Sex Ratio

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Definition

In sexually reproducing species, sex ratio is the proportion of males to females in a given population. It is usually expressed as the number of males per 100 females.

Introduction

Depending on the context, sex ratio might be measured in a particular life stage, e.g., ratio at the time of fertilization (also called primary sex ratio), ratio at birth (secondary sex ratio), ratio in organisms that have reached sexual maturity or adulthood (tertiary sex ratio), ratio of sexually active and fertile organisms (operational sex ratio), or ratio in organisms past reproductive stage (quaternary sex ratio). The ratio tends to be approximately 1:1, which is explained by Fisher's principle (see below). However, a significant deviation from that rule is observed in many species, either permanently or periodically. In humans, sex ratio at birth is sometimes skewed because of factors such as infanticide, sex-selective abortions, age of mother at birth, or environmental factors (Davis, Gottlieb, & Stampnitzky, 1998).

In 1982, Eric L. Charnov, an American evolutionary ecologist, published a book on the prediction of sex ratios based on a species' natural history. He attempted to identify the equilibrium when allocating resources to female versus male function in simultaneous hermaphrodites, equilibrium of time of sex change and sex order in sequential hermaphrodites, and equilibrium in the ratio maintained by natural selection in dioecious species (having both male and female reproductive organs). He also analyzed when natural selection favors an individual's ability to adjust its allocation to female versus male function, as a reaction to particular life history or environmental variables. He analyzed the conditions favoring evolutionary stability for various states of dioecy or hermaphroditism, and when mixtures of various sexual types are stable (Charnov, 1982).

Fisher's principle

Fisher's principle is an evolutionary model outlined by Sir Ronald Fisher, British geneticist and statistician, in his book *The Genetical Theory of Natural Selection,* published in 1930. It explains why the sex ratio in sexually reproducing species is close to the so-called "Fisherian" ratio of 1:1, which is considered evolutionarily stable (Fisher, 1930). Fisher argued that the process of natural selection leads to sex ratio adjustment. If the total parental investment (such as resources, energy, or time) in the offspring of both sexes is equal, then the birth ratio of sexes should be 1:1.

An important addition to Fisher's theoretical discussion of sex ratio was provided by Trivers and Willard (1973) that stated that, in mammals, females are able to adjust sex ratio of their offspring in response to the maternal condition. Despite the fact that Fisher's principle secures the 1:1 sex ratio, evolution will favor deviations from this rule if one sex has a probability of achieving greater reproductive payoff than the other. The findings of Trivers and Willard suggest that the reason for promoting such disproportion is that, in good condition, mothers should invest more in producing males, because sons of a high quality are expected to out-reproduce daughters of high quality. Consequently, mothers who are in poor condition should invest more in producing females, because daughters of low-quality are expected to out-reproduce sons of low quality. The implication is that parental ability to adjust offspring sex ratio depending on the quality of conditions should be favored by natural selection. Data on sex ratio of mammals supports this hypothesis: as maternal condition increases, females tend to produce more males than females.

Sex ratio in non-humans

Most animals maintain a relatively stable operational sex ratio, but some are known for having their sex determined not just by genes, but also by, e.g., environmental factors or hormonal changes (e.g., Ferguson & Joanen, 1982; Pike & Petrie, 2005). Proper assessment of a sex ratio is neither easy nor straightforward. It has been observed that deviation from the 1:1 ratio is widespread in marine crustacea; there are male-female relationships of discrete patterns, so instead of overall sex ratio, calculation of different within-size-class ratios should be taken into consideration (Wenner, 1972).

