Introduction to Evolutionary Dynamics
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Lecture - 25
Dynamics of a Moran process with Selection

Hi. And let us continue our discussion of the Moran process, and in particular its application in a system where there is one single individual which has arisen which whose fitness is unequal to that of the parent genotype associated with the system. So, let me just draw the system we are interested in.

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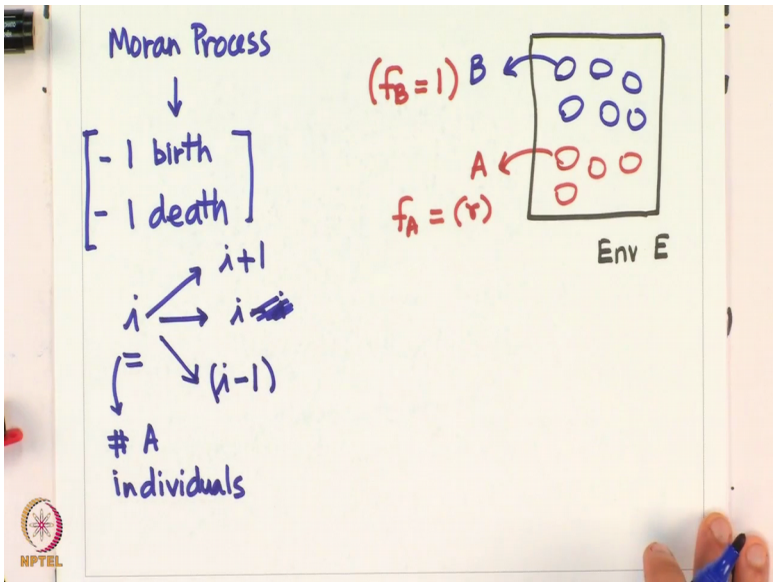

This is my environment E, the carrying capacity associated with this environment is n. And now I have two particular genotypes coexisting let us call this genotype B, and individuals which belong to genotype A. The fitness associated with genotype A is r this is f of A and the fitness associated with genotype B is f of B, which is equal to 1. And now we are interested in understanding what is the probability that these A type individuals are going to overtake the population and completely eliminate B from the system.

And we do that with the help of Moran process. And if you remember in the in the Moran process we had said that there is 1 birth and 1 death event that takes place and this leads to transition of the system from state i, which is number of A individuals. In this

one step of the Moran process where there is 1 birth and 1 death event being modeled the system could go from i to i plus 1 where the number which implies the number of individual goes up by 1. The system could remain in the same state, it remains at i or the number of A individuals could decrease from i to i minus 1.

And we are interested in finding out the probabilities associated with these three transitions in a setting where the fitness associated with the two genotypes is non-identical. So, how do we think about this? The way where it is going to make a difference the fact that the two genotypes have unequal finesses; where it is going to make a difference is in the birth process, because births process represents the probability that an individual divides in this delta t time.

Now, if a particular genotype has a fitness associated with it which is higher than the other genotype in the system chances are that this fitter genotype is going to lead to division faster than the other less fit genotype. Hence, if a birth event is taking place in this delta t time chances are that the progeny and the individual which is giving birth in this delta t time belongs to this more fit genotype. That is the probability. There is no certainty about the system, but it is more likely that the progeny is coming from an individual which is more fit.

So, how do we think about this?

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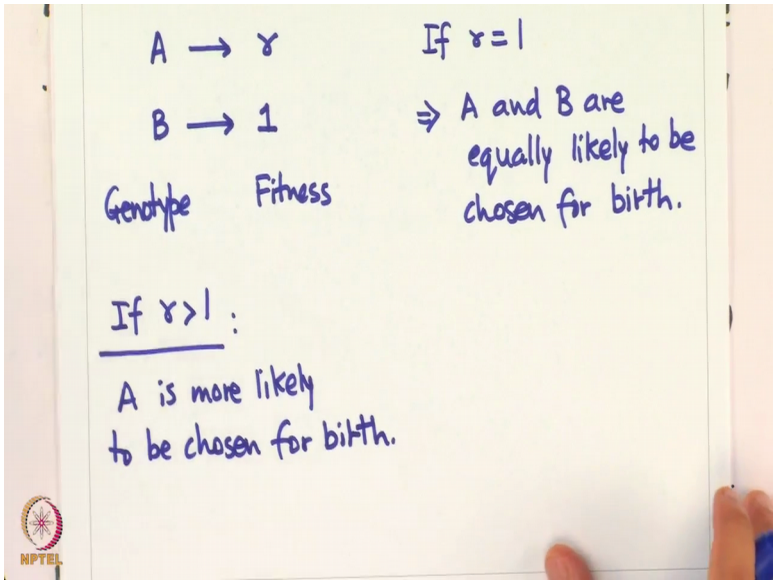

