1. (13 points) Imagine a site in DNA where there are 4 possible bases (the usual A, C, G, and T), so four alleles. Suppose we have a symmetric model of change of the bases, so at this site there is a mutation rate $u$ from each of these bases, and when a base mutates it is equally likely to change to each of the other three bases. Let the frequencies in an infinite random-mating population of these three alleles in generation $t$ be $x_A(t)$, $x_C(t)$, $x_G(t)$, and $x_T(t)$.

(a) Write out the four equations for the frequencies of these four alleles in the generation $t+1$, as a function of $u$ and of their frequencies in generation $t$.

(b) Make a good guess as to what the frequencies of the four bases will be at mutational equilibrium. Verify that this is correct using these equations.

(c) How quickly will the population approach these frequencies? [Hint – consider the difference between the frequency of A and the average of the three other frequencies, those of C, G, and T, then note what the relationship must be between $x_A$ and $x_C + x_G + x_T$, then see if you can write the first equation, the one for $x_A(t)$ simply in terms of that variable. Now find out how fast $x_A(t)$ approaches its equilibrium value. This will take some algebra but will all work out nicely.]

2. (12 points) Suppose we have a chromosome rearrangement that changes the gene order on the chromosome back or forth between two gene orders, which we will call I and II. Suppose that it has no effects on fitness when you have two of the same gene order, but has 10% lower fitness when you are a “chromosome heterozygote” which has both of the two gene orders. If you have a rate $u$ of rearrangement in both directions between these, what will be (approximately, using the formulas for equilibrium between mutation and selection) the equilibrium frequency of II in a population that starts from gene order I? What will be the equilibrium frequency of gene order I in a population that starts with gene order II? Give a formula in terms of $u$, and calculate the frequencies for $u = 10^{-6}$ and $u = 10^{-4}$. 