

Sex Ratios and the Power of Game Theory

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Ever see a family with five sons and feel really sorry for the mom? How unlucky. Indeed, the probability of having five boys is a scant .03, or $(\frac{1}{2})^5$.

The underlying odds of sex determination are surely one of the most widely known biological facts. It's a coin flip. But the ubiquity of a roughly 50-50 ratio in humans and most sexually reproducing species is puzzling.¹

First, it's inefficient. In animals like elephant seals, one male controls a harem of up to a hundred females, and many (relatively) scrawny bros are stag for life. Why not bias the sex ratio in favor of females so that no dudes die without reproducing? It'd certainly be better for the species—one male and three females can have more kids than can two males and two females. Second, a 50-50 ratio at birth does not guarantee a 50-50 ratio at adulthood, since males are more likely to die young. Why should the ratio matter at birth but not maturity?

Fisher's (1930) solution to the problem bears a striking similarity to Nash's fundamental work in game theory twenty years later.²

It goes like this: Pretend you're choosing between investing in a son or a daughter, and your only goal is to maximize your number of grandchildren. Assume, for simplicity's sake, that (a) the costs of rearing are the same for both sexes, (b) everyone in the next generation will have an equal shot at reproduction and (c) there's no inbreeding. Then if sex ratios are lopsided and there is only one male born for every two females, the choice is obvious: you should invest in a son.

Why? If the 50 males and 100 females from this generation have 200 kids, each male would on average have four kids ($200/50$) and each female would have two ($200/100$). Even if some males have zero kids while others have eight, you'd still expect a greater number of grandkids from a son. In reality you wouldn't be able to choose, but mutations favoring sons would increase until the expected number of grandkids was the same for either sex, that is, a 50-50 sex ratio.³

What's the relationship with Nash's later work? Nash Equilibrium, informally, means that no one can benefit by changing her behavior when everyone else stays the same. Thus, in the case above, this occurs at 50-50, when no parent can increase her expected number of grandkids by having more boys or girls. At all other ratios, given the assumptions, a parent could fare better by unilaterally biasing her births in favor of the less-born sex. Note that this theory not only explains the ubiquity of 50-50 ratios—it is also consistent with the 50-50 ratio at birth despite polygyny and high male mortality. These increase the *risk* of having a son, in terms of number of grandchildren, but not the *expectation*, which determines which genes get passed to future generations.

¹ The human sex ratio is slightly biased toward men, 105:100 (United Nations, 2004)

² Darwin made a similar argument in an early edition of *The Descent of Man* (Osborne, 1996).

Some of the most powerful predictions of Fisher's insight come from the exceptions to the 50-50 rule. If we look carefully, we can see that each of these is the result of breaking one of the assumptions above.

First, let's violate assumption (a) and imagine females are more costly to bear. We know from Fisher that equilibrium occurs when you're indifferent between investing in a son or daughter. But if daughters cost twice as much as sons, then the ratio should be biased by the simple principle of more-bang-for-your-buck. Sure enough, Trivers and Hare (1976) showed that, across ant species, the ratio of female to male weight—a proxy for the additional amount of investment required by females—predicts the sex ratio. Species such as *Aphaenogaster rudis*, or the winnow ant, with a female to male weight ratio of 13:1, produce much fewer females than leaf-cutter ants, where females are only about three times as heavy.

Further, assumption (b) is that all parents expect the same amount of grandkids from their sons (or daughters). But parents might not be completely in the dark about their sons' prospects. Trivers and Willard (1973) predicted that if females are dominant and healthy, they should invest more in sons, as they have a good indication that their son will be an alpha male, with more offspring than is physically possible for a daughter.

In a recent large-scale study on animals at the San Diego Zoo, the sons of mothers who gave birth to disproportionately more sons had much more offspring than the sons of mothers who had equal numbers sons and daughters. In other words, mothers with sex ratios biased in favor of males had sons who were more successful (Thogerson, et al., 2013). Perhaps they knew, in some deep, physiological sense, that sons were the right bet.

(Interestingly, humans might also exhibit this tendency: families in a Forbes list of billionaires have 60% sons, which is significantly different from a coin flip (Cameron & Dalerum, 2009). But this was a small, and certainly weird, sample.)

Finally, assumption (c) is that there is no inbreeding. But if there is, females should be more common since, from a grandkid-maximizing perspective, you'd rather have one son and three daughters rather than two sons fighting over sexual access to two daughters. Herre (1987) showed that, across thirteen species of fig wasps, female bias was positively correlated with the degree of inbreeding. Further, females in some species were found to adjust their sex ratio in favor of males when they anticipated the presence of another family in the same fig, responding as predicted to increased competition.

Fisher's insight has inspired thousands of studies, and is still cited as one of the most triumphant moments in theoretical biology—all for the intuition that deviation from equilibrium presents an opportunity for participants in the game. Notably, these strategies arise not through conscious calculating but rather the brute mechanics of natural selection (Smith & Price, 1973). We'll see shortly that this equilibrium concept provides deep insights well beyond the world of elephant seals and leaf-cutter ants.

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