Simple Math:
Sex Ratios

1 Introduction

There are roughly the same number of men as women out there. The validity of this statement depends on what age group you are talking about. Below are some statistics gleaned from the U.S. National Center for Health Statistics (National Vital Statistics Reports, vol. 50, no. 5, Feb. 12, 2002). These data represent the number of live births per year in the United States, arranged by gender.

Year	Males	Females	Males : Females
1995	1,996,355	1,930,234	1.05:1
1996	1,990,480	1,901,014	1.05:1
1997	1,985,596	1,895,298	1.05:1
1998	2,016,205	1,925,348	1.05:1
1999	2,026,854	1,932,563	1.05:1
2000	2,076,969	1,981,845	1.05:1

The sex ratio of live births – the ratio of boys-to-girls (1.05 : 1) born – is remarkably constant from year to year. Why are there more boys born than girls born? From an evolutionary perspective, this pattern might be selected for, because the death rate of males is greater than that of females across all age groups. This pattern becomes readily apparent when we consider the sex ratios of older Americans; the sex ratio of males-to-females aged 85 and older was 0.42 : 1 in the year 1998.

In general, there are approximately equal numbers of men and women in the world. Furthermore, this is true for most species of animals. Why is this so? It is this question that I want to discuss.

First, let's examine how males and females are created. In mammals, males possess 2 sex chromosomes (the chromosomes that determine their gender), an X and a Y (abbreviated as XY). Such males are called heterogametic. Females also possess 2 sex chromosomes, an X and another X (abbreviated as XX). Such females are called homogametic. When males and females produce gametes (sex cells: eggs or sperm) via meiosis, their sex chromosomes are packaged singly into their sex cells. When these sex cells join during fertilization, the resulting union of cells (a zygote) can be either female (XX) or male (XY). The probability of creating a male or a female is exactly 50 : 50 because the offspring is male if and only if the father contributes a Y chromosome, which happens half of the time.[1]

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[1] If there is some reason why the Y chromosome is more likely than the X to be the father's representative in the zygote, then the 50 : 50 ratio will not be attained exactly.

This story says that the structure of chromosomes determines the sex ratio. The structure of chromosomes is different in different animals (more on that below). So it is perfectly reasonable to ask why we haven't evolved in a way that creates a different sex ratio.

Not only is this a reasonable question, one could argue that the optimal sex ratio would have a large number of females for each male. The reason is that pregnant females can't do any additional reproducing until they give birth. A man, however, can continue to spread his seed. Think about the problem this way. In a "breeding" society with 50 men and 50 women, you could hope for 50 babies every nine months (or maybe a few more if there are some twins). In a "breeding" society with 1 man and 99 women, you could hope for 99 babies every nine months. So if evolution operated to maximize the number of members of a species, then you would expect the sex ratio to be greatly biased in favor of females. Evolution does not work that way (although there has been confusion about this point among scientists). A simple discussion about how evolution works leads to an explanation for why the sex ratio is approximately 50 : 50 (and also helps us understand situations in which the sex ratio is different).

What would happen if one gender gained a reproductive advantage over another – for example, if males produced many more offspring than females in their lifetimes (what evolutionary biologists refer to as improved fitness)? Roughly 80 years ago, statistician Ronald Fisher explained why sex ratios should remain around 1 : 1.

Consider a fictitious human population in which a single male prolifically mated with many females. Whereas each female might produce a few offspring in her lifetime, some individual males might produce hundreds of offspring.

Now, if males have better fitness than females – that is, if they produce more offspring, then wouldn't it be better (from the standpoint of producing offspring) to be a male? If you wanted to have more grandchildren, wouldn't it be better to have more male offspring than female offspring? If a genetic mutation enabling the parent to control the gender of their offspring evolved in the population, more males could be produced than females. (This phenomenon does occur in some animals.) Let's consider what would happen if this were the case in a human population:

If more males were born than females, soon there would be tremendous competition among men to mate with the less common women. Thus, the tables would turn, and now it would be advantageous to be a female or to have more female offspring (because each woman would mate, but few men would mate). The sex ratio would now shift towards more females being produced. The sex ratio would thus return – and be maintained – around 1 : 1.