And remember that our two genotypes are: genotype A which is fitness r and genotype B which is fitness 1. So, this is genotype and this is fitness. Now, if r is equal to 1 that means, A and B are equally likely to be chosen for birth. If r is bigger than 1; as in our case if r is bigger than 1 A is more likely to be chosen for birth.

And the way we do this is the following: if our system is present at state i and remember the state of the system represents the number of A types individuals which are present in the system.

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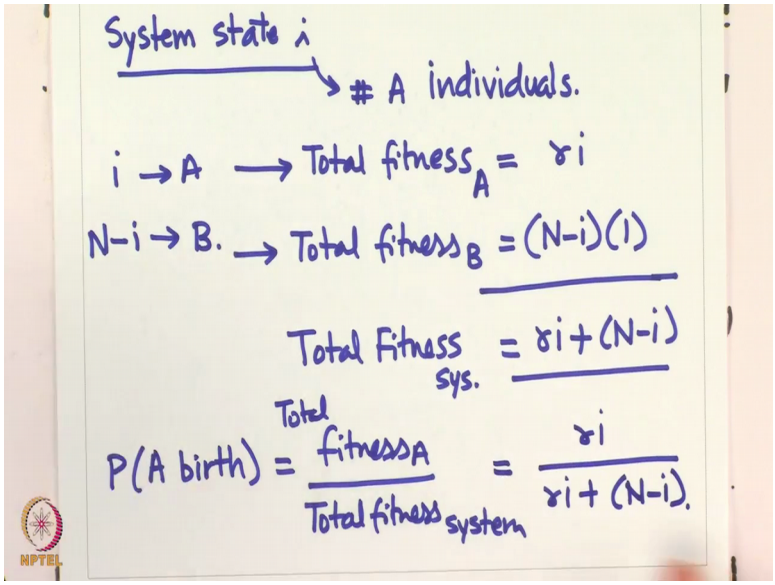

So, our system is at state i which means number of A individuals. That means, there are i A individuals and N minus i B individuals. That means, the total fitness associated with A type individuals is equal to total fitness associated with A type individuals is r times i. The total fitness associated with B type individuals is equal to N minus i times 1. And hence the total system the grand total fitness of the system when the population composition is represented by I and N minus 1 is just going to be equal to sum of the fitness is associated with genotype A and B. That is just equal to r i plus N minus i.

Now, out of this total fitness I am drawing one individual for replication. And now what this process says is the probability that a gets chosen for birth is just equal to fitness associated with A type individuals divided by total fitness of the system. Probability that I choose an A type individual for birth is just equal to the total fitness associated with A

type genotype divided by the total fitness of the system at this particular composition. This is just equal to r i divided by r i plus N minus i.

