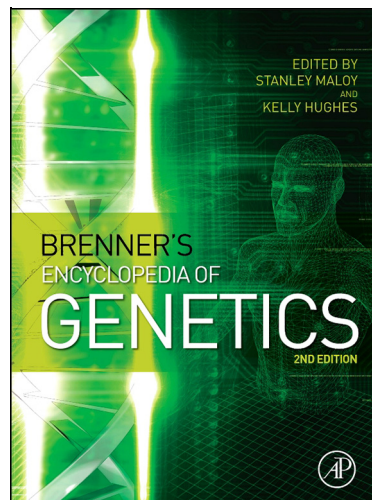


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Sex Ratios

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Glossary

Adaptation Biological design; the problem of adaptation, which was solved by Darwin, is the need to explain the fact that organisms appear designed.

Evolutionarily stable strategy The strategy (or behavior) which cannot be beaten by (i.e., has higher fitness than) any other strategy.

Fitness Genetic contribution to the next generation.

Local resource competition The offspring of one sex lead to greater competition for resources.

Local resource enhancement The offspring of one sex provide a greater benefit than the other.

The Düsing–Fisher's Theory of Equal Investment in the Sexes

Fisher, in 1930, famously provided an explanation for why most animal species, including humans, produce approximately equal numbers of males and females. If there were an excess of males, they would on average obtain less than one mate, and so the fitness of females would be greater, favoring parents that produced a relative excess of female offspring. In contrast, if there were an excess of females, males would on average obtain more than one mate, and so the fitness of males would be greater, favoring parents that produced a relative excess of male offspring. Consequently, the fitness of males and females is only equal when equal numbers of the two sexes are produced (a sex ratio of 0.5). This argument assumes that equal amounts of resources are put into the production of sons and daughters. If this is not the case then the argument is phrased in terms of investment, and the evolutionary stable strategy (ESS) is to invest resources equally in male and female offspring. Although usually attributed to Fisher, who provided a particularly lucid explanation, a mathematical treatment of this idea had already been published in 1884, in German, by Düsing.

Biased Sex Ratios

Fisher's principle clearly shows the frequency-dependent nature of selection on the sex ratio, and it provides a null model (equal investment in the sexes) which is the foundation upon which most areas of sex-ratio research have been built. However, it assumes that the fitness returns from the production of sons and daughters are identical (or linear). Many different biological mechanisms break this assumption and, in these cases, biased sex ratios are predicted. Here, we review two scenarios where there is a rich experimental literature exploring the predictions of many theoretical models: (1) sex-biased interactions between relatives, and (2) differential effects of the environment on male and female fitness.

Sex-Biased Interactions between Relatives

Fisher's principle assumes that the fitness returns from producing sons and daughters do not differ. This will not be the case if there are sex differences in the interactions of offspring with each other, or their parents.

If production of one sex leads to a greater increase in fitness of the parents or their offspring, then an excess production of that sex is favored by a process that has been termed local resource enhancement (LRE). One example of this process is observed in African wild dogs, which are wolf-like social carnivores found in sub-Saharan Africa. These live in packs and young males help more than young females in the rearing of pups. This favors an excess of males, and 60% of offspring are males. Another example is provided by allodapine bees, primitively social bees which communally nest in burrows. Sisters nest together, and increasing nest size leads to fitness benefits through increased survival and reproduction, in part due to efficiency gained from division of labor. This favors an excess of females, and less than 20% of offspring are male.

In contrast, if competition between siblings and/or parents is greater for one sex, then an excess production of the other sex is favored by a process that has been termed local resource competition (LRC). One example of this comes from African primates in the Galagidae family. In these species, females disperse much less than males, and related females compete for resources, especially during breeding season. This favors an excess of males, and 70% of offspring are male. A special case of LRC that has received considerable attention is the competition for mates between brothers in structured populations, termed local mate competition (LMC). If brothers compete for mates (including their sisters) before the females disperse, then LMC theory predicts a female-biased sex ratio to reduce this competition. Support for LMC theory has come from a wide range of animals and plants, especially insects (e.g., parasitic wasps, aphids, thrips, and beetles), other arthropods (e.g., mites and spiders), protozoan parasites (e.g., blood parasites such as those causing malaria, and intestinal parasites such as *Toxoplasma*), and selfing plants. In these cases, not only do populations show female-biased sex ratios (sometimes with just 1–5% males), but also, in many cases, individuals have been shown to adjust the ratio of their offspring in response to variation in the level of LMC.

Both LRE and LRC can occur in the same species. One of the clearest examples of this comes from studies of the Seychelles warbler. This small bird is extremely territorial, and in situations where there are few new territories available, some young will remain at their natal nest and help raise siblings. The majority (80%) of helpers are daughters. Importantly, whether a helper is advantageous or disadvantageous for her parent depends upon the quality of the territory occupied, which depends upon the availability of insects for food. On high-quality territories, helpers are beneficial from the point of view of their parent, and increase the number of young produced (LRE). On low-quality territories, the increased competition for food with helpers means that their presence is disadvantageous from the point of view of their parent (LRC). As predicted, predominantly (90%) females are laid on high-quality territories where their presence as helpers will be beneficial (LRE), and predominantly (80%) males are laid on low-quality territories, from which they will disperse, and avoid competition with their relatives (LRC).

Differential Effects of the Environment on Male and Female Fitness

Fisher's principle assumes that variation in environmental conditions affects the fitness of sons and daughters equally. If this is not the case, then individuals can be selected to adjust the sex of their offspring in response to the environment.

This idea was first applied to explain sex-ratio patterns in mammals caused by variation in maternal condition. For example, in red deer, higher-quality (indicated by rank) females are more likely to produce sons, and lower-quality females are more likely to produce daughters. This is thought to occur because (1) higher-quality females are able to provide more resources to their offspring, and (2) competition for mates between males is intense, with only the highest-quality males being successful, and so sons benefit more from increased resources than daughters. The same concept can explain why in many species of parasitic wasp, where only one individual can develop per host, females lay male eggs on small hosts, and female eggs on large hosts. In this case, it is presumed to be advantageous because the resultant increase in

body size provides a greater benefit for daughters (through effects on fecundity) than sons.

The same concept can also apply in response to variation in mate quality. In several bird species (e.g., zebra finches, collared flycatchers, and blue tits), females have been shown to adjust the sex of their offspring in response to the attractiveness of their mate. This is advantageous when male attractiveness is an indicator of genetic quality and heritable. Consequently, if a female mates with a relatively attractive male there is an advantage to producing sons, who will inherit their father's attractiveness. This pattern is observed, and some bird species show remarkable ability to shift their offspring sex ratio in the predicted way.

Conclusions

Evolutionary biologists have developed an excellent understanding of the selective factors that shape the sex ratio. More generally, studies of the sex ratio have provided some of the best support for the adaptationist approach. In particular, they have provided an area in which theory is able to make predictions that can be tested qualitatively and sometimes quantitatively, with experimental and observational data. Perhaps one of the greatest questions remaining is how do species with chromosomal sex determination, such as mammals and birds, achieve such striking facultative shifts in offspring sex ratios?

See also: Fundamental Theorem of Natural Selection; Sex Reversal.

Further Reading

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