Introduction to Evolutionary Dynamics

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Lecture – 26
Evolution, Selection, and Genetic Drift

Hi everyone, in the last lecture we had ended by deriving a very important result which was which we depicted as x subscript 1 which represented the probability that in a marble in a jar kind of an experiment should we have one individual which is different from the rest of the population, what is the probability that that particular individual takes over the entire population and eliminates a rest of the n minus 1 individuals from the population.

In the context of our bacterial evolution what this represents is that in an isogenic population of size n, should a neutral mutation happen such that the new individual is not genetically identical with the rest of the population, but at the same time is equivalent to the rest of the population when it comes to the fitness associated with these individuals. So, the fitness is do not change, but the genotype has changed which means there has been a neutral mutation what is the probability that this individual is able to take over the entire population and eliminate the rest of n minus 1 individuals, that are present in this environment that we are interested in.

And for this to happen if this were to happen that is not going to happen via selection because fitnesses of these individuals are equal, but what is going to enable this transition of this individual taking over the entire population is just poor random chance. So, we had derived an expression equivalent to that; in addition we had also derived an expression of the of the probability associated with the event that this mutant individual takes over the entire population when this mutant actually does hold of fitness advantage over the rest of the population. So, if the in the example that we had built our frame work with the rest of the population was working with the fitness equal to 1and the mutant individual that we are interested in had a fitness r where r was bigger than 1.

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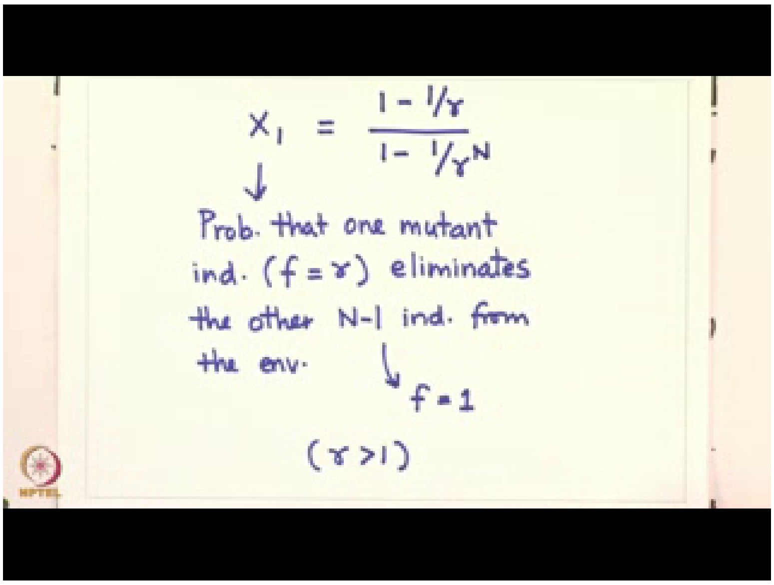

And what we noted was that X 1 which is the probability that this 1 individual. So, this was probability that 1 mutant individual whose fitness is equal to r eliminates the other N minus 1 individuals from the environment and these individuals have a fitness which is equal to 1 and we were given that r is bigger than 1 and we derived the expression that we developed was X 1 is equal to 1 minus 1 divided by r divided by 1 minus 1 divided by r to the power N, and we have ended up by doing one particular example we had assumed a situation where a beneficial mutation of a particular benefit arises in the population what is the chance that this mutant is able to eliminate the rest of the individuals in the population and spread in the environment that we are talking of.

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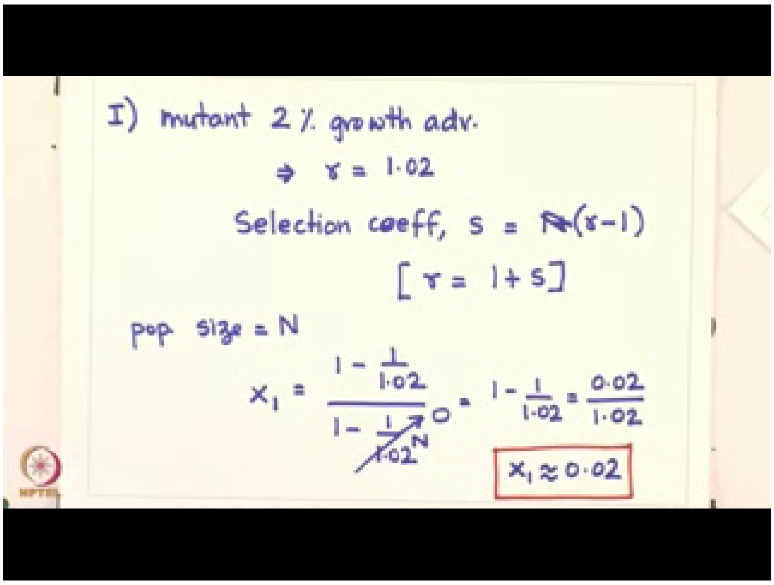

