $R_a = M_a$.

The average harem size H equals the number of mates per *mating* male. H is usually larger than the sex ratio ($H > R$). This is true because, whenever one male secures two or more females, other males are excluded from mating (Darwin 1874). The average mating success per mating male equals the number of females in each mating class, multiplied by the number of males in that class, added up over all classes, and then divided by the sum of the males who *actually mate*. Thus, $H = (\Sigma\ k_i\ m_i)/[(\Sigma m_i) - m_0]$. Since m_0 in fig. 1.12a equals zero, $R_a = M_a = H_a = 1$.

In fig. 1.12b, mating occurs approximately at random. In this situation, $M_b = [(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)]/100 = 1$, and here again, $M_b = R_b$. However, $H_b = [(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)]/[100 - 36] = 1.56$. Thus, with random mating, R_b still equals M_b, but H_b exceeds both values. This condition changes further when some males obtain more mates than expected by chance. In fig. 1.12c, again, $M_c = [(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)]/100 = 1 = R_c$. However, $H_c = [(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)]/[100 - 54] = 2.17$. Thus, in this example, as well as in general, as fewer males obtain more mates, R and M are equivalent and remain unchanged, but H increases still further.

How do such changes in the distribution of females with males affect the variance in mate numbers? The answer is this: As average harem size changes, so does the variance in mate numbers among males. The variance in mate numbers describes the "spread" of the distribution of mates per male around the population average. This variance can be calculated by squaring the value of each mating class, k_i, multiplying each squared value by the number of males in each mating class, m_i, adding up the products, and then subtracting this quantity from the squared average in mate numbers per male. Thus, V_M equals the average of the squared number of mates per male, minus the square of the average number of mates per male (Sokal and Rohlf 1995). That is, $V_M = [(\Sigma\ k_i^2 \mathrm{m_i})/\Sigma\ m_i] - [\Sigma\ k_i\ m_i/\Sigma\ m_i]^2$.

When all males in the population secure one mate, the variance in mating success among males is zero, that is, $V_{Ma} = \{[(0)^2(0) + (1)^2(100) + (2)^2(0) + (3)^2(0) + (4)^2(0) + (5)^2(0) + (6)^2(0)]/100\} - \{[(0)(0) + (1)(100) + (2)(0) + (3)(0) + (4)(0) + (5)(0) + (6)(0)]/100\}^2 = 0$ (fig. 1.12a). When some males mate more than once *by chance*, other males must still be excluded from mating. Consequently, the distribution of male mating success around the average widens. That is, $V_{Mb} = \{[(0)^2(36) + (1)^2(38) + (2)^2(18) + (3)^2(6) + (4)^2(2) + (5)^2(0) + (6)^2(0)]/100\} - \{[(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)]/100\}^2 = 1$ (fig. 1.12b). The more some males mate with more than one female, the larger the variance in mating success becomes. Thus, $V_{Mc} = [(0)^2(54) + (1)^2(22) + (2)^2(12) + (3)^2(4) + (4)^2(2) + (5)^2(2) + (6)^2(4)]/100\} - \{[(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)]/100\}^2 = 2.32$ (fig. 1.12c). Clearly, as the variance in mating success, V_M, becomes larger, the average mating success of mating males, H, must also increase.

As the example above graphically demonstrates, when there are equal numbers of breeding males and females, and if some males have many mates, then, necessarily, some males will have no mates at all. If a male loses in competition with other males for mates, then he has a reproductive success of zero (0). Conversely, a winning male might mate with one or more different females. As we have shown above, R equals the average number of mates per male. The parameter R also equals the sex ratio, $N_{\text{females}}/N_{\text{males}}$. In future examples, we will let V_{mates} be the variance in mate numbers among males.

Males might win or lose mates owing to either the Darwinian mechanism of sexual selection, direct male-male combat, or female choice. We will consider the relative effects of these mechanisms later (chapters 4 and 5). For now, to allow comparison of the effects of natural and sexual selection on both sexes, we must consider male and female fitness using the same units. Let O be the average number of offspring per female. Different females may produce more offspring or fewer offspring than the "average" female and we represent this variation in offspring numbers among females by V_O, the variance among females in fecundity fitness. The opportunity for fecundity selection in females, I_{females}, equals V_O/O^2. Because half of the genes in the offspring of our hypothetical species come from these females, half of the genes experience natural selection *against* the trait, possibly as strong as I_{females}.

The average male enjoys a reproductive success equal to RO, i.e., R times the reproductive success of the average female (O). When we say that the average number of offspring per male is the product RO, we are assuming that mate numbers and offspring numbers are independent of one another, i.e., not correlated. We will relax this assumption in chapter 4. If the breeding sex ratio is one male to every female, then for every male with k mates, there must be $(k - 1)$ males with 0 mates. As a result, the *least successful* males have a *lower fitness* than the least successful breeding females. In addition, unsuccessful males *outnumber* winning males whenever $k < 1$. Conversely, the fitness of the *most successful* males exceeds that of the most successful females *by a factor greater than R*. Differently put, there are many males with a fitness lower than the lowest in the female distribution and some males with a fitness much, much higher than the highest in the female distribution. The mean fitness is the same for both sexes when R is 1, because each offspring has one mother and one father (Fisher 1930). However, *the variance in fitness is much greater for males than it is for females.*

The average number of mates per male, R, is the total number of reproducing females, N_{females}, divided by the total number of available breeding males, N_{males}, which is also the sex ratio R. When the sex ratio R is expressed in this way it has the advantage that it is equivalent to the average number of mates per male. In many other discussions, the sex ratio is expressed as the reciprocal of R or $N_{\text{males}}/N_{\text{females}}$, as a means of expressing the degree of competition among males. This ratio of the number of mating males to the number of sexually receptive females is called the *operational sex ratio* or *OSR* (Emlen and Oring 1977). We will use the symbol R_O (i.e., $[1/R]$) for the OSR.