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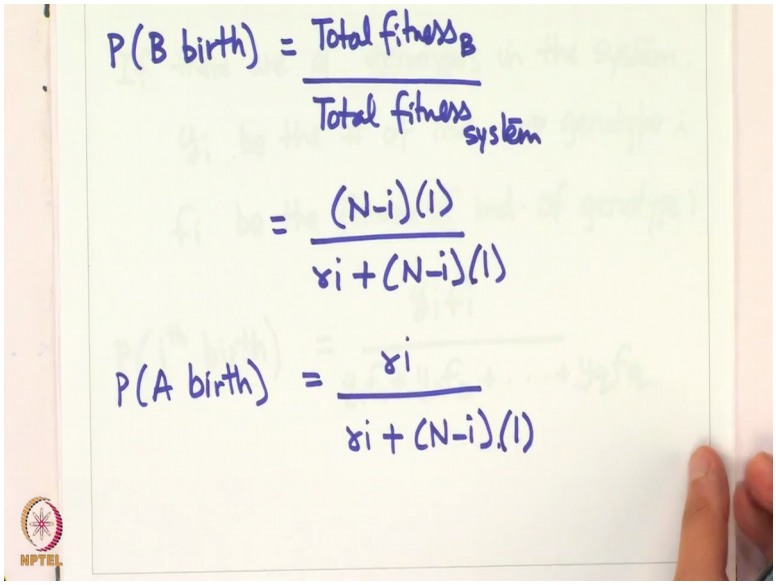

Similarly, what is the probability that I am going to select a B type individual for birth in such a setting is this just equal to probability that I select a B type individual for birth is just equal to total fitness associated with genotype B divided by total fitness of the system, which is just equal to N minus i divided by r i plus N minus i.

So, these definitions give me the likelihood of choosing A and B type individuals. And now these likelihoods are not evenly distributed between individuals of type A and type B, they are weighted by their respective finesses of each of a particular genotype that we are talking about. So this is B, let me rewrite the probability of A birth; A being chosen for birth again and that is just equal to r i divided by r i plus N minus i.

Very evident to note from here is that when you add the two probabilities you get back 1. The denominator is N minus i and r i, this is N minus 1 N minus i in the numerator this is r i in the numerator when you add the two you just get the same quantity in the denominator and numerator summation equals 1, which is to be expected because either you are selecting A for birth or you are selecting B for birth there is no other genotype present in the system.

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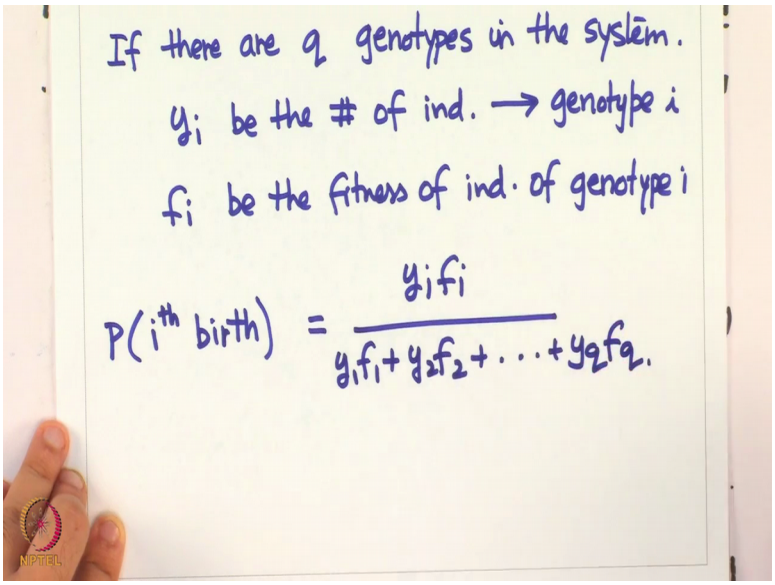

And the way you should think about this is that; if we can generalize this, if there are q genotypes in the system. And let y i be the number of individuals which belong to genotype i. And let f i be the fitness of individuals of genotype i. Then the chance the probability that an individual of i-th genotype is chosen for birth is just equal to the total fitness which is associated with that particular genotype which in this case is just going to be equal to y i divided by f i divided by total fitness of the system which comprises of all the q genotypes that we have which is just going to be equal to y 1 f 1 plus y 2 f 2 going all the way up to y q f q.

And this is exactly what we have done in this derivation where q is just equal to 2 because we have two genotypes present in the system and f 1 and f 2 are just 1 and are in the way we have defined our system. So, the way about to think about this is that the probability of being selected by the birth is proportional to number of individuals, but this is weighted by the respective fitness associated with that particular genotype.

So, if this is the case then again we go back to the Moran process the version where we had no selection advantage of A over B; what were the four transitions possible in that system? And if you were to write them again the four transitions are.

