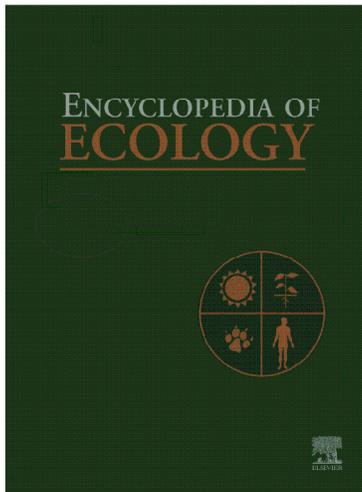


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See also: Age-Class Models; Biological Control Models; Competition and Coexistence in Model Populations; Competition and Competition Models; Fisheries Management; Fundamental Laws in Ecology; Limits to Growth; Metapopulation Models; Prey–Predator Models; r-Strategist/K-Strategists.

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## Mating Systems

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### Introduction

Measuring the Sex Difference in Fitness Variance  
The Mean and Variance in Mate Numbers

### The Opportunity for Sexual Selection

Genetic Correlations between the Sexes  
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## Introduction

Most humans have the sense that males and females are different. Much has been made of battles between the sexes, of sexual dialectics, even of the possibility that men and women have different planets of origin. But we are hardly unique; any observant naturalist can list several species, in addition to our own, in which male–female differences are clear. Many of us can also produce an even longer list of species in which external sex differences are inscrutable. Songbirds, for example, often lack external sexual differentiation. A large number of marine species, such as fucoid brown algae, sea urchins, polychaete worms, and red snappers, also have separate sexes that are nearly indistinct. Sexual differences in land plants too are often obscure, although botanists may assert that this is because both sexes often exist within each individual. But why should monoecy cause monomorphism? And if it does, why should sex in both cottonwoods and junipers be apparent only upon close examination, whereas sex among marijuana plants, even for aficionados, is simple to diagnose? Invertebrate zoologists might now chime in with examples of physical uniformity among hermaphroditic barnacles, flatworms, and freshwater snails, as well as

among gonochoristic comb jellies, kinorhynchs, and veneroid clams. What explanation can possibly exist for extreme sexual differentiation in some species, and for virtual monomorphism among others, especially those lacking gender?

The answer to this question is the mating system. That is, the circumstances in which reproduction occurs within individual species. It is here that sexual differences arise – or do not. In the current literature, mating systems are described in two distinct ways, and each description has different implications for how sexual differences may or may not appear. The first description of mating systems, one that is familiar to botanists and coevolutionary biologists, emphasizes the genetic relationships that exist between mating males and females. Random mating, positive assortative mating (inbreeding), and negative assortative mating (outbreeding), all are examples of mating systems described in terms of the genetic relationships that may arise among, or are imposed upon, breeding pairs. Because certain heritable traits will tend to co-vary between the sexes within each breeding scheme, genetic correlations may arise that lead to, or prevent, the appearance of sex-specific phenotypes. A second description of mating systems, familiar to behavioral ecologists,

considers mating systems in terms of the numbers of mates per male or per female. For example, monogyny and polygyny are descriptions of mate numbers per male, whereas monandry and polyandry are descriptions of mate numbers per female. Monogamy, polygamy, polygynandry, and polyandrogyny, each describe male and female mate numbers in relative terms (Table 1). These relationships are fundamental to sex differences in fitness variance and thus to the strength of sexual selection – or to its absence as an evolutionary force.

When these two schemes for describing mating systems are combined, genetic covariances that may arise between male and female mating phenotypes, because of the circumstances in which mate number may vary among individuals, can be incorporated into discussions of mating system evolution. Such considerations provide simple explanations, that is, explanations that do not imply wilful intent on the part of the participants, for interspecific differences in promiscuity or mate guarding, for tendencies to aggregate or to release gametes synchronously, and for apparent coevolutionary arms races involving genitalic morphology or between prostatic and uterine secretions. This combined description of mating systems identifies the nature, as well as the rates, of possible runaway processes that may arise when

particular associations between mating individuals cause male and female traits to co-vary. Such considerations explain a larger range of the sexual dimorphism that is observed, within and among species, than descriptions of mate number alone.

However, two other issues have led to controversy for the study of animal mating systems: (1) the source of sexual selection and (2) the intensity of sexual selection. These issues lie at the foundations of mating system research because the emphasis taken to explore them determines (1) the processes that are presumed to underlie sexual selection, (2) the procedures that are undertaken to observe these processes, and (3) the variables that are measured to test specific hypotheses regarding mating system evolution.