The OSR captures the intuitive idea that the greater the excess of males over females at the time of breeding, the greater the intensity of reproductive competition among males for mates. We show below that R_O is only one component, albeit an important one, of the sex difference in the opportunity for selection. Although it is a reasonable idea, R_O is *not* equivalent to the sex difference in the strength of selection (see Reynolds 1996; Kvarnemo and Ahnesjo 1996 for discussions to the contrary). Thus, two mating systems with the *same* value of OSR (our $1/R$ or R_O) can *differ* in the strength of sexual selection. Conversely, two mating systems with *different* OSRs can have the *same* strength of sexual selection. Because the OSR is not always predictive of the variance in male reproductive success, it is not always correlated with the strength of selection affecting male-female dimorphism.

We can divide males into two categories: those that are unsuccessful at mating, and thus have a fitness of zero, and those males that are successful and have one or more mates. We let H be the average number of mates of the successful males. We define p_m as the proportion of mating males, and p_0 as the proportion of nonmating, unsuccessful males. (Remember that $\{p_m + p_0\} = 1$.) These two frequencies are connected through the sex ratio R. The average number of mates per male, R, equals the average number of mates across our two categories of males. We can express this in terms of our definitions as

$$R = (H)p_m + (0)p_0. \qquad [1.16]$$

Writing the frequency of successful males, p_m, as $[1 - p_0]$, we find

$$p_0 = 1 - (R/H) \text{ or} \qquad [1.17]$$

$$p_0 = 1 - (1/[R_O H]). \qquad [1.18]$$

It is clear from eqs. [1.18] that the greater the number of mates per successful male, H, the larger must be the proportion of males with no mates at all,

p_0. As Darwin put it, females are a scarce or limited resource from the perspective of males competing for mates. Success in reproductive competition for some males *necessarily* means failure for others. Thus, whenever we add successful males with many mates to the right-hand side of the distribution of male fitness, we also must add one or more unsuccessful males at zero, the opposite side of the distribution.

To calculate the total variance in male fitness, V_{males}, we need to know the distribution of the number of mates of males. Let p_k represent the fraction of males that have k mates, where k ranges between 0 and a maximum of N_{females}. Thus, p_0 is the frequency of males with no mates at all and p_5 is the frequency of males with five mates, i.e., $k = 5$. The frequency of successfully mating males, p_m, is equal to the sum $\Sigma p_j = (1 - p_0)$. For all categories of mating males, we assume that the family size of each female is a random draw from the distribution of female reproductive success with mean O and variance V_O, which, in this case, is V_{females}. (We later relax this assumption in chapter 4 and permit male mate numbers to affect O.) The population of males can be viewed as consisting of the k categories given in table 1.3.

The total variance in male reproductive success is the sum of two components: (a) the average variance in offspring numbers among males within the categories of table 1.3; and (b) the variance in average in offspring numbers among the categories. Thus, we now have

$$V_{\text{males}} = \Sigma\, p_j(jV_{\text{females}}) + \Sigma\, p_j(jO - RO)^2 \qquad [1.19]$$

$$= RV_{\text{females}} + O^2 V_{\text{mates}}. \qquad [1.20]$$

Equation [1.20] illustrates the insight of Bateman (1948): *the fundamental cause of the sex difference in fitness variance is the variation of mate numbers among males*. However, the variance in male mating success is not as useful a comparative measure of relative male mating success as I, the opportunity for selection (Crow 1958, 1962; Wade 1979, 1995; Wade and Arnold 1980).

Table 1.3

The distribution of mates among males.

Number of Mates	*Frequency*	*Mean Number of Offspring*	*Variance in Offspring*
k	p_k	kX	kV_X
0	p_0	X	0
1	p_1	X	$1V_X$
2	p_2	$2X$	$2V_X$
3	p_3	$3X$	$3V_X$
4	p_4	$4X$	$4V_X$
k	p_k	kX	kV_X
Total: N_{females}	1	$N_{\text{females}}X$	$N_{\text{females}}V_{\text{females}}$

The opportunity for selection on males, I_{males}, equals the variance in male fitness, V_{males}, divided by the square of mean male fitness, $(RO)^2$. Dividing eq. [1.20] by $(RO)^2$, we have

$$(V_{\text{males}}/[RO]^2) = (RV_{\text{females}}/[RO]^2) + (O^2V_{\text{mates}}/[RO]^2), \qquad [1.21a]$$

$$I_{\text{males}} = (1/R)(I_{\text{females}}) + I_{\text{mates}}, \qquad [1.21b]$$

$$I_{\text{males}} = (R_O)(I_{\text{females}}) + I_{\text{mates}}. \qquad [1.21c]$$

When R and R_O are equal to 1, this expression reduces to

$$I_{\text{males}} = I_{\text{females}} + I_{\text{mates}}. \qquad [1.22]$$

When we say that the opportunity for sexual selection, I_{mates}, is the *only* cause of the sex difference in the strength of selection, we mean that

$$\Delta I = I_{\text{males}} - I_{\text{females}} = I_{\text{mates}}. \qquad [1.23]$$

I_{mates} is necessarily greater than zero whenever there is variation among males in the numbers of mates. Thus, I_{mates} provides a *standardized measure of the intensity of sexual selection on males and the sex difference in strength of selection* (Wade 1979; Wade and Arnold 1980; Wade 1995).

