ESS

- Optimality models are often organism vs. environment where the individual is reacting to a stable environmental condition
- ESS thinking allows for analyzing the fate of strategies in a population *when the benefit of the strategy depends on the frequency* of all the strategies in the population. So, though the physical environment of the organism might remain constant, its biological environment is subject to change
- Earliest use was in evolutionary arguments for the sex ratio of populations (Fisher 1930). We'll see this in another two weeks
- Makes use of similar assumptions about evolution as optimality models. Namely heritability, and the variability was there at some time in the past
- Given those assumptions, which strategy would one expect to find in a population? It is not necessarily the one that would optimize the mean fitness of the population—it is the one which, if everyone has adopted it, cannot be invaded by any other strategies (John Maynard Smith)
- This is best explored in an example. We use the "Hawks-Doves" scenario
- Toy problem that somewhat simulates the costs/benefits of contests between individuals. For example, elk during the rutting season in contests. In that case you achieve mating rights if you win, and you may be penalized with injury if you lose.
- Assume that the value of winning and the cost of energy can both be measured on the same scale.

$$\begin{aligned} V &= \text{Benefit Available} \\ C &= \text{The Cost of Fighting and Being Injured} \end{aligned}$$

- The Players are "You" and "Opponent"
- The possible strategies you might "play" are
  1. H = Hawk = Fight Always
  2. D = Dove = Never Fight
- The game can be represented in terms of the expected payoff matrix:

$$\begin{array}{cc} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} E(H,H) & E(H,D) \\ E(D,H) & E(D,D) \end{pmatrix} \end{array}$$

- Putting some numbers in there:

$$\begin{array}{c c} & \begin{array}{cc} H & D \end{array} \\ \begin{array}{c} H \\ D \end{array} & \begin{pmatrix} \frac{V-C}{2} & V \\ 0 & \frac{V}{2} \end{pmatrix} \end{array}$$

- This is because
  1. Doves split the value of the benefit available fairly
  2. Doves never fight hawks—they don't get injured, but they don't benefit either
  3. hawks always win everything from doves
  4. When two hawks encounter each other, half the time one of them gets injured and the other gets the benefit, while the other half of the time it's the other way around.

- Recall that to find the ESS we ask whether the strategy cannot be invaded

- Consider a population that is all doves, then imagine introducing a single hawk. In such a population does the hawk do better? You betcha! In *every encounter* it will make V benefit while doves will make only $V/2$ benefit in *almost* every contest. So Dove is not an ESS.

- Consider a population that is all hawks. If you were a lone dove in the population, you would always benefit 0 from each interaction, while hawks would benefit $(V-C)/2$ from almost every contest. Therefore, if the cost of injury is less than the benefit of victory (i.e. $V > C$), hawk is still the more profitable strategy; it is called a *pure* ESS. (Pure because everyone in the population should adopt it.)

- The above argument is that which is embodied in Maynard Smith's "condition number one"

- If $V < C$ then doves could invade an all-hawk population, so there is no longer a pure ESS.

- There might be a mixed ESS. This is a situation in which the two strategies should be maintained at a particular frequency. That frequency is the one at which the expected payoff to a dove encountering an individual drawn at random from the population is the same as for a hawk encountering an individual drawn at random from the population.

- Hence, if p is the proportion of hawks in the population the mixed ESS will have:

$$p \cdot 0 + (1-p)\frac{V}{2} = p\frac{V-C}{2} + (1-p)V$$

  which implies that p = V/C. So if injury is very costly, you'd expect to find far fewer "hawks" in the population.

- ESS theorists openly admit that they have tossed genetic rigor out the window, but feel it allows them to look more broadly at different possible sets of strategies.