Until recently, the analysis of mating systems, particularly for animals, has emphasized sex differences in parental investment as the source of sexual selection. According to this view, female reproduction is limited by the availability of resources required for energetic investment in ova and young. Because resource abundance may vary in space and time, male reproduction is presumed to be limited, in turn, by the spatial distribution of materials required by females, and by the temporal distribution of sexually receptive females themselves. Stated differently, males are expected to compete for females because male reproduction is limited by the availability of parental care that only females can provide. Parental investment theory (PIT) thus holds that the intensity of male–male competition reveals the intensity of sexual selection.

As a means for determining how female spatiotemporal distributions may influence this selection intensity, two measures have been defined: the operational sex ratio (OSR) and the environmental potential for polygamy (EPP). The OSR was originally defined as the ratio of potentially receptive males to receptive females at any time. The simplest quantitative description of OSR in these terms can be expressed as  $N_{\delta}/N_{\text{f}} = R_o$ , where  $N_{\delta}$  and  $N_{\text{f}}$  indicate the total number of males and females in the population, respectively. However, many researchers have focused instead on instantaneous measures of OSR that include only the individuals who are receptive at any particular time. With this emphasis, when  $OSR > 1$ , females are numerically rare, and male competition for mates can appear to be intense, although this assumption depends on the degree to which male mating success is consistent among males throughout the breeding season. When  $OSR < 1$ , females are numerically abundant, and male competition for mates can appear to have relaxed; but again, depending on the cause of the surplus in females and how males respond to it, such conditions may still allow certain males to contribute disproportionately to the next generation.

**Table 1** A classification of mating systems based on male and female mate numbers

Mating system	Definition	Variance in mate number	
		Females	Males
Monogamy	Each sex mates once	0	0
Polygyny	Females mate once; male mate numbers vary	0	++++
Polygynandry	Both sexes have variable mate numbers; mate numbers vary more among males than among females	+	+++
Polygamy	Both sexes have variable mate numbers; mate numbers are equally variable within each sex	++	++
Polyandrogyny	Both sexes have variable mate numbers; mate numbers vary more among females than among males	+++	+
Polyandry	Males mate once; female mate numbers vary	++++	0

The EPP identifies the degree to which social and ecological conditions allow males to monopolize females. However, standardized methods for quantifying female distributions, or the scale on which EPP can be consistently measured, have never been clearly defined. As a result, while serving as a conceptual surrogate for the intensity of sexual selection, the uncertain relationship between EPP and selection intensity itself, within as well as among species, makes the practical use of this measure imprecise.

Researchers emphasizing PIT have encountered further difficulties in putting its assumptions to rigorous empirical tests. Despite PIT predictions, a sex difference in relative parental investment has proven extremely difficult to compare within and among species. Not only are the amounts of energy, cost, and risk associated with relative parental investment difficult to quantify, but the correlation between sex differences in parental investment and sexual dimorphism itself is often poor, particularly in species with reversed sex roles. Measures of sexual selection intensity based on PIT, such as comparisons of potential reproductive rates among males and females, require laboratory conditions that are rarely encountered in nature. Other PIT estimates, which emphasize the number of individuals qualified to mate, require assumptions about who is breeding and who is not, that may underestimate the actual variance in mating success within the population. Like other research paradigms grounded in optimality theory, PIT also has an unfortunate tendency to emphasize adaptive outcomes. Thus, researchers may find themselves first identifying traits they consider likely to evolve due to sex differences in parental investment or in expected fitness returns, and then searching in earnest for evidence of adaptations that are consistent with their initial predictions. As creationists, astrologists, and politicians have shown, research methods aimed at hypothesis confirmation tend to be less rigorous than those aimed at hypothesis falsification.

Below, an approach for measuring the source and intensity of sexual selection that provides such empirical rigor is described. This framework emphasizes measurement of the actual selective forces responsible for shaping male–female differences instead of *ad hoc* proxies for sex differences in parental investment. Using data commonly available from ecology, life history, and behavioral analyses for sexual species, the author shows how the magnitude of the sex difference in fitness variance, estimated by measuring male and female offspring numbers, can be used to classify the mating systems of sexual species. The author also shows how the sex difference in the opportunity for selection can be influenced by runaway processes caused by genetic correlations. This approach provides an explicitly quantitative and easily interpreted means for classifying mating systems and for predicting sexual differences in adult phenotype.

