

These cheats make many small gametes, thus fertilizing more eggs (the larger gamete) per unit investment. This disruptive selection therefore gives rise to the evolution of anisogamy.

An attractive feature of the model is that it does suppose that isogamy can exist stably. Tests of the PBS model have been limited. As mentioned, the model requires that females attempt to maximize zygote volume. In this light, the activity of stripping off sperm cytoplasm prior to fusion is clearly contrary to expectations. However, this may be derived secondarily.

Only two sorts of tests have been performed. First, it has been questioned whether with increasing organism size the degree of anisogamy goes up. It appears that a prediction of the model is that as organisms get larger, the potential benefits for producing larger zygotes may accelerate, and thus larger organisms should be more anisogamous. The volvocales, relatives of *Chlamydomonas*, have been used to test this prediction. The volvocales are a group of organisms that are simple multicellular balls of relatively few cells. A few tests have been done to see whether the size of the parent that produces the eggs is a predictor of the degree of anisogamy (ratio of egg to sperm volume). The evidence appears to suggest that this is true, although the answer from the comparative analysis is sensitive to the choice of which phylogeny is employed.

Second, the model predicts that within the same group, as the size of the organism goes up, so should the size of the egg. Phylogenetically controlled analyses suggest that this may be true, but, again, the result is sensitive to the choice of phylogeny. Alternative reasons as to why these two predictions may be upheld within the volvocales have also been presented.

The situation remains ambiguous, and other models should be considered. For example, it has been suggested that anisogamy arose through disruptive selection, with one sex favoring staying put and emitting pheromones to attract the other, whereas the other was not a pheromone producer but an active searcher instead.

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SEX RATIOS

The sex ratio is the numerical ratio of male to female individuals, usually expressed as the proportion of males within a group (such as a family) or population. Evolutionary studies of sex ratio variation are some of the most successful applications of predictive theoretical biology, and they have provided classic tests of kin selection theory, with great relevance for the debate con-

cerning levels of selection. However, much is still not known about sex ratios—in particular, why the same theory works well in some taxa but less well in others. Nevertheless, in studies of those organisms where the theory works well, there is currently great interest in using measurements of the sex ratio to perform “reverse engineering,” and to deduce other aspects of an organism’s biology that may be much more difficult to measure directly.

Development of Theory. Most animal populations seem to be composed of approximately equal numbers of males and females. It is sometimes claimed that Darwin avoided trying to explain this observation on the grounds that the problem seemed too difficult, leaving R. A. Fisher to suggest what is now accepted as the correct explanation in 1930 (see Edwards, 1998). In fact, Darwin suggested an explanation in the first edition of *Sexual Selection and the Descent of Man* (1871), closely matching that attributed to Fisher, and it seems that the idea was widely known in the early decades of the twentieth century—perhaps so widely that Fisher felt no need to give any attribution to the explanation. Nevertheless, Fisher expressed the idea very succinctly, and his explanation remains the first clear statement of the principle of frequency-dependent selection, and of evolutionarily stable strategies.

Fisher reasoned that if there were an imbalance of one sex, say fewer females, in a population, then any individuals that had a heritable tendency to produce more of the rarer sex (in this case, females) would produce offspring that had higher reproductive success. Hence, the frequency of genes causing overproduction of females would increase in the population, so that this sex would become commoner. As the population sex ratio approached equality, the strength of selection on the genes producing more of the rarer sex would decline, until at equality they would have no net selective advantage. This argument works no matter which sex is initially rarer, and so it predicts that an equal sex ratio is the only evolutionarily stable outcome. One criticism of Fisher’s theory is that if sex is determined by sex chromosomes inherited in a Mendelian fashion, then an equal sex ratio is also expected as an outcome of random Mendelian inheritance. However, the few experimental tests of Fisher’s idea that have been performed have supported it.

In cases where the two sexes cost differing amounts for the parents to produce (for example, because of one sex being larger than the other), Fisher’s theory still works, but in this case it is the total amount of resources invested in each sex that is predicted to be equal. This will lead to an unequal sex ratio. The quantity that is predicted to be equal is the amount *allocated* to the two sexes; in fact, most sex ratio theories are actually theories about *sex allocation*, although the sex ratio is often

assumed to be closely correlated with sex allocation in empirical studies. In this broader guise, simple theory is also able to predict, for example, how simultaneous hermaphrodites should divide their resources between male and female reproductive function. Because the theory predicts what parents should do, and because it is based on an economic concept of expenditure, processes happening after parents cease investing in their offspring may not influence the parents’ optimum sex ratio. For example, if sexual dimorphism develops after offspring become independent, or if mortality is sex-biased after independence, biased sex ratios at birth are not expected.