Temperature-dependent species have a higher within-species variance in sex ratios than chromosome-determined species (Bókony, Milne, Pipoly, Székely, & Liker, 2019). For example, in American alligators, sex of the individual is dependent on incubation temperature of the egg. Females are hatched from eggs incubated at a lower temperature than males, who require higher temperatures (Ferguson & Joanen, 1982). Temperature-based sex determination is also found in turtles. However, a study performed on eggs incubated in the same temperature shows evidence that some heritable differences in sex determination exist as well (Bull, Vogt, & Bulmer, 1982). Temperature can also influence sex in fish, such as in Nile tilapia (Abucay, Mair, Skibinski, & Beardmore, 1999), and the effect for interaction of genotype and temperature is observed in species such as the Atlantic silverside (Conover & Kynard, 1981).

Environmental determination of sex ratio is also observed in the potato root eelworm, a parasite. In eelworms, the ratio can differ depending on primary and lateral roots, and on the intensity of their parasitic infection (Ellenby, 1954). Environmental influence on primary sex is also observed in dioecious plants. Maternal parents in close proximity to males produce female-biased progeny sex ratios (Stehlik, Friedman, & Barrett, 2008). In copepods, sex ratio differs between families depending on whether females produce eggs continuously after just one mating, or they require several matings (Kiørboe, 2006). In fig wasps, females adjust offspring's sex ratio in response to the level of inbreeding and the intensity of mate competition in the local population (Herre, 1985). Parasitic wasp females adjust offspring sex ratio depending on whether they are the first or second wasp parasitizing the host. The first one biases strongly towards daughters, and the second one varies sex ratio depending on local mate competition level (Werren, 1980). In collared flycatchers, females manipulate offspring sex ratio depending on the male partner's genetic quality (Ellegren, Gustafsson, & Sheldon, 1996). To summarize, not all species of flora and fauna follow the strict Fisherian ratio rule; in some species, sex is moderated by various environmental factors. In short, the sex ratio tends to be that which is most likely to propagate copies of the parents' genes in that environment.

In mammals, one way of increasing eventual offspring production is to vary the sex ratio of offspring as a function of the benefits and costs of producing daughters versus sons. There are at least three factors that may affect sex ratio in mammalian offspring: cooperation or competition between siblings or between parents and siblings; differences in the relative fitness of female and male offspring; and sex differences in viability during early growth or in energy requirement. There is growing evidence that in many species there remains significant variation in mammalian birth sex ratio, which suggests continued adaptive manipulation of sex ratio. However, there are also other mechanisms affecting sex ratio at birth, and they are not likely to reflect adaptive manipulation, because the distribution of observed trends in sex ratio does not conform to the assumptions of any adaptive theory in a significant way. Some studies, however, argue that such trends might be adaptive within a particular population if the sex ratio differs with the benefits or costs of producing female and male offspring, such as a hypothetical population finding a very good and stable source of food, and therefore being able to afford the more costly sex of offspring (Clutton-Brock & Iason, 1986).

Potentially adaptive significance of sex ratio variation caused by parental and environmental conditions is reported not only in mammals, but also in birds. Findings suggest that sex ratio at birth could have been interfered with by steroid hormones and gonadotropins; however, whether it is an adaptive sex ratio adjustment or merely a consequence of physiological constrain is a subject of debate (Krackow, 1995; Navara, 2018).

There are, however, exceptions to the expectations of the Trivers-Willard theory. For example, in American kestrels, the sex ratio of offspring is correlated with female body size. Parents can adjust the sex of their offspring depending on the amount of resources available and as the food supply declines, the proportion of males hatching increases. Also, parents in poorer health produce more male-biased offspring and smaller females produce more males (Wiebe & Bortolotti, 1992). In Seychelles warblers, biased sex production, not embryo mortality, is the cause of a bias in hatching sex ratios. Pairs on bad-quality territories produced 77% sons, and pairs on good-quality territories produced 13% sons. Pairs that transferred from a poor to a high quality territory subsequently produced significantly more females (Komdeur, Daan, Tinbergen, & Mateman, 1997). These exceptions may be caused by, for example, reversed sex characteristics in the species, such as females being physically larger in order to compete for mates.

