Next two lectures...

1. Games against the field: continuous strategies.
2. The Fisherian sex ratio
3. Hamilton’s tweak: Local Mate Competition (LMC)
4. The barnacle game
5. Diminishing returns on allocation
6. Advanced topic: Evolutionary Stability vs. Convergence Stability
1. Games against the field: continuous strategies.

Consider the evolution of sex ratio. It is clearly not an evolutionary game like the hawk-dove game in which individuals are selected at random to contest a resource.

Instead the sex ratio can be thought of as a maternal strategy, where the question is, how many sons and how many daughters should she produce? Here, even though the morphs (male, female) are discrete, the strategy is continuous, at least in theory. The maternal parent could make anywhere from 0 to 100% sons.

We need a new formulation to deal with this continuum.

The new formulation is, in general, to write the fitness of a target individual as a function of its own strategy, and that of the remaining individuals in the population (the residents).
In what follows, \( a_i \) stands for allocation of the resource \((R)\) to males by the target individual (often thought of as a mutant), and \( a_{res} \) stands for the allocation of the resource base to males by the resident population. In general, then, \( W_i \), the fitness of our target individual is a function of \( a_i \) and \( a_{res} \). In other words

\[
W_i = f(a_i, a_{res})
\]

Natural selection will favor mutations that increase \( a_i \) when

\[
\frac{\partial W_i}{\partial a_i} > 0
\]

Natural selection will favor mutations that decrease \( a_i \) when

\[
\frac{\partial W_i}{\partial a_i} < 0
\]

Note that by taking the partial derivative, we are assuming that \( a_{res} \) does not depend on \( a_i \) in an infinite population, because the mutation only affects the strategy of our target individual.
The candidates for the ESS are found by setting the first derivative = 0, and solving for $a^*$ (the stable value) when $a_i = a_{res}$. In other words, when

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

The solution is Evolutionarily stable (an ESS) if the second derivative is negative:

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

And the solution is Convergence stable (a CSS) if

$$\left. \frac{\partial^2 W_i}{\partial a_i \partial a_{res}} \right|_{a_i = a_{res} = a^*} < 0.$$
Rate of change = \frac{y + \Delta y - y}{x + \Delta x - x} \quad \text{Hence,}

\frac{\Delta y}{\Delta x} = \text{rate of change near } (x, y)

\frac{dy}{dx} = \text{slope of tangent line at } (x, y)
I show that \( \frac{dy}{dx} = 2cx \) for \( y = cx^2 \)

1. \( y = cx^2 \)
2. \( y + \Delta y = c[x + \Delta x]^2 \)
3. \( y + \Delta y = c[x^2 + 2x\Delta x + \Delta x^2] \)
4. \( y + \Delta y = cx^2 + 2x\Delta x < \)
5. \( \frac{\Delta y}{\Delta x} = \frac{\Delta y}{\Delta x} \)
6. \( \frac{\Delta y}{\Delta x} \approx \frac{dy}{dx} = 2cx \)

\( \Delta x \) is very small.

This is \( y \)

More generally, for \( y = cx^N \)

\[
\frac{dy}{dx} = Ncx^{N-1}
\]
Note that there is a local max for fitness at \( q = 0.25 \)

where the first derivative is zero AND the second derivative is negative

Q: what if the second derivative is \( > 0 \)?

see: L567 Lecture 9 CalcRefresh.xlsx
2. The Fisherian sex ratio

Fisher predicted that the best strategy for the sex ratio is for mom to allocate equal amounts of resources to the production of sons and daughters. Note: this is not the same as saying that the optimal sex ratio is 50% males, although it is often presented that way. Part of what we want to do is prove that to ourselves.

Fisher assumed an infinitely large population of randomly mating individuals. He also assumed that all the females would be fertilized, even if there were very few males in the population.

The first step is, under this assumption, to write the equation for fitness of our target individual in terms of its own strategy and the strategy for the rest of the population (which is infinitely large).

One way to do this is to add up the number of expected grandchildren that result from the sex ratio

Fitness = contributions through daughters plus contributions through sons.
Let the cost of each daughter be $C_d$; let the cost of each son be $C_s$; and let the amount of resources available for reproduction be $R$.