We need not assume that R and R_O are equal to 1. More generally, we find that the sex difference in the opportunity for selection can be found by subtracting I_{females} from both sides of eq. 1.21c. This expression becomes

$$I_{\text{males}} - I_{\text{females}} = (R_O - 1)\, I_{\text{females}} + I_{\text{mates}} \qquad [1.24a]$$

or

$$I_{\text{males}} - I_{\text{females}} = (1/R - 1)\, I_{\text{females}} + I_{\text{mates}}. \qquad [1.24b]$$

When R and R_O equal 1, eq. [1.24a] and eq. [1.24b] both reduce to eq. [1.23]. From the more general expression (eq. [1.4]), we see that the sex difference in the opportunity for selection is clearly affected by R_O, the OSR, as Emlen and Oring (1977) argued. When the OSR is less than 1, so that there are more females than males competing for them, then the sex difference in the strength of selection is diminished. When the OSR exceeds 1, so that there are more males than there are available females, then the intensity of selection on males exceeds that on females by more than I_{mates}. However, it is also clear from eq. [1.24], that the OSR *does not* estimate the sex difference in the strength of selection, which is important for the evolution of sex dimorphism by sexual selection. The OSR is *only one* component of the sex difference in strength of selection. Whenever I_{mates} is much larger than I_{females}, then $(R_O - 1)\, I_{\text{females}}$ will be only a small component of the sex difference in selection. On the other hand, when I_{mates} is much smaller than I_{females}, then the OSR will explain much of the sex difference in the strength of selection that results from sexual selection. We will provide an example of the influence of OSR on the sex difference in the opportunity for selection in chapter 5.

The Dimensionality of I_{mates}

In his definition of the opportunity for selection, I, Crow (1958) emphasized that the variance in fitness, divided by the square of the average fitness, is the variance in *relative* fitness. Thus, it measures the maximum change in a populational phenotype that can result from a single episode of selection. Note that I_{mates} equals the variance in mate numbers, V_{mates}, divided by the square of the average number of mates per male, R. This expression is the component of male relative fitness that results from reproductive competition among males. Since both the numerator and denominator of I_{mates} are expressed in units of $(mates)^2$, the opportunity for sexual selection associated with differences in mate numbers between the sexes is *dimensionless* (although "I_{mates}" remains a convenient, specific notation).

Other examples of dimensionless numbers include coefficients of variation, pondural indices, and drag and growth coefficients (Vogel 1988; Charnov and Berrigan 1991). In evolutionary biology, examples include the ratio of gene flow distance to spatial change in selection coefficient (Slatkin 1973, 1987; Kirkpatrick 1996), and the measures of population subdivision, G_{ST} and F_{ST} (Hartl and Clark 1989). Such parameters are extremely useful in cross-taxonomic comparisons because they capture the essence of the process independent of scale. Thus, I_{mates} permits comparisons of the strength of sexual selection within and among taxa. In later chapters, we will show how I_{mates} arises from the microspatial and temporal distributions of females. This is an important point. In our attempt to resolve the Quantitative Paradox of sexual selection, we will link microevolutionary processes to macroevolutionary patterns. Such explicit within- and between-taxonomic comparisons of processes and their outcomes require dimensionless parameters.

Potential Difficulties with I_{mates}

Several authors have criticized the use of I_{mates} as a means for identifying the intensity of sexual selection. Grafen (1987) argued that the study of sexual selection is "historical" (emphasizing taxonomic patterns) rather than "empirical" (emphasizing microevolutionary processes), and thus that quantification of the intensity of sexual selection has no intrinsic value. Grafen (1987, p. 222) noted that, "Darwin (1871) discovered almost everything important now known about sexual selection and did so without measurement." Grafen also reasoned that, because the study of sexual selection has proceeded at a vigorous rate without measures of its intensity, ". . . the desirability of precise mathematical modeling does not imply the desirability of measuring the parameters of any of these models in the field." He further concluded that empirical studies of selection intensities seem unlikely to increase our understanding of its process or its outcomes and "quantification has no intrinsic virtues . . . and can set back the cause of science." This argument, while extreme, is not surprising. It is the same one used by molecular geneticists and cell biologists, when biology departments discuss whether or not statistics and calculus should be required courses for biology majors.

Our response to this perspective is that one can seldom understand nature less by studying it more. While Darwin's mechanisms of sexual selection are clear, so too is the Quantitative Paradox of sexual selection. The discrepancy between microevolutionary theory and historical pattern *requires* quantitative measures of the sex difference in the strength of selection in natural populations to be assessed and resolved. We hope readers may share our view by the end of this book.

