

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. Continuous Stability
ESS or CSS?
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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 I 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 , which is a reasonable assumption, 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 stable if [the second derivative is negative](#):

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

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 we can write V as

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

Thus we have,

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

Taking the first derivative, we get

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

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

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

$$a^* = \frac{1}{2}.$$

Thus, the candidate ESS is to **allocate half the resources** for reproduction to sons.

What is the frequency of males at equilibrium? (see lecture10, page1)

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

Is the equilibrium an ESS? If yes why, If no, why not?

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