Hamilton’s Sex Ratio Theory. Fisher’s theory makes many simplifying assumptions (for instance, random mating within an infinite population and parental control of the sex ratio), and it is the cases where these assumptions are violated that have yielded some of the most spectacular predictions and confirmations of modern sex ratio theory. The first major development was that by W. D. Hamilton in a groundbreaking paper published in 1967. Hamilton pointed out that if individuals mate within highly structured populations, then the logic of sex ratio selection will be changed. To take the most extreme example, if one imagines that matings are only between full siblings, then much of the investment in males would be wasted if the sex ratio were equal, because a single male might potentially fertilize all of his sisters. In such a situation, a sex ratio biased very strongly in favor of females would be the evolutionarily stable strategy. Hamilton termed this *local mate competition*.

In the same paper, Hamilton pointed out that the optimal sex ratio for a gene, or a chromosome, might depend on its mode of inheritance. For example, because the cytoplasm present in sperm generally does not become incorporated in the zygote, males represent an evolutionary dead end for any genetic element residing in the cytoplasm of the cell (for example, mitochondrial DNA), and therefore they should “prefer” a sex ratio composed of all females. On the other hand, for a gene on a Y chromosome, female offspring represent an evolutionary dead end (or “no entry” sign), so genes on the Y chromosome should prefer a sex ratio composed of all males. If either cytoplasmic genetic elements or genes on the sex chromosomes influence the sex ratio, then Fisher’s assumption of parental control of the sex ratio is violated, and spectacular departures from sex ratio equality may be seen. Hamilton’s arguments can be interpreted in terms of relatedness, and they were one of the first examples of explicit gene-level selection thinking; the arguments can also be extended easily to organisms where relatedness differs between different classes of individuals—for example, in many social insects.

The most familiar social insects (ants, bees, and wasps) have haplodiploid sex determination: females are diploid and develop as normal from a fertilized egg, but males are haploid and develop from unfertilized eggs. This creates a *relatedness asymmetry* and affects the reproductive value of different sexes of relatives. For queens, sons and daughters are worth an equal amount. For workers (female offspring of the queen), however, the relative worth of sisters and brothers depends upon how many times their mother has mated. In the simplest scenario, when a queen has mated only once, sisters are worth three times as much brothers. Sisters receive an identical genetic endowment from their fathers and have a 50 percent chance of sharing genes via their mother, so they are related by 0.75; their relatedness to their brothers is only 0.5, however (genes shared via mother only). When these relatedness values are multiplied by the mean reproductive value of each sex of siblings, they yield a 3:1 female:male ratio. Thus, the queen and workers are potentially in conflict over the sex ratio of reproductives produced by the colony: for the queen, an equal sex ratio would be best, but for workers, three females for every male would be best. Data from a wide range of ant, bee, and wasp species suggest that, on the whole, workers win this conflict, since sex ratios of reproductives are strongly female-biased.

Variable Sex Ratios. The theory discussed above has generally been concerned with fixed situations in which there may be a single optimum sex ratio for a population, or for a group of individuals. R. L. Trivers and D. E. Willard first pointed out, in 1973, that the sex ratio that individuals produce might also be subject to selection. Their idea was related to ungulate mammals, but it can be expanded greatly to cover any situation where there are potentially different fitness returns to be obtained from investing in offspring of one sex or the other (see Charnov, 1982, for discussion of many applications of this idea).

As an example, imagine that a female insect lays solitary eggs on patches of food of limited size, and that the food patch represents all of the resources that the developing offspring will have access to before reaching sexual maturity. In this imaginary species, the fitness of female offspring is determined largely by how many eggs they lay, which in turn is determined by their body size at maturity. For male offspring, however, fitness is independent of size. Under these conditions, the fitness of daughters will be higher than sons when a brood is produced from a large food patch, but the reverse will be true in small patches. Selection then favors a male-biased sex ratio in small food patches, and a female-biased sex ratio in large food patches. This simple model can be extended to almost any situation in which an environmental variable has differential effects on the

value of male and female offspring—for example, mate attractiveness in birds, or rearing temperature in reptiles. Precisely the same argument can be used to predict at what point a sequential hermaphrodite (e.g., sex changing fish) should switch from being one sex to being the other, or how much a simultaneous hermaphrodite should expend on male and female gametes.

