

From last time, we had solved for the stable sex ratio when the population size was infinite and mating was random. This is called the Fisherian sex ratio. Remember that the allocation of resources to sons and daughters was equal at equilibrium $a^*=0.5$. The sex ratio is only equal if the cost of producing a daughter is the same as the cost of producing a son.

Specifically, the proportion of males in the population at the ESS is predicted to be

$$\text{Male frequency} = \frac{Ra^*/C_{sons}}{Ra^*/C_{sons} + R(1-a^*)/C_{daughters}}$$

Then we discussed some **advanced points** about the Fisher model. Here they are.

1. Strictly speaking, the solution for a^* is not an ESS, because the second derivative is equal to zero. That is a consequence of the assumption of infinite population size, and as such, there are linear gains associated with allocation to male function.
2. The assumption of infinite population size also means that no single individual that deviates from $a^*=0.5$ affects the sex ratio. So, if the population is at equilibrium ($a^*=0.5$) the sex ratio can drift. But if it drifts away from 0.5, there is an advantage to individuals that are closer to 0.5 than the population mean. This is very similar conceptually to condition 2.4b in Maynard Smith's chapter. Do you see why?

3. This tendency to move toward the attractor of $a^*=0.5$ when the population mean is away from 0.5 is called convergence stability (or continuous stability). Mathematically, the attractor is convergence stable strategy (a CSS) if:

$$\left. \frac{\partial^2 W_i}{\partial a_i \partial a_{res}} \right|_{a_i = a_{res} = a^*} < 0$$

The Fisherian sex ratio is a CSS. So it is not an ESS, but it is a CSS.

4. Finally, the Fisher sex ratio model is very good at showing an important point: as the sex ratio gets closer to the attractor of $a^*=0.5$, the selection differential becomes less steep, and drift becomes more likely.

End of **advanced points**.

Hamilton's tweak:

Bill Hamilton new that sex ratios were often female biased, even though the sexes were apparently equally costly. He wrote a very famous paper in 1967 called Extraordinary Sex Ratios (Hamilton 1967). In that paper, he relaxed the assumption of infinite population size and random mating. Instead organism could be mating in small groups, like wasps or barnacles. This means that an individual's allocation to sons or male function in hermaphrodites could greatly affect the mean of the group. He called this local mate competition.

As an historical note, Hamilton also introduced the idea of the "unbeatable strategy." It was in fact the same idea as the ESS, but

Hamilton's unbeatable strategy predated the concept of the ESS by 6 years. ESS caught on, but unbeatable strategy did not.

To get an intuitive feeling for Local Mate Competition, we played the barnacle game.

Local Mate Competition: **The Barnacle Game**

Rules: you have 100 units of resources

1. One egg costs 10 units
2. One sperm costs 1 unit.

So you could make 10 eggs and no sperm,

Or you could make 9 eggs and 10 sperm,

Or 5.5 eggs and 45 sperm

Or 0 eggs and 100 sperm.

Get into groups of two and cross-fertilize. Then count the number of zygotes that you contributed to. Goal, maximize the number of gametes that you contributed to.

Now groups of 4...

Literature Cited

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477-488.