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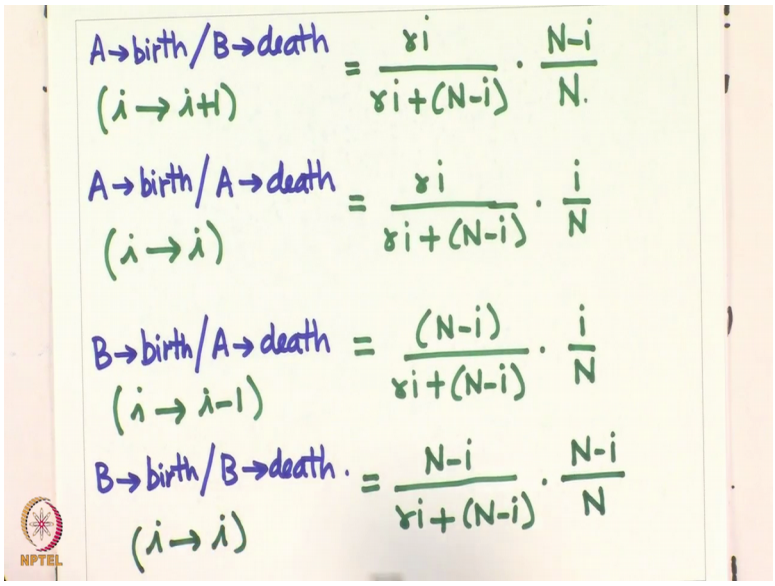

That A gets selected for birth, B gets selected for death; A gets selected for birth, A gets selected for death; and similarly the other two cases B for birth, A for death; and B for birth and B for death. Let us write down the probabilities associated with these transitions; now depending on the new rules for being chosen for birth as we have just defined them.

What is the probability that A gets selected for birth; that is we have just seen is equal to r i divided by r times i plus N minus i. What is the probability that B get selected for death? The probability of being chosen for death does not change. Aeath is independent of fitness of the genotype which is independent of the birth rate; an individual is equally likely to get selected for death in the Moran process as its defined. So, the probability of birth is has nothing to do with being baited with fitness and that is just equal to N minus i divided by N.

And in terms of transition of the system this transition, this birth and this death event taking place mean that the system has changed from i to i plus 1. The number of individuals associated with genotype A has gone up by 1. If you are choosing A for birth and A for death that is just equal to r i divided by r i plus N minus i times I divided by N. And the transition associated with this is that a system remains in the state i, because it is the same genotype which is being chosen for birth and death.

Similarly choosing B for birth is just equivalent to N minus i divided by r i plus N minus i; A for death is just equal to i by N, and this means the system transitions from i to i minus 1 the number of individuals associated with genotype A goes down by 1 and this is just equal to N minus i divided by r i plus N minus i times N minus i divided by N. And the system remains in its current state. So, we have the probability expressions in terms of i and N for all three transitions that are taking place: system could remain in the state i, system could move from i to i plus 1 or system could go from i to i minus 1

So, we have expressions for all these transitions. And now what we are interested in is solving those set of equations that we had derived for the simpler version of the Moran process when there was no selection advantage and defining and coming up with expressions for x i.

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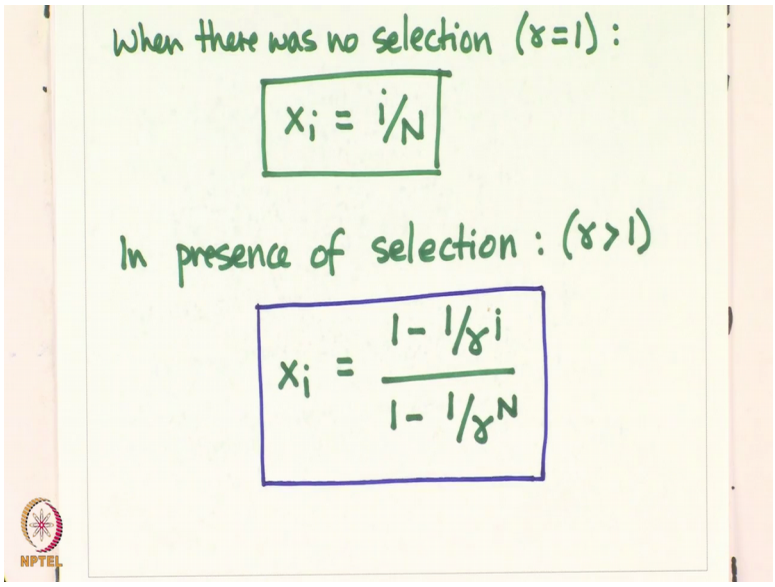