The fact that I includes all of the variance in fitness, both selected and random, has disturbed other authors. For example, Sutherland (1985) argued that, since chance alone (i.e., random mating) can generate nonzero values for I ($= I_{\text{mates}}$), this estimator is a poor measure of sexual selection. Indeed, Crow (1958, 1962) addressed this very point and showed that, *when random or chance deaths occur, the effectiveness of selective deaths must be diminished.* By chance, bad things happen to good genes and vice versa. If one eliminates the random variation in mortality and reproduction, one *overestimates* the strength of selection. This is another reason why I_{mates} sets an *upper limit* on the response to sexual selection: not all mating is differential with respect to male characters. By chance, some males obtain more mates than others, just as, by chance, some individuals die before expressing their good (or bad) genes for viability. Mutations with deleterious effects late in life accumulate in populations to a greater degree than deleterious mutations expressed early in life for this very reason: random, early mortality interferes with their expression.

Wade (1987) illustrated this same point in an analysis of laboratory data on the difference in mating success of male *Panorpa* scorpion flies with claspers intact and claspers immobilized (Thornhill 1981). Although males without functional claspers obtained no mates, and some males with intact claspers obtained more than one mate, many other males with intact claspers also did not mate. There was variance in mating success within as well as between the two artificial categories of experimental males. Because the variance in mating success between these two types of males was only a small part of the total variance in mating success, the strength of selection on claspers as a male trait (present or absent) was actually quite small. This was true despite the fact that the difference in average mating success between the two male groups was large and, statistically speaking, clear-cut.

Consider the hypothetical example introduced earlier in this chapter (tables 1.1–1.3). All of the opportunities for selection in table 1.3 or eq. [1.23] will have random or environmental components. They are not unique to I_{mates} nor are they necessarily larger for mate numbers than for viability or offspring numbers. In our hypothetical example, not all individuals with large tails have genes influencing development toward larger tails. Some simply experienced better environments for tail development. As stated above, only the heritable fraction of the differences between selected and nonselected individuals can be transmitted across generations. One thing is certain: if eq. [1.23] is not greater than zero with random variations in mate numbers, it will not become greater when the random component of variation is excluded.

More to the point, since variance in mating success among females is small in most species, even random variation among males in mate numbers will result in sex differences in the opportunity for sexual selection on males (fig 1.13b). Since some males will mate more than once, other males will not mate at all. This statement is identical to Darwin's (1871, p. 332) own definition of sexual selection: "The practice of polygamy leads to the same results as would follow from an actual inequality in the number of the sexes; for if each male secures two or more females, many males will not be able to pair."

Clearly, if R remains constant and harem size H increases, an increasing number of males *must* be excluded from mating as shown by eq. [1.18] and in fig. 1.13. For this reason, I_{mates} will increase and the sex difference in the strength of selection will increase with it.

Downhower et al. (1987) raised four arguments against the use of the measure I to examine selection. Their first criticism is that I is sensitive to the units commonly used to measure fitness variance. Thus, when different units are used in different studies, they are not comparable using I. This criticism is based upon a misunderstanding of how I is used and why it is a dimensionless parameter. The choice of what to count or measure when describing selection in the currency of fitness will certainly vary from organism to organism and often from study to study of the same organism. The conceptual issue is, how do we link different studies in order to obtain an integrated picture of total selection?

Consider a specific example. Suppose that two microevolutionary research programs are investigating the body size evolution in ambystomatid salamanders. One program studies how larval body size affects the development of paedomorphic reproduction and the other investigates how adult body size influences mating success. The former study uses age at first reproduction and clutch size as measures of fitness while the latter uses mate numbers and duration of courtship. Each finds a relationship between body size and fitness and reports the direction of selection on body size, invoking *ceteris paribus* (all else being equal), as though the other study did not exist, a scenario depressingly typical of microevolutionary studies. Neither study can claim to know *the* adaptive significance of body size for several reasons including the following: (1) many of the same genes and developmental processes are involved in the determination of *both* larval and adult body size; (2) different traits and different genes are correlated phenotypically and genetically so their effects (and the effects of selection on them) are not independent of one another; and (3) natural selection operates on total fitness, yet each study has measured only a component of fitness or (as is common) a surrogate thereof. The common assumption of *ceteris paribus* not only sweeps away these concerns for any particular study but also isolates the results of different studies that should be integrated. It gives the evolutionary biologist license to carve nature up into manageable fragments and to describe selection in whatever fitness currency is expedient. Unfortunately, it also impedes the cogent and necessary integration of the separate descriptions of nature. The measure I provides a rigorous method of combining results across studies, even studies that use different fitness currencies, because it is both dimensionless and based on the single common currency of evolutionary theory, namely, the *variance in relative fitness*.