So, let us just to a few more fitness cases associated with this probability and let us start with the first case where we say that the mutant has a 2 percent growth advantage over the wild type, over the wild type or over the parent genotype that we are talking of. What that means, is that r is equal to 1.02 and we define something called a selection coefficient which is represented by the variable s which is just equal to 1 plus I am sorry which is just equal to r minus 1. So, in other words r is just equal to 1 plus s. So, s in the case that we are talking of comes out to be equal to 0.02 because r is equal to 1 plus s and r in our case is 1.02.

So, this selection coefficient associated with this mutant individual which holds a 2 percent growth advantage over the rest of the population is equal to 0.02. So, the probability that given the population size is N the probability that this individual this single individual takes over the entire population is just given by x 1 which is equal to 1 minus 1 divided by 1.02 divided by 1 minus 1 divided by 1.02 raise to the power N. Now N for any reasonable bacterial setting is going to be a very large number we just going to mean that this ratio of 1 divided by 1.02 to the power N approaches 0 as N for as n approaches a number such as 10 to the power 6 10 to the power 7 which is very common for bacterial environments.

So, the denominator we are just left with approximately equal to 1 and this comes out to be equal to 1 minus 1.02 which is equal to 0.02 divided by 1.02 which is approximately equal to 0.02. You should realize that the denominator here is 1.02 which is bigger than 1. So, the exact number for x 1 is going to be slightly less than 0.02, but for our approximation this is good enough. So, that is that is case number one.

So a 2 percent a mutant that confers a 2 percent growth advantage has a likelihood of taking over the population which is equal to probability 0.02; let us do another case. So, bacterial mutants large beneficial mutations via a single nucleotide substitution that occur in a bacterial population that occur in a bacterial genome are thought to conferred an advantage of 4 to 5 percent in terms of growth rates these. So, any nucleotide substitution that confers a 5 percent change to growth, 5 percent increase in the growth rate associated with bacteria is relatively rare mutant mutation and 5 percent growth rate is a large benefit that has occurred to this mutant.

So, let us just calculate quickly what is the probability associated with this mutant which has acquired this large beneficial mutation of spreading to the population and eliminating everybody else which is growing at 5 percent lower growth rate than itself.

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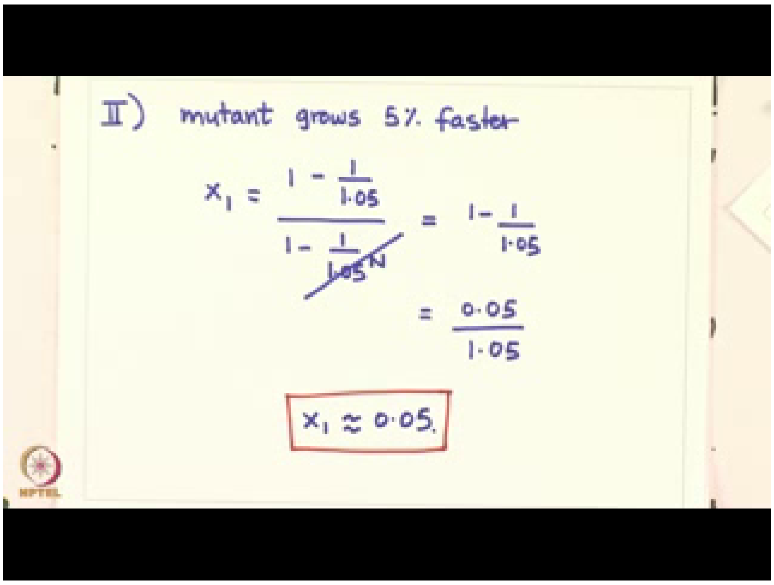

So, the second case is when mutant grows 5 percent faster and everything at that we have done in our analysis remains the same and the answer that we get is 1 minus 1 divided by 1.05 divided by 1 minus 1 divided by 1.05 to the power n again this quantity approaches 0. So, the denominator approaches 1 and we end up getting 1 minus 1 divided by 1.05 which is equal to 0.05 divided by 1.05 and x 1 is approximately equal to 0.05 correct.