This is an example of how frequency-dependent selection can maintain the different "types" of individuals in a population (different "types" can include different genders or different genotypes). In frequency-dependent selection, the less-frequent types in a population may have better fitness than the more-common types. The less-frequent types would enjoy better mating opportunities until they become more- or equally-common in the population. Then, the less-frequent types would have a fitness advantage.

2 Some Simple Evolution

The idea of evolution through natural selection is perhaps the biggest scientific discovery of the nineteenth century and one of a small number of transcendent insights. I will give a short example to highlight some of the ideas. Image a population consisting of 200 mice, 100 of which are white and 100 of which are black. The fitness of a population member is its relative success at reproducing. Let's suppose that 10 of the dark mice get killed by owls and 40 of the (easier to see) white mice get killed. Further, two-thirds of the remaining mice die of other causes before reaching reproductive age. That leaves $30 = \frac{1}{3}(100 - 10)$ dark mice and $20 = \frac{1}{3}(100-40)$ white mice. Let's suppose that these remaining 50 mice pair off and breed and each pair has eight offspring. This reproduction rate is sufficient to replicate the original population of 200. Now, however, it is likely that more than one half of the population of mice is dark. If mice always take on the color of their mother, then 120 mice will be dark and 80 will be white. (If light color is the result of a recessive characteristic, then roughly 116 of the 200 members of the second generation will be dark.)

I will not focus of the mechanism that determines the color of mice, but want to emphasize the differential mortality between light and dark mice leads to changes in the frequency of the characteristics in the next generation. In the example, the fraction of dark mice grow because they are better able to escape attacks from owls. Natural selection predicts that dark mice will eventually dominate the population.

There are three features of natural selection. The first is fitness, roughly the relative reproductive rate of different traits or individuals in a population. In the example, dark mice are fitter than white mice: they better able to survive and produce children. Notice that fitness would change if the different types of mice differed in more than just their visibility to owls. If for some reason light mice had more children than dark mice or found it easier to get food, then the fitness of white mice relative to dark ones will improve. In order for relative survival rates to make a difference, there must be limits to population growth (so that the relative success of one group comes at the expense of another). Second, natural selection works on variation in the population. If everyone in the population is the same, then there would be no variation in fitness. We typically assume that the variation comes from random mutations. Small random changes in traits are possible. Third, natural selection depends on the fact that traits are passed from one generation to the next. If there was no relationship between the color of a mouse and the color of its offspring, then natural selection would have nothing to say about how the color of the population changes over time. (So natural selection influences the distribution of height, intelligence, and hair color, but not the number of people who have tattoos, pierced ears, or Shakespeare's sonnets committed to memory.)

At the end of *The Origin of Species* Darwin summarized the mechanism in the following way:

- If there are organisms that reproduce, and

- If offspring inherit traits from their progenitor(s), and
- If there is variability of traits, and
- If the environment cannot support all members of a growing population,

then those members of the population with less-adaptive traits (determined by the environment) will die out, and those members with more-adaptive traits (determined by the environment) will thrive, leading to evolution of species.

These simple statements turn out to be controversial and complicated. They are controversial because they run counter to some intuition and religious beliefs. They are complicated because the formulation leaves open many of the details of the process. For one thing, Darwin did not know much about how traits were transmitted from one generation to the next. (Mendel came later and Crick and Watson came later still.) For another, there has been refinement in the idea of what is the current object of selection. I described evolution as operating on a "trait." Some authors argue that evolution operates at the level of groups – like species. The most intuitive discussions have selection operating at the level of the individual. But it is now understood that the transmission operates at the level of genes, which are generally viewed as the true object of selection. Since there are so many genes, the selection pressures are complicated. Since there are so many forms of life that operate in so many different environments, there will be many puzzles for natural selection to explain and many ways to apply the reasoning.