A second criticism raised by Downhower et al. (1987; see also Ruzzante et al. 1996) is that measurements of I are sensitive to differences in average fitness between populations. These authors argue that two populations may have equal fitness variance, but if they differ in average fitness, the values of I calculated for each will differ accordingly. Therefore, variation in average fitness may falsely imply that differences in fitness variance exist between populations. This criticism arises from a lack of understanding of how I is defined and what it measures, and the further confusion of I with analysis of variance. In evolutionary theory, natural selection on a trait results from the correlation between values of that trait (z) and heritable differences in relative fitness ($w[z]$, see above). The effect of natural selection can be quantified explicitly as the covariance between trait value and relative fitness whether expressed as the familiar "breeders' equation," $\Delta Z = h^2 \mathrm{Cov}(z,w[z])$, or as the equally familiar Δp from population genetics When the trait is fitness itself, the *relative* change in mean fitness by natural selection, $\Delta W/W$, equals the variance in relative fitness, V_w (see eq. [1.7] above). Because the denominator of V_w is mean fitness W, differences in mean fitness do change the strength of selection even when the variance in absolute fitness is the same; *by definition*, they have to! If one wants to compare only fitness variances, which do not describe the amount of evolutionary change, then we do not recommend using I, but use of ANOVA instead. Unfortunately, as useful as ANOVA is as an experimental tool, it is not a good comparative measure of the strength of selection for evolutionary genetic studies in the field or laboratory.

A third criticism by Downhowner et al. (1987) states that measurements of I are sensitive to sampling error. Since I is based on the mean and variance in population fitness, this criticism simply restates difficulties encountered with any parameter estimation method based upon sampling. For example, the range is much more sensitive to sample size or sampling effort than is the variance, thereby conferring greater utility on the latter. This difficulty does not weaken the usefulness of our approach for studies of mating systems any more than insufficient sample sizes weaken the usefulness of other parametric statistical procedures, including ANOVA, where estimates of main effects are confounded with interactions in small experiments (Wade 1992). Indeed, Wade (1995) showed that the statistical properties of I_{mates} are the same as those of the negative binomial distribution, a distribution that has "probably been used more frequently than any other contagious distribution" (Sokal and Rohlf 1981, p. 95). This permits us to employ tests of significance when making taxonomic comparisons of different values of I, a feature we consider one of the strengths of our approach. As with most test statistics, increasing sample size increases the power of the test.

This last point addresses the fourth criticism of Downhower et al. (1987) as well. That is, no reference values exist against which a given value of I may be compared. Although several values have been published since 1979 (Wade 1979; Wade and Arnold 1980; Fincke 1986; in Clutton-Brock 1988; Yezerinac et al. 1995; Dinsmore 1985; Rajanikumari et al. 1985; Hed 1984, 1986; Clutton-Brock 1991b; Marzluff and Balda 1992; Souroukis and Cade 1993; Lande et al. 1994; Murphy 1994; Fleming and Gross 1994; Webster et al. 1995; Iribarne 1996; Morgan and Schoen 1997; Coltman et al. 1999; Stanton et al. 2000; Herrera 2000; Ferguson and Fairbairn 2001; Webster et al. 2001; Fairbairn and Wilby 2001), including those calculated by Downhower et al. (1987), we hope that our discussion of I in this book will stimulate its further use for measuring selection in natural populations and thereby provide cross-taxonomic values for the opportunity for selection. In the meantime, the similarity of the theoretical distribution of I to a negative binomial distribution with its well-known statistical properties puts the final criticism of Downhower et al. (1987) to rest.

Chapter Summary

We have seen how the two mechanisms of sexual selection, male-male combat and female choice, proposed originally by Darwin, permit the evolution of sex differences. However, understanding the Darwinian mechanisms of sexual selection does not address the apparent conflict between the macroevolutionary patterns and the microevolutionary process of sexual selection. The macroevolutionary comparison indicates that sexual selection is one of the *fastest and strongest* of the evolutionary forces, capable of producing large phenotypic differences among the males of even closely related taxa.

Our microevolutionary analysis reveals not only that the effects of sexual selection are sex-limited, but also that conflict exists in the direction of selection between the sexes as well as between different life history stages within the male sex. These are the features of a very *slow and weak* evolutionary force.

Our Quantitative Paradox of sexual selection vis-à-vis natural selection is resolved when we take into account the variance in male fitness that results from the variations among males in the numbers of mates. The success of one male in competition for mates necessarily results in the failure of one or more other males (eq. [1.18]). Thus, points are added to the distribution of mate numbers in groups such that, for every point added above the mean, one or more points are added below the mean at zero. A large variance among males in mating success ensures that selection in the male sex will be stronger than opposing viability selection in the female sex and in the male sex at earlier life stages. In subsequent chapters, we investigate how other genetic and ecological factors can enhance or diminish evolution by sexual selection. In particular, we examine the roles of spatial and temporal variation in female receptivity in their effects on I_{mates}.

2

The Ecology of Sexual Selection

We will now develop the concepts introduced in chapter 1 in greater detail, in order to apply them, quantitatively, to the evolution of animal mating systems and to a lesser degree, the mating systems of other sexual organisms. A great deal of research in animal behavior over the last three decades has focused on animal mating systems. Although this work has been very successful in identifying the *mechanisms* by which sexual selection operates within a mating system, it has not been as successful in quantifying the relative *strength* of sexual selection as it varies with mating system. Thus, we do not know whether and to what degree differences in mating system explain variations in the pattern of sex dimorphism, nor do we have a clear understanding of the relative importance of different features of a mating system. In this chapter, we develop a comparative method for measuring the variance in fitness of both males and females. We show how the *sex difference* in fitness variance (the strength of sexual selection) is strongly influenced by the variance in the distribution of male mating success. As we explained in chapter 1, identifying the mechanism of sexual selection is different from quantifying its evolutionary effect. We will demonstrate the comparative utility of our quantitative approach by applying it to examples from natural populations.