Flexibility in the sex ratio may also be expected when male and female offspring cost their parents different amounts depending on the circumstances in which they are produced. For example, in some vertebrates, one sex of offspring may stay with the parents and assist them with rearing subsequent broods of offspring. In that case, they are sometimes said to “repay” the cost of their production, which leads to selection for overproduction of the helping sex. However, producing more of the helping sex may not always be beneficial: if the family inhabits a limited range, at some point production of the sex of offspring that remain behind to help may cost more than producing a dispersing offspring, because the helping offspring will deplete resources that could be used for further offspring by the parents.

Empirical Evidence—Invertebrates. Evidence in support of the predictions of sex allocation theory has been gathered in many ways. In some organisms (particularly invertebrates with haplodiploid sex determination), the support for a range of predictions is so good that it is probably safe to assume that the theory is correct. In some cases where data do not fit theoretical predictions, it may be that this represents a failure by the researcher to understand the biology of the system, rather than a failure of theory.

Support for the effect of local mate competition on the evolution of sex ratios has come from a wide range of invertebrate species, especially wasps, ants, beetles, mites, and spiders. Some of the most striking of these studies have been carried out on fig wasps. Figs and the tiny wasps that pollinate them have evolved intricate interrelationships throughout the tropics; each species of fig is associated with one or more species of pollinating wasp. Figs produce flowers inside a closed fruit (the synconium) and rely on females of their particular pollinating wasp species to crawl into this fruit and pollinate their flowers. While doing so, the wasps lay their own eggs, which develop within the fruit, feeding upon some of the flowers. The wasps mature just before the fruits ripen. In many cases, the male wasps are nondispersing (they may lack wings altogether) and mate with females that hatch within the same fruit as them; it is the mated females that disperse to other fruits. This life history creates the possibility for strong local mate competition. If only one female has laid eggs within the fruit, then her sons will compete among themselves to fertilize their sisters. In this case, the optimum sex ratio is to lay just enough male eggs to fertilize all of the females;

the clutch should consist of a small number of males, with all the rest females. However, as increasing numbers of females lay eggs within the same fruit, the relatedness among competing males falls, with the result that the optimum sex ratio creeps up toward an equal number of males and females.

Work by Allen Herre in Panama has shown that multiple species of fig wasps obey this rule relating number of ovipositing females to sex ratio, but it has also added an intriguing twist that demonstrates the explanatory power of evolutionary theory. Although the same basic theory governs the optimum female response, different species may not all evolve identical responses. For example, some species almost never encounter a situation in which another female has oviposited in the same fruit, while others may do so frequently. In that case, one may expect the species that frequently encounters a range of situations to demonstrate a closer fit to the predicted relationship, because it is more often exposed to that particular selective regime. Herre showed that this is indeed the case: wasp species that are exposed regularly to a range of degrees of local mate competition show a closer fit to the theoretically expected relationship.

Experimental studies of parasitic wasps (parasitoids) also have confirmed the predictions of local mate competition, and these results have been used frequently to demonstrate that sex ratios are adjusted in response to environmental conditions. The fitness of female offspring is more strongly affected by the size of the host in which they develop than is male fitness, because female fitness is determined largely by fecundity (number of eggs laid), which is in turn determined by body size when the wasp emerges from its host. Consequently, there is selection for females to lay male eggs in small hosts, and female eggs in large hosts. Careful experiments show that it is the relative size of the host, rather than its absolute size, that determines the egg-laying female's sex ratio response. By exposing a newly emerged female to undersized hosts followed by an average-sized host it is possible to shift the sex ratio response relative to that of females that have experienced a normal range of host sizes.

Empirical Evidence—Vertebrates. In contrast to the work on invertebrates such as parasitoid wasps and social insects, which often shows a beautiful match between theory and data, the question of whether vertebrates (particularly birds and mammals) can adjust their sex ratio in an adaptive fashion has long been controversial. One reason for this is that in birds and mammals sex is determined chromosomally, rather than by whether an egg is fertilized or not (as in haplodiploid systems). It thus seems reasonable to assume that the sex of an offspring will ultimately be determined by which sex chromosome it inherits from its heterogametic parent (father in mammals, mother in birds), which will in turn

be determined by random Mendelian segregation. However, a large number of studies have reported finding correlations between the sex ratio within families and some environmental factor, and a small but increasing number of experimental studies have demonstrated similar effects on the sex ratio. In many cases, these findings are still compatible with the idea that random Mendelian segregation controls the sex ratio, because it is virtually impossible to measure the sex ratio at fertilization in either birds or mammals. As a consequence, it is possible that mortality may be sex-biased between fertilization and the point at which the sex ratio is measured.