## Measuring the Sex Difference in Fitness Variance

Most research on sexual selection and its effects on mating systems has focused either on the context in which sexual selection occurs (i.e., via male combat or female choice), or on the evolutionary outcome of sexual selection (i.e., on descriptions of sexual dimorphism or mating behavior). This research has led to fascinating results; it is the same approach used by Darwin himself, but unfortunately, these results do not consider either the process or the extent to which sexual selection may achieve its evolutionary effects. To understand whether and to what degree the sexes may become distinct within a species, and to understand if sexual selection could be responsible for such divergence among related species, it is necessary to measure the fitness variance for males and females within as well as among species. This method illustrates when and why sexual selection can be strong enough to overwhelm the effects of natural selection and, therefore, how it can produce the sex-specific phenotypes researchers find so compelling.

Consider a hypothetical population, say of albatrosses or penguins, consisting of 20 individuals and a sex ratio equal to 1. If, in a given breeding season, a single ovum from each of the 10 females in the population is fertilized by a different male, the total number of offspring,  $N_{\text{total}}$ , equals  $(1 \text{ ovum}) \times (10 \text{ females}) = 10$ . Because each mating pair produces 1 offspring, the total offspring produced by all females,  $N_{O\text{♀}}$ , equal the total offspring produced by all males,  $N_{O\text{♂}} = 10$ . Because there are 10 females and 10 males in our population, the average offspring per female,  $O_{\text{♀}}$ , equal  $N_{\text{total}}/N_{\text{♀}} = 1$ , which equals the average offspring per male,  $O_{\text{♂}}$ , evaluated similarly as  $N_{\text{total}}/N_{\text{♂}} = 1$ . Also, because each individual in the population produces the same number of offspring (=1), no variance in offspring numbers can exist for either sex. Thus, if  $V_{O\text{♀}}$  and  $V_{O\text{♂}}$  equal the variance in offspring numbers among females and among males, respectively,  $V_{O\text{♀}} = V_{O\text{♂}} = 0$ . This example shows that, regardless of whether the number of fertilized ova each female produces is 1, or  $10^6$ , when each female is mated by a single male and the sex ratio equals 1, barring sex differences in juvenile viability, there can be no sex difference in the variance in fitness between the sexes.

This example goes a long way toward explaining why wind-pollinated plants, marine species with external fertilization, and even hermaphroditic organisms, all tend to show little sexual dimorphism. In each of these cases, population sex ratios equal to or are nearly 1, and pollen or sperm are either so widespread or so restricted in their distribution that individual males and individual females both have similar probabilities of reproduction and tend to contribute approximately equally to the next

generation. In the case of hermaphrodites, both sexes are represented in each individual, thus reproduction by one sex means reproduction by the other, and unless some individuals emphasize one sex or the other sex (as occurs in some marine flatworms), the population-wide variance in fitness through male and female functions is approximately equivalent. When such conditions apply, neither sex is likely to become distinct from the other, except as is specifically required for the production of ova or sperm.

Now consider a case in which 1 of the 10 males secures 2 mates instead of just 1. The total offspring produced by our population,  $N_{\text{total}} = 10$ , remains unchanged. Similarly, because  $N_{\delta} = N_{\varphi} = 10$ , the average offspring per male,  $O_{\delta} = N_{\text{total}}/N_{\delta} = 1$ , equal the average offspring per female,  $O_{\varphi} = N_{\text{total}}/N_{\varphi} = 1$ . Because each female still secures 1 mate with whom she produces a single brood, the variance in offspring numbers for females,  $V_{O_{\varphi}} = 0$ . However, because 1 male has 2 mates, 1 male must be excluded from mating. When this happens, the variance in offspring numbers among males,  $V_{O_{\delta}}$ , must increase.

If paternity data were available for our population, we could estimate the magnitude of the increase in  $V_{O_{\delta}}$  simply by calculating the statistical variance in offspring numbers for males. When such data are available, this is indeed the simplest approach. However, as is more often the case, when paternity data are lacking, an equally accurate and in fact more informative approach involves partitioning the variance in offspring numbers within and among the classes of mating and nonmating individuals. In the example above, only males were variable in their numbers of mates, but in many species, both sexes may vary in mate numbers, and in sex-role-reversed species, including certain sea spiders, giant water bugs, and pipefish, females are consistently more variable in mate numbers than males. Although they are seldom used for this purpose, the data necessary to calculate the mean and variance in mate numbers for males, and the mean and variance in offspring numbers for females, are often available in standard life history analyses. This quantitative approach allows us to measure the fitness variance within each sex, which is proportional to the intensity of selection. The sex difference in selection intensity, in turn, estimates the degree to which the sexes will diverge in phenotype.