The Emlen and Oring Hypothesis

In 1977, Stephen T. Emlen and Lewis W. Oring compiled the published observations of avian and mammalian researchers through the 1970s, and presented an ecological classification of animal mating systems. The mating system classification proposed by Emlen and Oring (1977) was predictive, based on the following logic:

1. Males compete with one another for access to females:
2. Like competition for scarce resources, male reproduction is limited by the spatial and temporal availability of sexually receptive females.
3. The intensity of sexual selection depends on the rarity of receptive females in relation to the abundance of competing males.
4. Sexual selection favors male attributes that permit their bearers to find and monopolize their mates.
5. Ecological constraints on male monopolization attempts lead to a species-specific pattern of male-female associations, called a "mating system."

The underlying cause of taxonomic variation in mating systems, according to this approach, is the interaction between ecological constraints and the process of male-male competition for scarce reproductive resources. Thus, quantifying the intensity of male-male competition is equated with quantifying the strength of sexual selection and the ensuing adaptive process.

In ecology, the intensity of competition is typically quantified as resources per head, that is, as the ratio of the units of available resource divided by the numbers of competing individuals. In mating system studies, therefore, it is reasonable to expect that the intensity of male-male reproductive competition should vary with the relative rarity of reproductive resources, that is, sexually receptive females. Hence, as explained by Emlen and Oring (1977), the intensity of male-male competition for mates can be expressed as the ratio of adult males to adult females. This *operational sex ratio* or OSR (we represent this ratio as R_O; chapter 1) is widely used in studies of mating systems (Emlen and Oring 1977; Borgia 1979; Wickler and Seibt 1981; Wittenberger 1981; Thornhill and Alcock 1983; Bradbury 1985; Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Arnold and Duvall 1994; Parker and Simmons 1996). Many researchers consider the operational sex ratio to be *the* measure that best quantifies the intensity of sexual selection (e.g., Reynolds 1996). Sexual selection and OSR are terms often used interchangeably (e.g., Kvarnemo and Ahnesjö 1996).

In discussing sexual selection, Darwin (1859, 1871), Bateman (1948), Williams (1966), and Trivers (1972) made observations similar to those of Emlen and Oring (1977). However, none proposed that a combination of ecological constraints on male mating behavior and the spatial and temporal availability of female receptivity could be used to classify mating systems. Emlen and Oring (1977) argued convincingly that the ecology of female reproduction determines the degree to which males are successful in reproductively monopolizing females. The ecology of female reproduction depends, in turn, upon the distribution and abundance of crucial resources, which include most aspects of nutrition and nesting. Thus, the distribution of reproductive resources fundamentally determines the intensity of sexual selection and subsequent mating system evolution under the Emlen and Oring (1977) hypothesis.

Emlen and Oring (1977) made specific predictions concerning the kinds of mating systems that would result from different features of female reproductive ecology. For example, they predicted that *polygyny*, a mating system in which individual males may reproduce with more than one female, is likely to evolve when females are spatially clumped and young are not dependent on male care. The authors further partitioned polygynous mating systems into four general forms. Under *resource defense polygyny*, males guard resources crucial to female reproduction and mate with those females aggregating around the guarded resources. In *harem polygyny*, females aggregate first around clumps of resource; then males are attracted to female aggregations and guard females directly. If males themselves are the resources, as in those cases where female mating preferences are strong, additional polygynous mating systems, such as *lekking* or "*hot spot*" *polygyny*, could evolve. In these systems, female mating preferences or historically successful breeding locations are hypothesized to mitigate the influence of resource ecology on mating (Bradbury and Veherenkamp 1977; Thornhill and Alcock 1983; fig. 1.1). In practice, for any of the above reasons, one or a few male "despots" may monopolize large numbers of females. In contrast, in *scramble competition polygyny*, neither females nor the resources important to their reproduction are spatially aggregated. Instead, males are temporally polygynous, encountering, guarding, and mating with individual females as they forage for resources (e.g., McCauley 1981; McCauley and Wade 1978). All systems of polygyny result in the clustering of *reproductive* resources (i.e., receptive females), either spatially or temporally, around mating males. Conversely, when females are dispersed, owing to scarce and/or widely dispersed resources, or when young are dependent on care from both parents, Emlen and Oring (1977) predicted that *monogamy* will evolve. Lastly, when resources and females are so scarce that males must form coalitions to acquire them, or when males are solely responsible for providing care of the young, *polyandry*, a mating system in which individual females may reproduce with more than one male, is expected to evolve (see review in Thornhill and Alcock 1983).