Sex ratio in humans

In humans, sex ratio at birth is approximately 1:1, and research measuring sex ratio has been conducted all around the globe, producing over 100 years of data. Sex ratio varies across age groups and geographical locations, and several factors can influence sex ratio, including race, birth order, plural birth, duration of gestation, and parental age, psychological stress, and health history. The sex ratio produced in relation to these factors, however, is not consistent over time for a given country, or across countries at a given time. It has been observed that in the United States, between 1950 and 1972, fetal and neonatal death more frequently occurs in females, which biases the birth sex ratio slightly towards males (McMillen, 1979); however, proper estimation of this bias is difficult and affected by factors such as sex-selective abortions. In infancy, boys have higher mortality rates because they are more susceptible to disease (Pongou, 2013). For the USA, sex ratio at birth for Hispanic and African-American ethnic groups is lower than for white ethnic groups. Also, in a white ethnic group, sex ratio at birth was 1.04 if the gestational age was 33-36 weeks, but if the age was shorter (<28-32 weeks) or longer (37 weeks or more), the sex ratio was 1.15 (Branum, Parker, & Schoendorf, 2009). Women tend to live several years longer than men, which biases sex ratio in older generations towards women.

In 1990, economist Amartya Sen analyzed whether birth sex ratios are affected by sex-selection, e.g., aborting female fetuses, or natural causes, such as greater vulnerability of male fetuses. Sen argued that strong socioeconomic factors, e.g., one-child policy in China or India’s dowry system, affect prenatal sex-selection. Some disagree with this argument; however, for example, Garenne (2004), who observed that, in many African nations, e.g., Nombia, Botswana, and Angola, there are fewer boys born than girls, which is not the case for other nations.

Sex ratio imbalance differs across the globe as a consequence of various factors, such as environmental stressors in the form of, e.g., cold weather; women exposed to colder temperatures tend to spontaneously abort (i.e., miscarry) male fetuses more frequently, and therefore, more females are born. It has also been shown that males living in colder temperatures tend to live longer, thus raising sex ratio in later life stages (Catalano, Bruckner, & Smith, 2008). Helle, Helama, and Lertola (2009) found the reverse effect; they documented that environmental stress, such as war or warmer temperatures, skew human birth sex ratio towards more frequent male births in Northern Europe. In females, experiencing stress during pregnancy, such as malnutrition, increases fetal deaths among males, in particular, leading to a female-biased sex ratio (Catalano, Bruckner, & Smith, 2008). Due to the contradictory results regarding stress experienced by mothers during pregnancy on survivability of fetuses, more studies are needed to fully understand the effect. It has been found that some types of environmental pollution leading to exposure to persistent organochlorine pollutants, which are endocrine disruptors, increases the amount of ejaculated spermatozoa carrying the Y-chromosome, which might alter the sex ratio of offspring (Tiido, et al., 2005). A longitudinal study on a Finnish population reported changes in sex ratio caused by environmental chemicals and showed that the birth sex ratio of males to females has decreased. It was found that the peak of male birth dominance occurred before the introduction of hormonal drugs and pesticides and the period of industrialization; after that, the sex ratio decreased. The researchers excluded the possibility that the change occurred because of other factors, such as birth order, age difference of parents, or parental age (Vartiainen, Kartovaara, & Tuomisto, 1999). Finally, there has been identified an effect of father's age on sex ratio of offspring. Younger fathers had significantly more sons than older fathers. Mother's age did not affect a child's sex (Jacobsen, Møller, & Mouritsen, 1999). To sum up, sex ratio in humans is a subject to various pressures, and the final sex ratio observable in a given population is a resultant of all of them.

Cross-References:
Population
life stages
operational sex ratio (OSR)
Infanticide
Hermaphrodite
Evolutionarily Stable Strategies
parental investment
Trivers-Willard effect
Environmental influences
Chromosomes
Incubation
Genotype
parasitism
Mammalia
Aves (Birds)
gonadotropic hormone
Race
Stress
Fetus
Pollution
Ejaculate

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