So, even this large beneficial mutation whose relative contribution to fitness of the individual is pretty large in the sense that one substitution is conferring a 5 percent increase in the fitness associated with the individual only has a likelihood of survival and taking over the population which is equal to 5 percent. What that means, is that should 20 of such mutations occur nineteen are likely to be lost because of the randomness or genetic drifts associated with the population and only one of them one of these mutations will be able to eliminate the other individuals in the population and establish itself.

It just goes to illustrate the large role the very significant role that chance events play in dictating the evolutionary dynamics, because which of the 20 mutations which of these twenty large mutation goes on and eliminates the rest of the population establishes the course of evolutionary trajectory that this particular that bacteria in this particular environment are going to follow in the future generations all right.

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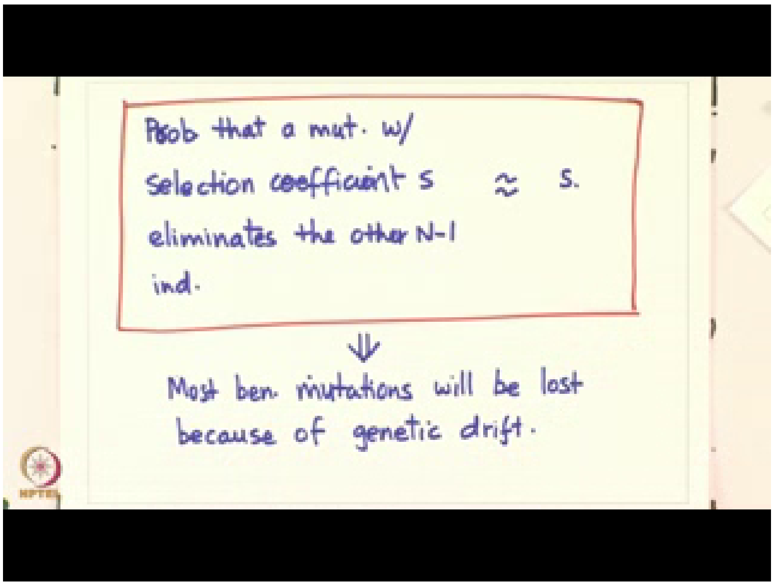

So, we can generalize the result that we have so far and we can say that the probability that a mutation with selection coefficient s eliminates the other N minus 1 individuals from an environment and this selection coefficient s is the advantage that this individual this mutant holds over all N minus 1 other individuals in the population, this probability is roughly equal to s. And this is a extremely important result because what this shows is that more often than not beneficial mutations are going to get lost because of chance events and it is only going to be a very it is only going to be a relatively rare phenomena that are beneficial mutations is going to be able to eliminate others in the population.

Which what that implies is that most beneficial mutations will be lost because of genetic drift. Again I cannot over emphasize the important associated with these results this is we say most beneficial mutations will be lost because we know that for any physiological setting the number s here is going to be less definitely less than 10 percent. Hence the probability that are beneficial mutation is going to be able to eliminate others in a population there is always going to be this probability is always going to be less than 0.1, which means at most at most you are only going to have 1 out of 10 mutations that survive and eliminates others in the population.

So, we have this result, but we want to understand the context in which we understand the actual experimental context in which this result is applicable.