3 Evolutionary Stable Strategies

Here is a simple mathematical model of the situation. Suppose that the population is governed by a reproductive system that produces male children with probability m and female children with probability f, $m + f = 1$, $m, f \geq 0$. In the next generation, we suppose that each female produces one child and paternity is uniformly distributed over the males in the population. This means that if $m = f$, then each male produces one child, but in general if the expected number of children for a representative male is $\frac{f}{m}$. If there are more males than females, however, then competition among males lowers a male's productivity, while if there are more females, then a representative male can impregnate more than one female. It follows that an organism that produces males with probability m will expect to have $m(\frac{f}{m}) + f(1) = 2f$ children. Notice that this formula confirms that our intuition that the growth rate of the population is faster the greater the percentage of female children.

A sex-ratio is stable if a "mutant" organism that produces males at the rate m^* and females at the rate $f^* = 1 - m^*$ produces fewer children that the existing organism. So how successful is the new organism? It produces

$$m^*(\frac{f}{m}) + f^* \tag{1}$$

if it is the only organism that has the mutant trait (so that its mix of children does not substantially change the sex ratio of the next generation). You need to modify the formula slightly if the mutation occurs in a "positive fraction" of the population. In this case, the sex-ratio in the next generation is not $m : f$, but slightly skewed towards $m^* : f^*$. I will include the details of this computation in a moment, but it really just interferes with the main point.

Writing $m^* = m + \mu$ (and so $f^* = f - \mu$), (1) becomes

$$m^*(\frac{f}{m}) + f^* = 2f + \mu(\frac{f}{m} - 1). \tag{2}$$

Equation (2) yields our conclusion. If the sex-ratio is not equal ($m = f$), then a properly selected mutant (produce more of the sex that is in the minority) will grow in size. The only possible stable sex ratio is $50 : 50$ (with $m = f$).

Now let me take into account the possibility that mutants influence the sex ratio. Suppose that a fraction ϵ of the population carries the mutation. We need to recompute the expected fitness of both the mutant population and the original population. If ϵ is the fraction of the population that produces m^* males and $1 - \epsilon$ is the fraction of the population that produces m males, then the number of males in the next generation is $m(\epsilon) = \epsilon m^* + (1 - \epsilon)m = m + \epsilon\mu$. Consequently, the number of offspring produced by the dominant strain is:

$$m(\frac{1 - m(\epsilon)}{m(\epsilon)}) + f = 2f - \epsilon\frac{\mu}{m + \epsilon\mu} \tag{3}$$

while the number of offspring produced by the mutant strain is

$$m^*\left(\frac{1 - m(\epsilon)}{m(\epsilon)}\right) + f^* = 2f - \epsilon\frac{\mu}{m + \epsilon\mu} + \mu\frac{1 - 2m(\epsilon)}{m(\epsilon)}. \tag{4}$$

The mutant is less fit than the rest of the population if and only if $\mu\frac{1-2m(\epsilon)}{m(\epsilon)} < 0$. When $m = \frac{1}{2}$, we have $\mu\frac{1-2m(\epsilon)}{m(\epsilon)} = -2\mu^2\frac{\epsilon}{m(\epsilon)}$, which is negative whenever $\mu \neq 0$. On the other hand, if $m \leq \frac{1}{2}$, when the mutation rate is small (ϵ is close to zero),a properly chosen μ (which determines whether the mutation biases the sex ratio in favor of males or females) will guarantee that the fitness of the mutants will exceed that of the rest of the population.

We can extend the notion of evolutionarily stable strategy to more general situations.

4 Why the $50 : 50$ Sex Ratio is not Universal

Sex ratios in different species differ from $50 : 50$. It is interesting to examine situations where Fisher's argument does not apply.