### The Mean and Variance in Mate Numbers

We begin by identifying the classes of mating males and their population frequencies. Here, we represent the proportion of the male population in each mating class as  $p_j$  where  $j$  represents the number of females in the  $j$ th mating class of males. There are three such classes: males who do not mate,  $p_0 (= 1/10 \text{ males} = 0.1)$ , males who mate once,  $p_1 (= 8/10 \text{ males} = 0.8)$ , and males who mate twice,

$p_2 (= 1/10 \text{ males} = 0.1)$ . The sum of all male mating classes,  $\sum p_j = (0.1 + 0.8 + 0.1) = 1$ . Next, we use these values to identify the average offspring produced by males in each of the  $j$ th mating classes,  $O_{\delta j}$ , as well as the average offspring produced by all males across all mating classes,  $O_{\delta}$ . The average offspring that males in each mating class produce,  $O_{\delta j}$ , equal the average offspring per female,  $O_{\varphi}$ , multiplied by the number of mates,  $j$ , that males in each  $j$ th mating class obtain, or  $O_{\delta j} = j(O_{\varphi})$ .

Clearly, the average number of offspring produced by males who do not mate,  $O_{\delta 0}$ , equals  $(0)(1) = 0$ . The average number of offspring for males who mate once,  $O_{\delta 1}$ , equals  $(1)(1) = 1$ , and for males who mate twice,  $O_{\delta 2}$  equals  $(2)(1) = 2$ . The average number of offspring produced by all males, across all mating classes,  $O_{\delta}$ , is equal to the number of offspring produced by the average female,  $O_{\varphi}$ , multiplied by the number of females mated by males in each mating class,  $j (= jO_{\varphi})$ ; then, each quantity is multiplied by the fraction of the males belonging to that  $j$ th mating class,  $p_j$ , and summed over all  $j$  mating classes, so that

$$O_{\delta} = \sum p_j (jO_{\varphi}) \quad [1]$$

Using the values in our example above, we can easily see that  $O_{\delta} = O_{\varphi} = 1$ . Thus, although females are distributed unevenly among the 10 males, relative to females, as well as to the initial case in which all 10 males have equal mate numbers, the average number of offspring produced by all males in this example again equals 1.

The distribution of females across all classes of mating males is equal to the population sex ratio, which we can call  $R$ . This value can be calculated as the number of females mated by males in each mating class,  $j$ , multiplied by the fraction of the males in each mating class,  $p_j$ , and summed over all classes of males, or,  $R = \sum j p_j = 1$ . Because the distribution of all females with all males equals the average number of mates per male,  $R$  also equals  $N_{\varphi}/N_{\delta} (= 1)$ . That is,  $R$  is the reciprocal of OSR ( $= N_{\delta}/N_{\varphi}$ ). But whereas OSR measures the apparent intensity of male–male competition,  $R$  measures a slightly more useful quantity for estimating how selection works;  $R$  measures the population-wide average in the number of mates per male (in sex-role-reversed species,  $1/R = R_O$  measures the analogous quantity). By substitution, we can see that the average offspring per male,  $O_{\delta}$ , equals the average mates per male,  $R$ , multiplied by the average offspring per female,  $O_{\varphi}$ , or  $O_{\delta} = R O_{\varphi} = 1$ . Furthermore, while the distribution of females is now uneven among males, the average mates per male,  $R$ , the average offspring per female,  $O_{\varphi}$ , and the average offspring per male,  $O_{\delta}$ , all remain unchanged relative to our initial example.

We can now express the total variance in offspring numbers for males,  $V_{O\delta}$ , in terms of the average number of mates per male and the average number of offspring per female. As in a standard analysis of variance (ANOVA) problem, the total variance in male fitness can be partitioned into the sum of two components: (1) the average variance in offspring numbers for males within the classes of males who sire offspring, and (2) the variance in the average number of offspring sired by males among these same categories.