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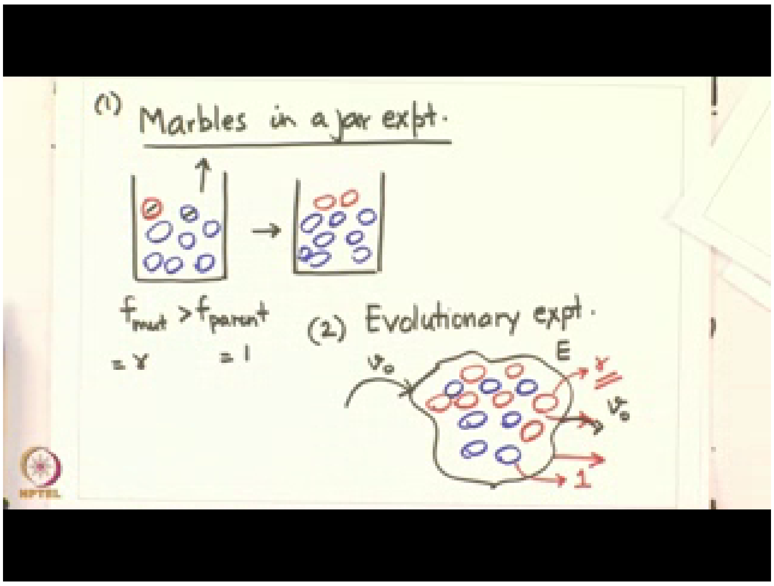

So, we had started our discussion on genetic drift and randomness associated with populations with the marbles in the jar experiment. So, the equivalent here is going to be the in a marbles in a jar experiment what our analysis that we have just completed represents is the case that we have a jar and we have 1 red marble, and we have N minus 1 marbles of another color. Now this in the case that we just did fitness of mutant is more than fitness of parent we said this was equal to 1 this was equal to r. So, the equivalent setting in the marbles in a jar experiment is that when you draw a marble randomly for some reason, the chance that you draw a red marble is slightly higher than chance that you draw any of the any one of the blue marbles ok.

So, individually the chance of drawing red is more than chance of drawing blue, but because there are so many blue and only one red overall the chances of drawing a blue marble is more than chances of drawing a red marble, but if you want to compare this red and this blue the chance of drawing the red this red marble is more than chance of drawing this blue marble. So, that is the equivalent setting that we have in the marbles in a jar experiment, now what is going to be the fate of this. Everything that we have done the result that we have derived here holds for the marbles in a jar experiment too. So, what is the equivalent meaning of this experiment here it is that as we as I go to jar number 1 to jar number 2 or in an evolutionary experiment generation number 1 to generation number 2, this red may or may not survive. If I never pick up red from here it will get eliminated and I will get only blue, but it is also possible that i ended up picking red twice and hence I have 2 red marbles in the next generation and subsequently I might have another red marble I might have three red marbles in the next generation and so on and so forth.

On the other hand it is also possible that i loose both of these red marbles and i only have blue marbles in the next generation and all of that depends on chance events happening in the population and one of the very useful ways of representing this is a via the following, but before we get that this is the representation of a marbles in a jar experiment, the second representation is for an evolutionary experiment. The way you can visualize this happening is that let us say you have any environment E this is any physical chemical environment E and you have certain influx this is not a closed system it allows for exchange of material with the environment and because the environment that we are talking of is a fixed volume you have a certain incoming rate of v naught because the volume is conserved you have a certain outgoing rate of what is present in the environment also equal to v naught. So, if in is equal to out; that means, a volume of the system is conserved and if you have a case like this you need not have 1 entry and 1 exit from the system you could have multiple entries and multiple exits from the system all of them all the entries being added up is equal to v naught all the exits being added up is also equal to v naught, and hence we can represent the system such as this.

Now, in this environment suppose you have bacteria leaving and you have an original genotype which is all blue bacteria and again a random event happens and you have a beneficial mutation that is conferred to one of the individuals, one of the progenies that as a resulted from a division event and you have this red individual which is the mutant and now this individual is growing at fitness equivalent to fitness equal to r while the rest of the population has a fitness equal to 1.

What that means, is that this individual divides relatively faster as compared to in a individual of the parent genotype, but because there are these exits streams associated with the environment what could also happen is this red is this red mutant which is a fittest individual in this environment could just get washed away from this exit stream. And if that happens you lost that 1 mutant that was present in the environment, and now what is the individuals that are present in the environment are all of the same genotype that you started with and you lost that 1 individual which was growing at a faster rate r equal to more than 1.