Given a spatial distribution of females, the temporal pattern of female receptivity to mating further modulates the distribution of mate numbers across males. If there is a high degree of synchrony of female receptivity, then a male's ability to monopolize many mates simultaneously may be reduced. Emlen and Oring (1977, p. 216) predicted that extreme female synchrony could limit the opportunity for multiple mating by males, whereas extreme asynchrony would enhance the "environmental potential for polygamy" or EPP. (We consider the effect of the temporal pattern of female receptivity on sexual selection in detail in chapter 3.) The spatial distribution of females is itself determined in a complex way by many factors. For example, conspecific queing may lead to the overaggregration of females or female-female competition may lead to the overdisersion of females, as per Orians' threshold model of female nesting site choice in relation to male territories. In addition, runaway sexual selection can lead to a higher level of clustering of females at resources than is "adaptive" considering only the amount of resource (see below). We do not take up here the important questions of "why" females are spatially aggregated, whether they are "adaptively" or "maladaptively" clustered, or, if overclustered, whether it is owing to conspecific queing or runaway sexual selection. These are questions deserving of further study, and are considered in more detail in later chapters. In this chapter, we will show that our method applies to *any* spatial distribution of females, whatever the proximal or ultimate causes of the particular spatial distribution.

Trivers' (1972) earlier theory of parental investment made somewhat similar predictions but was founded on the widespread occurrence of *anisogamy*, that is, the sex difference in initial parental investment in gametes that exists in most in bisexual species. Trivers (1972) argued that asymmetrical parental investment in gametes is the cause of sexual selection because such asymmetric investment manifests itself as an asymmetry in the numbers of male and female gametes. Thus, reproduction by individuals of the sex investing less (generally the males) becomes limited by the availability of individuals of the sex investing more (generally the females). Because parental investment in gametes requires resources, Trivers' hypothesis is viewed by many as the foundation of the Emlen and Oring model. Trivers' argument also bears some similarity to that of Bateman (1948), who argued that the potential variance in fitness is greater among individuals of the sex producing more numerous but smaller gametes.

Most analyses of animal mating systems since 1977 have been conducted within the Emlen-Oring-Trivers framework, and excellent reviews have been provided by Bradbury and Veherencamp (1977), Borgia (1979), Wickler and Seibt (1981), Wittenberger (1981), Thornhill and Alcock (1983), Bradbury (1985), Ostfeld (1987), Clutton-Brock and Vincent (1991), Ketterson and Nolan (1994), Arnold and Duvall (1994), Parker and Simmons (1996), and Reynolds (1996; see also Verner and Willson 1966). Several parameters have been suggested for quantifying sexual selection under the Emlen-Oring-Trivers hypothesis. However, the OSR as proposed by Emlen and Oring (1977) captures the essential concept of the dependency of sexual selection on competition for reproductive resources. The OSR can be viewed as a "*reproductive competition coefficient*" among mating males because it expresses the number of competing males, N_{males}, per unit of resource, namely, sexually receptive females, N_{females}. The greater the number of mature males relative to the number of receptive females, the greater the OSR, and, correspondingly, the stronger the intensity of male-male competition for mates (Sutherland 1985; Kvarnemo and Ahnesjö 1996).

In a concept similar to the OSR, the sex difference in gametic investment has been quantified as the ratio of maximum potential reproductive rate (PRR) of males to females (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). The greater this ratio, the greater the potential difference in numbers of offspring between a successful male and a successful female. The PRR can also be interpreted as the number of females whose ova could be inseminated by a single male. This measure emphasizes the intersexual difference in maximum offspring numbers rather than the intrasexual intensity of competition or the sex difference in variance of offspring numbers. It is used often in discussions of maternal sex ratio strategy to summarize the potential fitness gain to a female of producing an offspring of one sex instead of the other (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992) and has been extensively used in discussions of sex-role reversed species (Vincent et al. 1994; Ahnesjö 1995; Parker and Simmons 1995; Simmons 1995; Kvarnemo 1996, 1997; Wiklund et al. 1998; Okuda 1999; Kvarnemo and Fosgren 2000; Masonjones and Lewis 2000; Ahnesjö et al. 2001). With multiple mating, the PRR can also be used to express the potential for postcopulatory reproductive competition. The PRR quantifies the maximal sex difference in reproductive fitness. When it is used to explain mating strategies, it is often assumed that every son is a “best” or “maximal” son, which is clearly impossible as we show later.

The breeding sex ratio (BSR) proposed by Arnold and Duvall (1994; Duvall et al. 1995) measures the ratio of *actually* breeding males, N^*_{males}, to breeding females, N^*_{females}, in contrast to the number of *potentially* breeding males, N_{males}, in the OSR, which is always greater than or equal to N^*_{males}. The BSR attempts to measure the *realized* male-male competition for mates, but, by ignoring nonbreeding males, it omits those males whose numbers dramatically increase the variance in male reproductive success (chapters 1 and 11). This convention is also applied when Q, the ratio of males to females qualified to mate, is first calculated, and then the OSR is calculated as $Q\ (\text{PRR}_{\text{males}}/\text{PRR}_{\text{females}}) = \text{OSR}$ (Ahnesjö et al. 2001). As we will show, both of these approaches ignore the fact that most of the variance in male reproductive success exists between mating and nonmating males when sexual selection is strong (see below). Arnold and Duvall (1994) also suggested using a measure from phenotypic selection theory, the sexual selection gradient, as a way of isolating the statistical relationship between male trait values and mating success relative to other components of selection. In artificial selection and selective breeding experiments, the selection gradient provides a standardized measure of the strength of selection, useful for making comparisons across different experiments.