4.1 Local Mate Competition

Fisher's theory assumes that there is 'population-wide' competition for mates. Hamilton (1967) first pointed out that the sex ratio will become biased in species in which an individual competes against only a limited part of the rest of its population. The condition is called local mate competition. The pyemotid mites are an extreme case. In this group, brothers inseminate their sisters while they are still inside their mother. A mother therefore only needs to produce one or two males in a brood to inseminate all her daughters; the sex ratio is female biased. In Pyemotes ventricosus, for instance, the sex ratio of a brood contains on average four males and 86 females. The males are not competing against the whole population for mates; they compete only against their brothers, and a mother can reduce the fruitless competition by producing fewer sons.

4.2 Dominant Females Produce More Males

In polygynous species, males have multiple wives. Hence, a small number of males do a disproportionate amount of the breeding. Many males die before reaching the breeding stage and even then some males (the ones that do not get mates) fail to breed. Fisher's argument demonstrates that a female cannot gain by producing more males, even if only a minority of them survive to breed. By producing more males, the average female would be as likely to produce more of the failures as successes.

There is a circumstance in which it can be advantageous to bias the sex ratio, however. It is when a female 'knows' that she is not an average female, and that her offspring will not be average sons and daughters. Consider the case of the red deer Cervusal megalocerus. The breeding system is polygynous, as females live in groups, which are defended by a single male. Within a group of female deer, there is a dominance hierarchy. The more dominant hinds are better fed and stronger, and they can better provide for their offspring. Their offspring in turn grow up to be stronger than average. In these circumstances, there can be selection on higher ranking females to produce more sons, and on lower ranking females to produce more daughters. A high ranking female can expect to produce successful sons, and a low ranking female to produce sons that fail to breed.

5 Alternative Chromosome Patterns

In mammals, apart from rare exceptions, one X and one Y chromosome makes you a man, and two X's make you a woman. Move outside mammals, though, and there is a lot of variability. Birds are just the opposite: roosters are XX, hens, XY.

Sex in butterflies is done just like sex in birds, but fruit flies are basically like us. This raises a question: flies and butterflies share a common ancestor (which must have had some sex determination scheme), but they have managed to evolve completely opposite ways to decide what sex they are. Humans much closer to birds than either birds or humans are to insects, but our sex-determination scheme is the same as the fly's.

That is not all. Praying mantisses have one X and several Y's: Females have two X's, while males have one X and a handful of distinct Y's: each Y is different, and each male has one Y of each kind. Other species turn this on its head, and have several X different chromosomes but only one Y: each female may have, say 3 different pairs of X's, while her mate has 3 X's and a single Y.

Some animals, like the voles, have gotten rid of their Y's altogether. One sex has two X's and the other has one. Spiders have several X chromosomes. Females might have six, while males have three – but no Y.

But there's constant threads running through all of this: Despite this wild diversity, there are always exactly two sexes, males and females (there may be exceptions even to this in algae). One has one sex-chromosome makeup; the other has a second. Also, one sex makes two kinds of gametes, in equal numbers, and the other only makes one. All human (or fly) eggs have an X chromosome, but each human male has two kinds of sperm: X sperm and Y sperm. If we were birds, males would make only make one kind of sperm, but our mates would make two kinds of eggs.

In spiders with three sets of X chromosomes, spider moms always make eggs with three X's, while spider dads make sperm that have either three X's or no X.

Ants, bees, and wasps take this to an extreme. Effectively, every chromosome is an X: An egg has one full set of chromosomes. Fertilized eggs (ones that get an additional full set from dad), become daughters, unfertilized eggs (one that get no set from dad – effectively an "empty sperm") become sons.

The regularity means that when you mate a male and a female, you get two kinds of offspring: sons and daughters. And the production of equal numbers of two kinds of gametes by one sex means that there are the same number of sons as daughters.