So if $a_i$ is the proportion of resources allocated to sons, the number of daughters produced is

$$= \frac{R(1-a_i)}{C_d}$$

And the number of sons produced is

$$= \frac{R(a_i)}{C_s}$$

Total fitness will depend on the number of sons and daughters produced. But (and this is key) the gains through sons depends on the frequency of females in the population.
One way to write the equation from mom’s fitness is

\[ W_i = \frac{R(1-a_i)}{C_d} + \frac{R(a_i)}{C_s} V, \]

which is simply the number of daughters + the number sons times the reproductive value \((V)\) of sons. What is \(V\)?

\(V\) depends on the number of females per male in the population. Hence, assuming a large, panmictic (random mating) population, we can write \(V\) as

\[ V = \frac{R(1-a_{res})}{C_d} \cdot \frac{C_s}{R(a_{res})/C_s} \]

Thus we have,

\[ W_i = \frac{R(1-a_i)}{C_d} + \frac{R(a_i)}{C_s} \left[ \frac{(1-a_{res})}{C_d} \right] \frac{(a_{res})}{C_s} \]
Taking the first derivative, we get

\[
\frac{\partial W_i}{\partial a_i} = -\frac{R}{C_d} + \frac{R}{C_s} \left[ \frac{(1-a_{res})}{a_{res}} \cdot \frac{C_s}{C_d} \right]
\]

now we set \( a_i = a_{res} = a^* \) and solve for the equilibrium, \( a^* \). The equilibrium is found at the value for which the first derivative is equal to 0, which is when

\[
\frac{R}{C_d} = \frac{R}{C_s} \left[ \frac{(1-a^*)}{a^*} \cdot \frac{C_s}{C_d} \right]
\]

\[
a^* = \frac{1}{2}.
\]

Thus, the candidate ESS is to allocate half the resources for reproduction to sons. (note: see Harman’s The Price of Altruism page 170 for how Williams realized that this result worked against the “good of the species arguments” by Wynn Edwards. See also page 171 for a simple game that shows the logic.)
What is the frequency of males at equilibrium?

Under what conditions would you expect a 50:50 sex ratio?

Male frequency = \( \frac{\text{Number of sons}}{\text{Number of sons} + \text{Number of daughters}} \)

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

Now solve for Male Frequency at the equilibrium, \( a^* = \frac{1}{2} \).

Male Freq = \( \frac{1}{1 + C_d/C_s} \)
Is the solution an ESS? If yes, why? If no, why not?

What is the second derivative? The second derivative is 0.

\[
\frac{\partial^2 W_i}{\partial a_i^2} \bigg|_{a_i = a_{res} = a^*} = 0
\]

The solution for \(a^*\) is not an ESS...

If the equilibrium is not as ESS, what would happen if the population mean drifts away from \(a_{res} = 0.5\)?

Is the solution a CSS? If yes, why? If no, why not?

\[
\frac{\partial^2 W_i}{\partial a_i \partial a_{res}} \bigg|_{a_i = a_{res} = a^*} = \frac{-R}{\frac{a^2_{res} C_d}{a^2}} < 0
\]
Plot the CSS (for $R = 1; \ C_d=0.1$)  

(see "graph the CSS_2.nb")

First derivative of $W$ against $a_i$ plotted against $a_{res}$
**Advanced points** about the Fisher model (borrowed from Lecture 10).

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. We are about to study that.

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 sex ratio drifts away from 0.5, then there is an advantage to individuals that are closer to 0.5 than the population mean. Thus the population mean will tend to be moved by selection back towards the equilibrium (converge on the equilibrium). Hence the equilibrium solution is Convergence Stable. In other words, the equilibrium is a CSS. We will graph that.
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. It is not an ESS, but it is a CSS.

4. Finally, the 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 step, and drift becomes more likely. We will study this in more detail today.

End of advanced points.
The barnacle game: to get an intuitive feeling for Local Mate Competition, we will play 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 offspring that you genetically contributed to. ...Now groups of 3 (or 4?)...