The temporal aspect of male competition for mates, which Emlen and Oring introduced as the synchronicity of female receptivity, was also recognized, but in a very different way, by Parker and Simmons (1996; see also Kvarnemo and Ahnesjö 1996; Ahnesjö et al. 2001; Wade 1979). These authors noted that, for males, display time costs energy. Thus, they added a temporal element of energy expenditure to male competition for mates. They proposed measuring the time budgets of males and females and emphasized the sex difference in the fraction of time spent on reproductive activity as critical to estimates of the intensity of sexual selection. All of these measures address aspects of the intensity of intra- or intersexual competition and its temporal modulation by the availability of females or by competing activities of males with limited time budgets. However, we will show below that, with the exception of Arnold and Duvall (1994), none of these approaches directly measures the sex difference in the strength of selection, although some, like the OSR, are often correlated with it.

In this chapter, we introduce a method for quantifying the spatial distribution of sexually receptive females and for making comparisons among species in the sex difference in the strength of selection. As mentioned above, we postpone discussion of the effect of variations in the temporal distribution of sexually receptive females until chapter 3. Our goals are to provide a statistical framework by which the predictions of the Emlen-Oring-Trivers hypothesis may be tested and extended to include all sexual species. We will focus our discussion mainly on animals, because sexual selection operates more strongly in animals than in most other sexual taxa (chapter 4). Thus, although our approach has broad application, we think animals provide the clearest examples of how our method may be used. Our framework yields many specific predictions, and, as we show in later chapters, it provides a quantitative way of classifying mating systems. Also, because we make extensive use of I_{mates}, the opportunity for sexual selection, as developed in chapter 1, our approach permits comparative analyses of mating systems that are not possible using either the measures suggested in the Emlen-Oring-Trivers hypotheses, or their recent methodological extensions.

Recall from chapter 1 that I_{mates} measures the strength of selection arising from the variance among males in mate numbers. Under assumptions explained in chapter 1, the sex difference in the opportunity for selection often arises entirely from the differences in mate numbers among males. That is, I_{mates} often equals the sex difference in the strength of selection. We now extend this concept to investigate how the spatial and temporal distribution of sexually receptive females affects I_{mates} and the other aspects of the sex difference in opportunity for selection. We illustrate the connection of our approach with concepts central to the thesis of Emlen and Oring (1977) and make explicit the role of the OSR in the sex difference in strength of selection. We also show that Lloyd's (1967) ecological measure of density-dependent competition, **mean crowding**, is a useful way to characterize the spatial distribution of receptive females because it is directly related to I_{mates}. Mean crowding quantifies the contagious clustering of females and, hence, reproduction, around males. In chapter 3, we extend this characterization to include the temporal distribution of receptive females.

Lloyd (1967) developed the concept of mean crowding, now widely used in ecological studies of natural populations. Estimates of mean crowding quantify how individuals experience the effects of crowding and competition when a population's membership is spatially distributed into clusters around patchily distributed resources. By incorporating mean crowding into the description of male-male competition for mates, our method permits us to make specific predictions about the activities males may engage in to monopolize clustered females. We can ask of any male behavior: Does it enhance or diminish the mean crowding of male reproduction? Since our method also distinguishes the mechanisms by which females may aggregate, the separate effects of male and female behaviors on sexual selection can also be quantified.

We will explicitly incorporate spatial effects of predation and viability selection, as well as female tendencies to copy the mate choices of other females, into our measurement of the spatial and temporal aggregation of female receptivity. In subsequent chapters, we will combine the spatial distribution of females not only with the temporal distribution of female sexual receptivity, but also with the tendency toward multiple mating, and examine the effects of semelparous and iteroparous female life histories. We show how our measure is affected by variations in male tendencies to guard females, to seek multiple mates, to employ alternative mating strategies, and to engage in parental care. Once we have established the effects on sexual selection of these male and female traits separately, we will then examine when and how conflict between the sexes arises and is resolved by selection. Lastly, since our method generates a dimensionless measure of the overall intensity of sexual selection, we show how it provides a basis for comparative analyses of mating system evolution.

The Mean Crowding of Sexually Receptive Females in Space

Lloyd (1967) developed a statistical framework for measuring the microspatial distribution of organisms in natural populations in relation to the ecological effects of crowding and competition. He proposed a measure m^* that identified the number of other individuals the average individual experiences as competitors. He called this measure "*mean crowding*." Lloyd noted that whenever individuals are clustered spatially and the clusters differ in size, individuals in the largest clusters experience *greater* competition than individuals in smaller clusters. Because there are more individuals in the larger clusters, by definition, the average *experience* of competition, m^*, exceeds that expected from the average density per cluster, m. Thus, Lloyd argued, average patch density is an inadequate measure of the way in which individuals experience competition and other density-dependent processes in ecology. On the other hand, if individuals are more uniformly distributed in space than random, the experienced competition may be *less* than that expected by the average density. Indeed, overdispersion is one manifestation of an ecological response to resource competition. Mean crowding captures both of these effects of the variance in size of the clusters on the intensity of competition.

We extend Lloyd's concept of mean crowding to sexual selection. We argue that, whenever females are clustered or clumped across a patchily distributed resource, OSR, EPP, PRR, BSR, Q, or other commonly used measures of reproductive competition, do not adequately reflect the variable ex-