The first component of variance in male offspring numbers is calculated in three steps. First, for each mating class of males, the variance in female offspring numbers,  $V_{O\varphi}$ , is multiplied by the number of mates obtained by males in each  $j$ th mating class ( $=jV_{O\varphi}$ ). Next, this product is multiplied by the proportion of males in the population,  $p_j$ , that belong to each  $j$ th mating class ( $=p_j(jV_{O\varphi})$ ). Finally, these products are summed over all  $j$  mating classes. Thus, the variance in offspring numbers within the classes of mating males equals

$$V_{O\delta(\text{within})} = \sum p_j(jV_{O\varphi}) \quad [2]$$

In this example, because all females produce exactly 1 offspring, there is no variance in offspring numbers among females ( $V_{O\varphi} = 0$ ), and, consequently, the variance in offspring numbers within the classes of mating males is also zero ( $V_{O\delta(\text{within})} = 0$ ). We will return to this point below.

The second component of variance in male offspring numbers equals the variance in the average number of offspring sired by males among these same categories. This quantity is calculated in four steps. First, for each  $j$ th mating class of males, we calculate the difference between the average number of offspring per male,  $O_\delta$ , and the average number of offspring produced by that mating class,  $O_{\delta j}$  ( $= [O_\delta - O_{\delta j}]$ ). Second, we square each difference ( $= [O_\delta - O_{\delta j}]^2$ ). Third, we multiply each squared difference by the fraction of males belonging to each mating class,  $p_j$  ( $= p_j [O_\delta - O_{\delta j}]^2$ ), and fourth, we sum across all classes to obtain

$$V_{O\delta(\text{among})} = \sum p_j(O_\delta - O_{\delta j})^2 \quad [3]$$

Substituting in the values from above, we have  $V_{O\delta(\text{among})} = 0.2$ .

The total variance in offspring numbers among males is the sum of the within and among male components in offspring numbers, or

$$V_{O\delta} = \sum p_j(jV_{O\varphi}) + \sum p_j(O_\delta - O_{\delta j})^2 \quad [4]$$

Because there is no variance in offspring numbers for females,  $V_{O\varphi} = 0$ , the first term in eqn [4] drops out. Thus,  $V_{O\delta(\text{among})} = V_{O\delta}$ , and we can easily see that the variance in fitness among males goes from 0 to 0.2 when a single male

mates with 2 females instead of 1. Note too that the increase in fitness variance comes entirely from the among-male component of total fitness variance. Now, if 1 male mates with all 10 of the females, the mean and variance in offspring numbers for females remains unchanged ( $O_\varphi = 1$ ;  $V_{O\varphi} = 0$ ), and there is no change in either the sex ratio,  $R = 1$ , or the average number of offspring per male,  $O_\delta = 1$ . But, because 1 male mates 10 times, 9 males do not mate at all. Thus,  $p_{\delta 0} = 9/10 = 0.9$ ,  $p_{\delta 1} - p_{\delta 9} = 0$ , and  $p_{\delta 10} = 1/10 = 0.1$ . When these values are substituted in eqn [4], we see that  $V_{O\delta}$  now increases 45-fold, to 9.

This exercise shows three important relationships. First, when the sex ratio equals 1, both sexes must have equal, average fitnesses. This is the reason why in most sexual populations, the sex ratio remains at 1. Deviations in sex ratio cause the average fitness of individuals of the majority sex to decrease relative to the average fitness of the minority sex, a condition that favors population-wide production of individuals belonging to the minority sex. Secondly, when some individuals are excluded from mating, the variance in offspring numbers within that sex will increase. This is the source of sexual selection. Exclusion of some individuals from mating means that the traits of the individuals who do mate will be represented disproportionately in the next generation. Third, if the fraction of individuals excluded from mating is larger in one sex than it is in the other, a sex difference in the variance in offspring numbers will appear. Because fitness variance is proportional to selection intensity, the magnitude of this sex difference in fitness variance determines the actual intensity of sexual selection. The larger the sex difference in fitness is, the more the sexes will diverge in phenotype.

