## AGE AND SEX RATIO

## Introduction

Sex ratio is the proportion of males relative to the proportion of females. Sexually reproducing organisms must find mates in order to produce offspring. Without comparable numbers of males and females, mating opportunities may be limited and population growth stunted. Thus, ecologists measure the number of males and females within a population to construct a sex ratio, which can help researchers predict population growth or decline. Much like population size, sex ratio is a simple concept with major implications for population dynamics. For example, stable populations may maintain a $1: 1$ sex ratio and therefore keep their growth rate constant, whereas declining populations may develop a $3: 1$ sex ratio favouring females, resulting in an increased growth rate. In species where males contribute significantly to offspring rearing, populations may instead maintain a ratio skewed towards males (Hamilton 1967).

## Concept of sex ratio

Sex ratio affects both the growth rates and the evolutionary trajectories of wild populations. The sex ratio of the population affects, and is affected by birth, death, immigration, and emigration rates. The production of males and females in a ratio of $1: 1$ is generally the most common evolutionary stable strategy (ESS), led by frequencydependent natural selection due to competition for mates among individuals of the same sex. Both population density and sex ratio shape competition for mates, resources and mating costs. Thus, they may critically affect the intensity of sexual selection in the populations. Susceptibility to inter- and intra-sexual competition, which changes with age in a large number of species, may additionally influence population response to these demographic factors.

Natural selection often appears to determine the differences within and among populations and species in sex ratio. The optimum sex ratio for a given individual in a given population depends on both the existing sex ratio of the population and on the relative costs and benefits of producing offspring of each gender. Patterns of natural selection on sex ratio may be affected by the quality and stability of the immediate habitat, as well as by life-history traits, competition and dispersal, which affect local competition on mate or resources.

Environmental effects, both temporal and spatial, can create a biased sex ratio by excess production of the sex that is cheaper to produce under poor environmental conditions. Interestingly, sex ratio is not always random, rather it can be manipulated at birth by environmental or physiological mechanisms. All crocodiles and many reptiles utilize a strategy called environmental sex determination, wherein incubation temperature determines the sex of each individual. Moreover, empirical studies have found that the sex ratio in plants can be modified at the individual level, following seasonal changes in the resources available.

In most sexually reproducing species, the ratio tends to be $1: 1$. In modern language, the $1: 1$ ratio is the evolutionarily stable strategy (ESS). Spending equal amounts of resources to produce offspring of either sex is an evolutionarily stable strategy: if the general population deviates from this equilibrium by favouring one sex, one can obtain higher reproductive success with less effort by producing more of the other. For species where the cost of successfully raising one offspring is roughly the same regardless of its sex, this translates to an approximately equal sex ratio. For various reasons, however, many species deviate from anything like an even sex ratio, either periodically or permanently. Examples include parthenogenic species, periodically mating organisms such as aphids, some wasps, bees, ants, and termites. The theory of sex ratio is a field of study concerned with the accurate prediction of sex ratios in all sexual species, based on a consideration of their natural history. The field continues to be heavily influenced by

Eric Charnov's 1982 book, Sex Allocation. Biological research mostly concerns itself with sex allocation rather than sex ratio, sex allocation denoting the allocation of energy to either sex. Common research themes are the effects of local mate and resource competition.

## Fisher's principle

Fisher's principle is an evolutionary model that explains why the sex ratio of most species that produce offspring through sexual reproduction is approximately $1: 1$ between males and females. Bill Hamilton expounded Fisher's argument in his 1967 paper on "Extraordinary sex ratios. Fisher couched his argument in terms of parental expenditure, and predicted that parental expenditure on both sexes should be equal. Sex ratios that are $1: 1$ are hence known as "Fisherian", and those that are not 1:1 are "extraordinary" and occur because they break the assumptions made in Fisher's model.

## Types of sex ratio

In most species, the sex ratio varies according to the age profile of the population. ${ }^{[7]}$

It is generally divided into four subdivisions:

- Primary sex ratio: sex ratio at conception (the point at which the sperm fertilize the eggs). This is usually near 50:50 in natural populations, though a few cases exist where parasites can change the primary sex ratio by for example, having lethal effects on sperm.
- Secondary sex ratio: sex ratio at time of hatch or birth. Often nearly 50:50 but more examples exist of skewed secondary sex ratios than of skewed primary sex ratios.
- Tertiary sex ratio: sex ratio at some later stage of life such as at age of first reproduction or "adult" stage. Skewed sex ratios are most often observed at this stage in sexually mature organisms. It is also
known as Adult Sex Ratio (ASR). ASR is defined as the proportion of adults in a population that are male.
- Quaternary sex ratio: ratio in post-reproductive organisms.


## Patterns of natality

Generally (birds, mammals), reproduction improves fairly quickly to a peak and then declines in old age, as indicated in the table below for three species of ungulates. For each example, the rate of pregnancy or the number of offspring produced starts low, increases in the middle years, and then declines toward the end of the life span. The decline at the end is senescence, but here it is acting on natality rather than survival.

| Species | Age-class | Measure of <br> natality |
| :--- | :--- | :--- |
|  |  | \% pregnancy |
| Elk (Yellowstone) | Yearling | 12 |
|  | 2-15 years | 97 |
|  | 16-21 years | 37 |
| Wood <br> (Canada) | bison | Yearling |
|  | 2 | 4 |
|  | 3-11 years | 67 |
|  | 12+ years | 35 |
|  |  | Fawns per doe |
|  | White-tailed | deer |
| (NY) | Yearling | 0.32 |


|  | 1.5 years | 1.54 |
| :--- | :--- | :--- |
|  | 2.5 | 1.57 |
|  | 3.5 | 1.65 |
|  | $4.5-7.5$ | 2.00 |
|  | 8.5 | 1.22 |
|  | 9.5 | 1.22 |
|  | 10.5 | 1.00 |

## References

Charnov, E. L. (1982) Sex allocation. Princeton University Press, Princeton, New Jersey. ISBN 0-691-08312-6

Fisher, R.A. (1930). "Chapter 6: Sexual Reproduction and Sexual Selection § Natural Selection and the sex-ratio". The Genetical Theory of Natural Selection. Oxford, UK: Clarendon Press. p. 141.

Hamilton, W. D. (1967) Extraordinary sex ratios. Science 156, 477488.