Sex-biased mortality is of particular concern in studies of mammals, where the sex ratio is rarely recorded before birth, and in which it is well established that the larger sex of offspring (usually males) is more likely to die before birth, particularly if environmental conditions are harsh. This association between the environment and sex-biased mortality can make it difficult to determine whether a correlation between the environment and the sex ratio represents an adaptation by the parent or not. For example, in red deer (*Cervus elaphus*), males are larger than females, and sons born to dominant females are disproportionately successful as adults. These conditions create selection for the sex ratio to be adjusted in relation to dominance status, with dominant females giving birth to a higher proportion of sons. However, recent analysis of a long-term dataset from the Scottish island of Rum shows that the effect of female dominance on the sex ratio is environmentally dependent. A correlation was present when the population's density was low, but this correlation disappeared as density increased, perhaps because sex-biased mortality then affected all females equally (Kruuk et al., 1999). It is not known whether the correlation between female dominance and the sex ratio at low density represents maternal control over the sex ratio, or simply the fact that only subordinate females suffered from male-biased offspring mortality.

In birds, where eggs are laid into a nest soon after fertilization, sex-biased mortality before laying seems less likely than in mammals, although it is hard to rule out with certainty. Recent development of genetic markers for the avian sex chromosomes has made possible some studies suggesting remarkable degrees of adaptation in the sex ratio. Foremost among these is a study of cooperatively breeding Seychelles warblers (*Acrocephalus sechellensis*) by Komdeur et al. (1997). In this bird, confined to a few islands in the Indian Ocean, daughters help their parents to rear subsequent offspring and thereby increase their parents' fitness. However, helpers are useful only on high-quality territories where there are plenty of insects to eat; on low-quality territories, the presence of helpers increases competition for food, leaving less for nestlings. Parents show

strong, and reproducible, biases in the primary sex ratio of their offspring depending on the quality of territory that they breed on, producing daughters on high-quality territories and sons (which disperse) on low-quality territories.

Despite some successes like those mentioned above, there are numerous studies of sex ratio variation in vertebrates where it appears that sex ratios are determined by chance processes. Vertebrates tend to have more complex life histories, with overlapping generations, than do the haplodiploid insects to which sex allocation theory has been applied so successfully. This may mean not only that it is harder for biologists to understand why (and whether) sex ratios should vary, but also that selection for sex ratio adaptation does not act in a consistent manner.

Applications of Sex Ratios. In cases where sex allocation theory can be shown to work well, it can then be used to deduce other things about an organism. One example of this with considerable applications to biomedical science concerns the use of Hamilton's local mate competition theory to work out the population structure of parasites, such as human malaria as pioneered by Andrew Read. Malaria parasites reproduce clonally inside vertebrate hosts, but they also produce sexual stages (gametocytes) that are taken up in blood meals by blood-feeding insects such as mosquitoes, which act as vectors of the parasite between hosts. Sexual reproduction occurs inside the gut of the vector. Because blood meals are taken so infrequently, mating is likely to take place between the gametocytes from a single blood meal. Consequently, mating will generally take place between the different parasite genotypes (clones) that infect a single host. This sets the stage for potential local mate competition if only a small number of parasite clones infect each host. If one then measures the sex ratio of gametocytes within a host, the simple theory developed by Hamilton can be used to predict how many clones the average host contains. This information can be obtained in other ways—for example, by using genetic markers to investigate the population structure of the parasite—but this is both expensive and time-consuming compared to the "reverse engineering" method using the sex ratio. All this involves is counting gametocytes in blood smears under a microscope. Remarkably, in the few cases where population structure has been estimated in both ways, there is a close agreement between the two estimates. Knowledge of the population structure of parasites is of considerable importance for the development of vaccines and in predicting the spread of drug resistance among parasites.

Why is simple theory sometimes so successful in predicting something so fundamental about an organism as how many male and female offspring it produces? There are probably two contributing factors. First, sex ratios are simple because there are often only two quantities—

the number of males and the number of females—which trade off with each other. Second, sex ratios may be under very strong selection. As a consequence, the study of sex ratios represents an excellent model for the study of the limits of adaptive evolution.

[See also *Cytoplasmic Genes; articles on Eusociality; Fisher, Ronald Aylmer; Meiotic Distortion.*]

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SEXUAL CONFLICT. See *Cryptic Female Choice*.