### The Opportunity for Sexual Selection

The above examples consider the absolute mean and variance in fitness for males and females, but selection is a relative process, and to account for this fact, certain adjustments are necessary. When the variance in absolute fitness,  $V_W$ , is divided by the squared average fitness,  $W^2$ , we obtain  $V_W/W^2$ , a quantity known as the variance in relative fitness,  $V_w$ , or as  $I$ , the opportunity for selection. The opportunity for selection provides a dimensionless, empirical estimate of selection's maximum strength that is comparable within and among species. Selection intensity can also be measured as the slope of the line that describes the correlation between phenotype and fitness within a population. However, to plot this relationship, it is necessary either to identify the specific trait that is under selection, or to vary the trait of presumed importance experimentally to generate the regression. Such considerations are not necessary for estimates of  $I$ , whose value places an upper limit on the change in average population fitness due to selection, regardless of its source, as well as

on the change in the standardized average of every other trait. In most cases,  $I$  can be calculated directly from field records of individuals who produce offspring and those who do not. When paternity can be assured,  $I$  can be calculated from estimates of mating success alone.

This approach is especially useful for understanding the strength of selection within each sex. Here, the value of  $I$  is expressed as the ratio of the variance in offspring numbers,  $V_{O\delta}$ , to the squared average in offspring numbers,  $O^2$ , among the members of each sex. Thus,  $I_\delta = V_{O\delta}/O_\delta^2$  and  $I_\phi = V_{O\phi}/O_\phi^2$ . Because each offspring has a mother and a father, the opportunity for selection on males,  $I_\delta$ , and the opportunity for selection on females,  $I_\phi$ , are linked through the sex ratio and mean fitness, which must be equal for both sexes. However, the sex difference in the variance in relative fitness,  $I_\delta - I_\phi = \Delta I$  may be positive, negative, or zero. Its value determines whether and to what degree the sexes will diverge in character because fitness variance is proportional to selection intensity.

How can we express these relationships for a natural population? Rewriting eqn [4], substituting values from eqns [2] and [3] and rearranging terms, we have

$$V_{O\delta} = RV_{O\phi} + O_\phi^2 V_{\text{mates}} \quad [5]$$

When  $R=1$ , eqn [5] shows that the variance in fitness for males,  $V_{O\delta}$ , equals the variance in fitness for females,  $V_{O\phi}$ , plus the quantity,  $O_\phi^2 V_{\text{mates}}$ . This latter term equals the average female fitness squared,  $O_\phi^2$ , multiplied by the variance in mate numbers among males,  $V_{\text{mates}}$  ( $=\sum p_j(R-j)^2$ ). For the above example,  $O_\phi^2 V_{\text{mates}} = 9$ . This shows that the sex difference in fitness variance is due to the fitness effects of a sex difference in the variance in mate numbers,  $V_{\text{mates}}$ . In this case, variance in mate numbers exists among males, but not among females. Now recall that  $I = V_W/W^2$ . We can obtain an analogous expression for the variance in relative fitness for males in terms of offspring numbers by dividing eqn [5] by  $[RO_\phi]^2$ , that is, by the squared average offspring number for males.

When we do this, we obtain

$$I_\delta = (1/R)(I_\phi) + I_{\text{mates}} \quad [6]$$

Or,  $I_\delta = (R_O)(I_\phi) + I_{\text{mates}}$ , because  $R$  equals  $1/\text{OSR}$  ( $=1/R_O$ ). Thus, the opportunity for selection on males,  $I_\delta$ , equals the opportunity for selection on females, adjusted by the sex ratio,  $(1/R)(I_\phi)$ , plus the opportunity for selection arising from differences in mate numbers among males,  $I_{\text{mates}}$ . This expression, like eqn [5], shows the relationship between male and female fitness. However, because this relationship is now standardized by the square of mean

fitness, it provides estimates of relative fitness, that is, of selection opportunities for each sex.

Contrary to PIT, which considers male-biased OSRs and sexual selection as equivalent, these expressions show that the sex ratio is only part of the total opportunity for selection. When the sex ratio equals 1 ( $R=1/R_O=1$ ), subtracting  $I_\phi$  from both sides of eqn [6] yields  $I_\delta - I_\phi = I_{\text{mates}}$ , demonstrating that the sex difference in the opportunity for selection, that is, the opportunity for sexual selection, is indeed due to differences in mate numbers between the sexes. It also shows, paradoxically from a PIT perspective, that the effects of a biased OSR ( $=R_O=1/R$ ) are strongest when  $I_{\text{mates}}=0$ , that is, when sexual selection due to differences in mate numbers is weak.