But before this is washed away it it is possible that this individual divides and goes up to 2. But even that 2 such individuals there is a chance that these 2 could go these could leave the system via the exit streams and hence you are back to this back to the situation where all individuals in the environment that you are interested in r of that fitness equal to 1. But it is also possible that this individual does not leave the system and it keeps on dividing and hence it has enough number of progeny now, that the chance that all of them get eliminated via the exit streams reduces significantly and if you enter into a situation like that, that is when you have red individuals taking over the blue individuals it is the blue individuals which are replicating slowly you are generating progenies slower than the red individuals and hence their relative numbers decrease and eventually they will be reduce to so few, that there will be the once which are eliminated from the environment.

But that event where 1 red individual is able to eliminate all the blue individuals is the is exactly the event that we have calculated the probability for and that is the probability that we have here that that probability that this one red individual is is able to eliminate all N minus 1 blue individuals from the population even though it is growing at a rate faster than everybody else that probability is just equal to s which is the selection coefficient or the advantage that this individual holds over the rest of the individuals in the population. So, again a very very important result and these 2 are the sort of the physical settings associated with this probability calculation in the context of marbles in a jar and an evolutionary experiment.

So, let us imagine that this we have this environment and we have this evolutionary experiment taking place and a genetically identical set of individuals give raise to one individual which is growing at a rate which is more than the parent genotype. So, how do we represent graphically the fate of such a mutation that has happened? So, we will talk about some of the graphical representation associated with the dynamics of this mutation.

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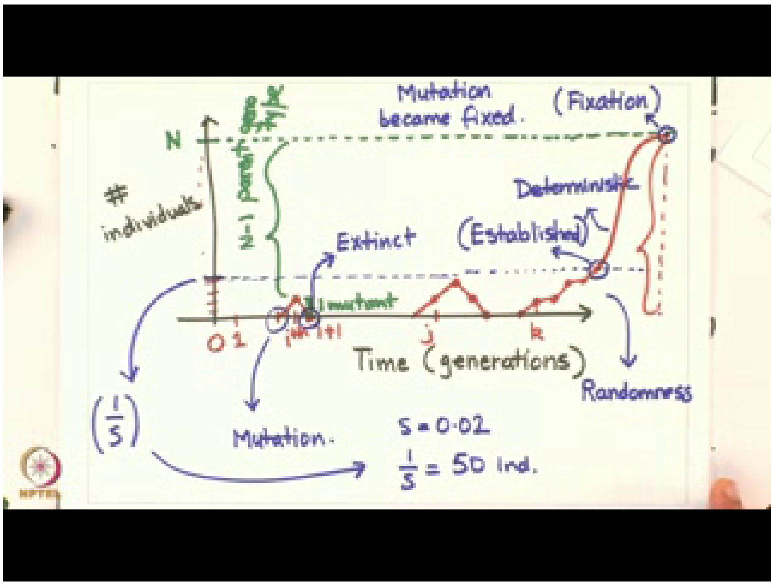

The first one. So, let us draw the 2 axis on x axis in the first one. So, remember this is these are just graphical representations and how do we graphically represent the evolutionary dynamics associated with an experiment.

So, we represent time in the context of generations number of generations represent time for me and on the y axis I represent number of individuals. Now because my environment is such that number of individuals never exceeds N this is the cap that I have, I am never going to go beyond this curve I am always going to be confine to this particular region I am not interested in numbers of individuals exceeding n because that that is the situation which is not relevant to my environment. Now what is happening here at t equal to 0 that is your first generation the parent genotype, everybody is genetically identical hence the individual number 1 2 3 and so on and so forth going all the way up to n are all genetically identical and that is the parent genotype that you started with.

So, you do not represent anything you have generation number 1 and let us say no mutation happened. So, even here all the individuals are of the parent genotypes. So, you do not represent anything, when you start representing is the ith is at ith generation when the first mutation has happened, where the first beneficial mutation has happened and you have an individual now which is growing at a rate other than everybody else in the environment. So, at ith generation you have this beneficial mutation take place and this how you would represent it that from i minus oneth individual this event happened. You have 1 individual now which is growing faster which is growing at rate r and the other n minus 1 are still equal to a parent genotype.