There is a famous counter example to this property, however. The swordtail is a Central American fish that has three different flavors of sex chromosomes: an X, a Y, and a Z. Here's how sex determination works:

Each individual only has two sex chromosomes: XY, YZ, XZ, ... but not XXX, $XYZZ$, or anything else with more than two. If you carry a Z, you're a female. Otherwise, if you have a Y, you're a male. This gives us the following possibilities: chromosomes sex YY male XY male XX female YZ female XZ female. Notice that ZZ pairs do not exist. A ZZ would have to get a Z from mom and a Z from dad. But swordtails with Z's are never dads.

This is very different system with lots of odd pairings. For example, $XX \times YY$ gives all sons, while three-quarters of the offspring of $XZ \times XY$ will be daughters.

There is one curious empirical pattern associated with the different chromosomal structure of birds and mammals. I can't argue that this is an instructive point about mathematical models, but it is curious and stimulating enough that I cannot resist mentioning it.

6 The Weaker Sex

It is the case that (human) males are the weaker sex in that they have higher mortality rates. Indeed, Fisher's argument really applies to the ratio of sexes at the reproductive stage. Since boys die at a higher rate than girls, it is likely that the 1.05 : 1 ratio that we observe at birth evolved to equalize the sex ratio at the time of mating.[2] This could happen, even within our reproductive system, if somehow XY pairs were more likely to form than XX pairs. The most natural mechanism would be if Y sperm were most robust that X sperm. In any event, it is certainly the case among humans that the older the sample population, the greater the fraction of females. This characteristic is true of humans but not birds.

The following table shows both a change in sex ratio (away from 50 : 50) with age, and a difference between birds and mammals in the direction of the bias. The three mammals at the end of the table all show a bias towards females. The birds show the reverse.

Species	Juvenile sex ratio (% males)	Adult sex ratio (males)
Hungarian partridge	50	56
Bobwhite quail	51	62
California quail	50	58
Ruffed grouse	50	54
Willow ptarmigan	54	60
Sharp-tailed grouse	49	55
Mallard	51.2	63.8
Black duck	48.6	61.3
Pintail	51.6	54.9
Canvasback	44.0	56.8
Scaup	49.7	61.4
Starling	52	66
Brown rat	51	41
Muskrat	57	50
Cottontail rabbit	50	46

Examples of ungulate sex ratios. Note the increasing bias toward females in the elk data (which are the only data for prenatal ratios):

Species	Prenatal sex ratio (M:F)	Adult sex ratio (M:F)
Elk	53:47	23:77
Mule deer	n.a.	35:65
Mt. goat	n.a.	43:57

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[2] Another possibility is that it requires less investment in parental resources to "make" male children.

So, the empirical data show that adult sex ratios in birds often tend to be male-biased, while those in mammals tend to be female-biased.

What might explain this pattern of sex ratio differences between birds and mammals? Biologists propose several alternative hypotheses that might explain the pattern. The first seems more elegant to me (but this does not make it the most important empirically).

The "Chromosome" Hypothesis asserts that the heterogametic sex is weaker than the homogametic sex. (In species with chromosome-derived sex determination, the sex that has the "different" chromosome is called the heterogametic sex. This means that males are the heterogametic sex in mammals and females are the heterogametic sex in birds.)

The logic behind this hypothesis is that recessive deleterious alleles can have more effect in the heterogametic sex. A recessive allele is a form of a gene that is expressed only when it occurs in a homozygote – when it occurs in a heterozygote it is blocked by the other "dominant allele." For XY males, a recessive allele on the X chromosome will be expressed, because there is no other X chromosome to carry the dominant allele that will prevent the recessive characteristic from expressing itself. So male mammals and female birds have less protection against bad recessive characteristics and die younger than their homogametic partners.

Alternate hypotheses have some empirical support, but are less elegant because they are not directly connected to the chromosomal structure of sex determination. For example, according to the hypothesis of density-independent mortality, female birds sit on nests more than male birds, so they are more exposed to predators. On the other hand, male mammals must fight for food (or social position) leading to greater mortality rates. There are also related stories involving, for example, different dispersal rates of the different sexes. Again, these stories do not have the beauty of being directly related to the mechanism that determines the sex ratio.