Inserting the values from our example into this latter equation, we see that when males and females have equal mate numbers,  $I_{\text{mates}}=0$ . When males vary in mate numbers,  $I_\phi$  still equals 0, so all of the opportunity for selection on males is due to sexual selection or,  $I_\delta = I_{\text{mates}}$ . If  $V_{O\phi}$  becomes nonzero, either because females vary in their mate numbers, or because females vary in their offspring numbers, or for both reasons,  $I_\phi$  will increase and  $I_{\text{mates}}$  will be eroded to a degree determined by the relative magnitudes of  $I_\delta$  and  $I_\phi$ . If  $I_\phi > I_\delta$ , the sex roles will reverse because sexual selection acts on females. However, erosion of  $I_{\text{mates}}$  may become negligible if the variance in mate numbers among individuals in one sex becomes large and in the other sex remains small. When this occurs, sexual selection on one sex can overwhelm the effects of natural selection acting on the other sex, leading to apparent cases of sexual exploitation. But such situations may not last for long. Mating systems with strong sexual selection tend to be invaded by alternative mating strategies that reduce the variance in mate numbers within the sex in which it is large. The important empirical points are: (1)  $I_{\text{mates}}$  appears to explain much about why sex differences exist; and (2)  $I_{\text{mates}}$  can be estimated for any population in which the mean and variance in offspring numbers among females and the mean and variance in mate numbers among males are known.

## Genetic Correlations between the Sexes

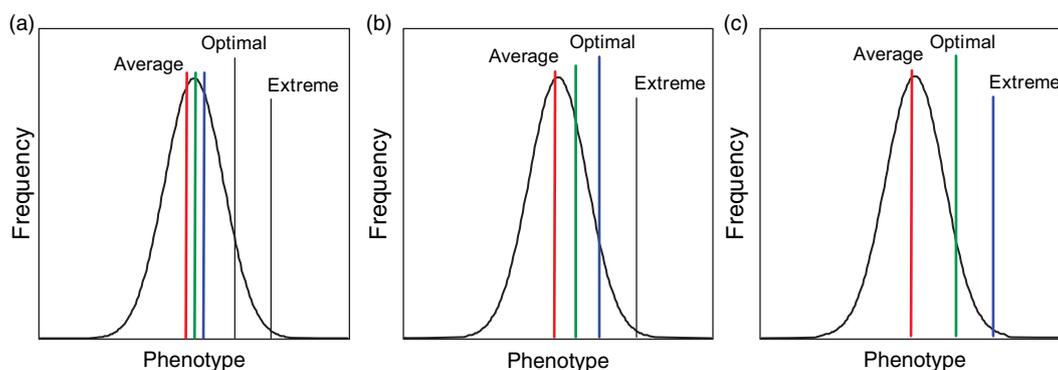
When particular males mate with particular females within a population, the traits within each sex that make these pairings distinctive are likely to become genetically associated. The best-known example of this phenomenon was proposed by R. A. Fisher in 1930, who argued that a self-accelerating evolutionary process known as 'runaway' selection could lead to extreme male and female phenotypes. Fisher noted that when females tend to vary in the strength of their mate preferences, that is, when some females are 'choosier' than others, and when choosy

females prefer to mate with males possessing extreme phenotypes, such males will gain disproportionate fitness relative to other males in the population. If male and female traits are heritable, the greater mating success of extreme males leads to an increase in the frequency of extreme male traits, as well as a corresponding increase in the frequency of females with preferences for such males, among the progeny of choosy females. With regard to male traits and female choosiness, mating in such cases is assortative rather than random. Thus, genes for extremes in male and female traits are brought together simply by the act of mating, and they occur in combinations that, directly or indirectly, enhance the fitness of individuals within each sex. Such conditions, Fisher claimed, will cause extremes in male traits and in female preferences for such traits to increase over evolutionary time.

This process is likely to operate for other male and female traits as well. A tendency for receptive females to aggregate, say at food or near shelter, could favor the reproduction of males who are attracted to such female aggregations. A tendency for females to resist matings with just any male could favor reproduction by males who are most persistent in their attempts to mate. A tendency for males to defend progeny from predators could favor the reproduction of females who leave offspring with such males, and a tendency for females to leave offspring with such males could increase mating opportunities for such females, which in turn could favor males who provide more parental care. If female tendencies to prefer particular males are heritable, a genetic correlation between the male and female traits that lead to particular matings will arise among the progeny of these pairs, and as variance in mate number becomes greater due to nonrandom mating by females, increases in the frequencies of particular male phenotypes

and particular female preferences, as well as increases in the strength of the genetic association between these male and female characteristics, will cause further increases in fitness variance for each sex. The rate of evolution accelerates too because direct selection on male traits causes an indirect response to selection on genetically correlated female traits and vice versa.