So, this is 1 mutant and this is the n minus 1 parents parent genotype all right. So, you have this 1, now what is going to happen in the context of the experiment that we talked about we noted that this mutation could spread in the population or it this mutant could eliminated from the environment that we are talking about. So, if it gets eliminated from the environment, then what we have is that this one individual comes back to 0 and again we get into a situation in the i plus oneth generation, we again get back to a situation where we have 0 number of individuals corresponding to the mutant and all n individuals correspond to the parent genotype and this might continue and I might have another beneficial mutation occur at generation number j. So, at j th generation at j minus 1 th generation I had all individuals belonging to parent genotype whereas, in the j th generation there is just 1 mutant which is arisen again which is beneficial in nature which is growing faster than everybody else in the population and now this individual may be this goes upto 2 in the next generation.

So, the numbers of this individual this particular genotype go up to 2 and the rest of the individuals which is the parent genotype go up to n minus 2 now. But then again because of genetic drift this loses out and the number of individuals of this particular genotype comes back to 0 and you have all n individuals which are of parent genotype.

So, this mutation got lost because of drift again, but eventually you will have one beneficial mutation whose numbers keep rising, and that is going to be somewhat random, but eventually this will start growing and take over the entire population. This at the k th generation another beneficial mutation happened and this mutation unlike the previous 2 did not get lost because of drift, but went on and established enough number of individuals such that it was by just by chance difficult to eliminate individuals of this particular genotype and hence as we move forward in time the number of individuals associated with this genotype are able to eliminate the individuals associated with the parent genotype and at this particular instances we have a situation where all n individuals in the population belong to the mutant genotype and the parents genotype has been eliminated totally ok.

So, this is one representation of an evolutionary experiment where you can represent beneficial mutations happening, beneficial mutations getting lost and so on and so forth and this particular graph represents three important time points that we want to capture; and those time points are this is the first one which is mutation. So, this we already know. So, this one is not one of the three that I am talking about this time point what this represents is that the mutation went extent, because I had one individual which was carrying this mutation and that individual got eliminated because of chance. So, that mutation got lost in the next generation hence the mutation got extent. At this point where all individuals are of the mutant type and there is no individual left which corresponds to the parent genotype is called fixation.

So, you say that fixation event happen happened and the mutation became fixed; that means, the frequency of individuals in the population which are carrying this particular mutation has gone up to 1. And the third important point which is associated is that there is a threshold below which randomness place an important part. As long as the number of individuals which correspond to this genotype mutants genotype is less than this threshold stochastic effects randomness plays an important part here whereas if the number of the individuals corresponding to this mutant genotype goes above this threshold, then randomness is not so important and its deterministic effects which dictate dynamics.

So, you have this transition happening in terms of how the numbers associated with that genotype are behaving, and if a mutation is able to cross this threshold then it is almost certainly going to go to fixation. Elimination extension of a mutation only happens when it is not able to cross this threshold number of individuals are associated with it and when the mutation crosses this threshold that is when you say that the mutation has become established right.

So, there are these three important definitions associated with the dynamics of a mutation, a mutation could go extent a mutation could go to fixation and the random fate of the mutation is no longer random if the number of individuals associated with that particular mutation go above a certain threshold and the if the numbers go above that threshold then you say mutation has become established in the population and it is very difficult to eliminate that mutation just by chance event now.

One more thing before we stop for this lecture is that how many individuals need to accumulate before you say that the mutation has gotten established, and that number which at which you say that mutation has been established is just equal to 1 by s. What that means, is that if you have a mutation with s equal to 0.02 then you need 1 upon s which is equal to 50 individuals of that particular genotype before you can confidently say that this mutation is not going to evolve lost now, but it is going to go to fixation ok.

So, this is the first representation associated with a dynamics of a mutation that might happen in an evolutionary experiment, mutation might become extent, mutation might go to establishment, mutation might go to fixation and in order to go to fixation mutation has to overcome the randomness associated with its fate, and its able to overcome that randomness if it achieves a certain threshold number of individuals, which are of its own genotype in the population.

Once that number is achieved the mutation is said to be established and then it goes on and goes to fixation, and the corresponding number which ensures that the establishment event has happened is given by 1 by s, where s is the selection coefficient of the mutation associated with the advantage that it holds over the rest of the individuals in the population. So, this is the first representation of an evolutionary experiment how you would represent it graphically, we will continue with the others in the next lecture.

Thank you.