Hawk/Dove example from Dawkins

Imagine a game with the following payoff structure:

	Hawk	Dove
Hawk	-25	50
Dove	0	15

The number in the box is the payoff that the row player receives when paired against the column player. So in this case, a hawk gets -25 when paired with a hawk while the receive 50 when paired with dove.

In this game, neither strategy is an ESS. Here is how we know:

Hawk is not an ESS. If everyone was playing hawk, the average payoff in the population would be -25. If a mutant dove came in, they would be paired against a hawk and so would get 0. But 0>-25 so doves would start to increase in frequency and invade. So hawk is not stable.

Dove is not an ESS. If everyone was playing dove, the average payoff in the population would be 15. If a mutant hawk came in, they would be paired against a hawk and so would get 50. But 50>15 so hawks would start to increase in frequency and invade. So dove is not stable.

As it turns out, this game has a stable polymorphism. That means that natural selection will push the population towards a state that has a mix of hawks and doves. To see what this state is like, note that for the state to be stable, hawks and doves would have be receiving the same payoff on average (otherwise selection would push one of them to increase in frequency).

The average payoff to a hawk is: -25*P(H) + 50*P(D) where 'P(H)' is the probability of meeting a hawk (which is the frequency of hawks in the population) and 'P(D)' is the probability of meeting a dove.

The average payoff to a dove is: 0*P(H) + 15*P(D). So hawks and doves get the same payoff when -25*P(H) + 50*P(D) = 0*P(H) + 15*P(D).

By algebra, this means that -25*P(H) + 50*P(D) = 15*P(D) and so 35*P(D) = 25*P(H) and so P(D)/P(H) = 25/35 = 5/7. That is, the stable ratio of doves to hawks is 5:7. If you want to solve for the actual frequency of hawks and doves, note that a 5:7 ratio means that 5/12 individuals will be doves. Since P(D) + P(H) = 1, that means that 7/12 individuals will be hawks.

Another way to think about it is to go back to the claim that 35*P(D) = 25*P(H) (or any other step along the way). Note that P(D) + P(H) = 1. So by substitution, 35*(1-

P(H) = 25*P(H). Thus 35-35*P(H) = 25*P(H). Thus 35=60*P(H) and so P(H) = 35/60 = 7/12.

We can verify that this is in fact the equilibrium by making sure that at this frequency, hawks and doves really do get the same average payoff.

The average payoff to a hawk is: -25*P(H) + 50*P(D) = -25*(7/12) + 50*(5/12) = -175/12 + 250/12 = 75/12

The average payoff to a dove is: 0*P(H) + 15*P(D) = 15*P(D) = 15*(5/12) = 75/12.

Thus when P(H) = 7/12 and P(D) = 5/12, hawks and doves get the same average payoff (75/12 = 6.25) and thus selection will not change the frequencies any further. And it is easy to verify that if the frequencies are any other numbers, then selection will push the population towards this state.

To help you understand the game, we can change the numbers and the story a bit. In humans, lets call 's' the name for the sickling allele which causes red blood cells to have a deformed shape but also gives the bearer resistance to malaria. The homozygous recessive situation ss gives the bearer sickle cell anemia. Lets say 'A' is the name for the 'normal' allele. Lets assign fitnesses as follows: Fitness of AA = 1.8, Fitness of As = 2.1, Fitness of ss = 0.1

As it turns out, it is useful to think of the two alleles A and s as playing a strategic game. How good the strategy is depends on who your partner is.

	A	s
A	1.8	2.1
s	2.1	0.1

So what will happen to the population? It is fairly easy to see that qualitatively, the ordering is the same as in hawk/dove and so just as neither hawk nor dove is stable, neither A nor s is stable. What will evolve instead is a stable polymorphism with some A alleles and some s alleles in the gene pool.

To determine what that equilibrium is, we find the frequencies at which the fitness of A = the fitness of s. If you did this in a genetics class, you might use the Hardy-Weinberg principle using p, q as the frequencies noting that p^2 will be the frequency of AA, q^2 will be the frequency of ss, and 2pq will be the frequency of As. We will just use game theory.

Average fitness of A = 1.8*P(A) + 2.1*P(s)
Average fitness of s = 2.1*P(A) + 0.1*P(s)

These are equal when 1.8*P(A) + 2.1*P(s) = 2.1*P(A) + 0.1*P(s) and so 2*P(s) = 0.3*P(A). This happens when P(s)/P(A) = 0.3/2. Remember that P(s)+P(A) = 1, we get that P(s) = 0.3/2+0.3 = .3/2.3 = 3/23 or approximately 13%.

If my fitness numbers were accurate (total guess!) then 13% of the alleles in the population would be s. Assuming random mating (definitely not true!), that means that 13% ^ 2 = approximately 1.7% would be the frequency of people with sickle cell anemia.