But how do such associations get started? Why might females develop a preference for extreme male phenotypes in the first place? One hypothesis suggests that females prefer traits in males that stimulate particular sensory channels. Positive responses to certain visual or auditory cues in their environment may have enhanced food capture or shelter location by females. If such tendencies enhance female fitness, they are likely to become widespread. Males who fortuitously possess traits that resemble these attractive stimuli are likely to encounter females more often, and because they are more readily available than less conspicuous males, a runaway process can ensue between attractive males and attracted females. Another hypothesis suggests that females prefer males possessing traits that enhance the survival of their offspring. That is, females prefer to mate with males who possess so-called good genes. Most good genes scenarios assume that traits associated with fitness are influenced by multiple genetic factors and thus are normally distributed (Figure 1). For many such traits (e.g., birthweight, body height, disease resistance), the average trait value for the population is also somewhat less than the trait value that provides optimum fitness. Individuals in such populations also may exhibit extreme values of these traits, although these individuals often have fitness less than the optimum. These relationships confirm that good genes can exist in this population. The question is, what sort of mate should the average female choose?



**Figure 1** The distribution of a quantitative trait in a hypothetical population in which females have the option of selecting among males who vary in their expression of this trait; (a) average females selecting males of average phenotype are likely to produce average offspring; (b) average females selecting males of optimal phenotype will produce suboptimal offspring; (c) only average females choosing males with extreme phenotypes will produce offspring of optimal phenotypes, a condition likely to cause runaway selection favoring extreme male phenotypes and female preference for extreme males; red line: female parental phenotype; blue line: male parental phenotype; green line: offspring phenotype. Redrawn from Shuster SM and Wade MJ (2003) *Mating Systems and Alternative Mating Strategies*. Princeton, NJ: Princeton University Press, Figure 7.1.

If an average female (red line, **Figure 1a**) chooses a mate with the average trait value (blue line, **Figure 1a**), she will produce average offspring (green line, **Figure 1a**). If she chooses a male with the optimal trait value (blue line, **Figure 1b**), she will produce offspring with phenotypes above the trait average, but these offspring will still exhibit phenotypes with suboptimal fitness (green line, **Figure 1b**). It is only when females mate with males possessing extreme phenotypes (blue line, **Figure 1c**) that their offspring will exhibit the optimal trait phenotype (green line, **Figure 1c**). Thus, even in this good genes example, it is clear that female mate preferences can rapidly favor extreme male phenotypes, here within a single generation. Such conditions are likely to establish genetic correlations between male traits and female preferences for them that, as the runaway process accelerates, will soon have little relevance to actual offspring fitness. Although natural selection may favor an optimum phenotype, by this mechanism, sexual selection favors phenotypes that exceed the fitness optimum. Furthermore, as explained above, when fitness variance within one sex becomes large due to a sex difference in mate numbers, the contribution of fitness variance by the other sex to total fitness variance can become comparatively small. For these reasons, again paradoxically from a PIT perspective, when sexual selection intensifies, mate choices based on good genes are likely to contribute little to the total response to selection.

See also: Sex Ratio.

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## Matrix Models

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## Introduction

### Matrices

By an  $m \times n$  matrix we mean an array of  $m \times n$  elements, for example,  $a_{ik}$  ( $i = 1, \dots, m$ ;  $k = 1, \dots, n$ ) arranged in a rectangular form:

$$\begin{pmatrix} a_{11} & \cdots & a_{1n} \\ \vdots & \ddots & \vdots \\ a_{m1} & \cdots & a_{mn} \end{pmatrix}$$

The element  $a_{ik}$  is called the  $(i, k)$ -element (entry or component). The notation for matrix is often abbreviated by writing  $\mathbf{A} = (a_{ik})$ .

Each horizontal  $n$ -tuple in an  $m \times n$  matrix is called a row of the matrix, and each vertical  $m$ -tuple is called a column of the matrix. The  $m \times n$  matrix  $\mathbf{B}$ , where  $b_{ik} = a_{ki}$  is called the transposed matrix of  $\mathbf{A}$  and denoted as  $\mathbf{A}^T$ .

An  $n \times n$  matrix is called a square matrix of order  $n$ . A square matrix is called diagonal matrix if all its components are zero except for diagonal components