In the last lecture we had seen that when there was no selection; that is when r was just equal to 1 x i was just equal to i by N. In this case in presence of selection when we solve the appropriate equations associated with this case, this is r greater than 1 case it can be shown that x i is just equal to 1 minus 1 upon r i divided by 1 minus 1 upon r to the power N.

This is a extremely important result to us because it tells me what is the likelihood now of their being i-th particular individuals belonging to this genotype A. Genotype A which is fitter than genotype B whose fit the genotype B has a fitness equal to 1 and genotype A

has a fitness associated with it which is equal to r, what is the likelihood that A eligible to eliminate individuals of B.

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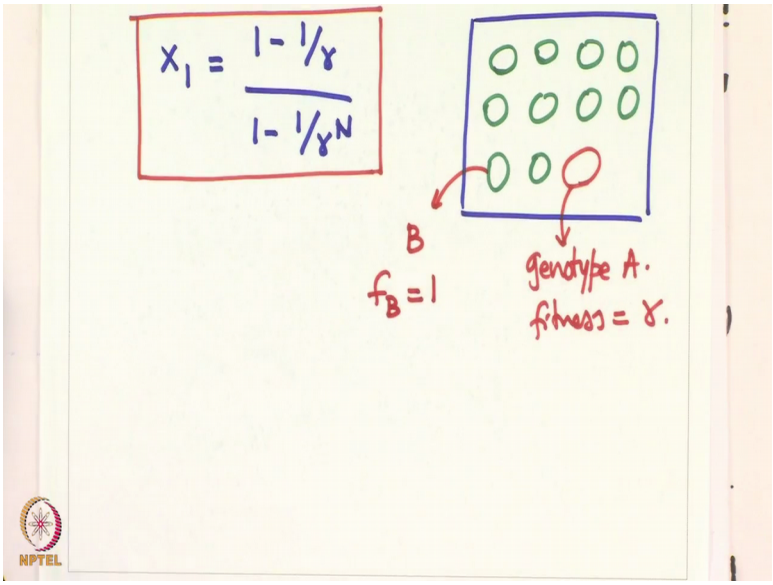

And in particular as we had discussed in the last section; in the last lecture the value of x i that we are most interested in is x 1, which represents the case that there is one individual of genotype A which has arisen via mutation event and that quantity can be estimated by this expression.

I want to reemphasize again that this represents the scenario that you have an environment and in this environment you have genotype B, and via mutations you have this one mutant that has arisen which is genotype A which has a fitness equal to it, which is r and the rest of them are genotype B; and fitness of b is just equal to 1. This quantity x 1 represents the likelihood that this one individual is able to eliminate all the other individuals from the population and eventually all individuals which are present in this environment are of genotype A.

And that probability is given by this expression. The probability of that event happening when we did not take randomness in to account was equal to 1 because a fitter genotype would always replace a less bit genotype if it has a selection advantage in an environment such as this where growth is going to be limited by the environment that this is being placed in, because of the environment only being able to support a maximum number of individuals.

So, what does this look like? Let us try to get a sense of; let us try to look at this expression that we have derived carefully and trying at a sense of what it actually means. Now if we look at the denominator associated with this expression its 1 minus 1 divided by r to the power N. Where, N represents the size of the population, the number to the total number of individuals which are present in the environment. Typically, because we are interested in bacterial cultures N is going to be very very large.

So, let us define a few mutations which would lead me to this lead me to looking at this system which has one individual of genotype A which has some relative advantage over the all the other individuals in the system. So, let us do a few cases like that.

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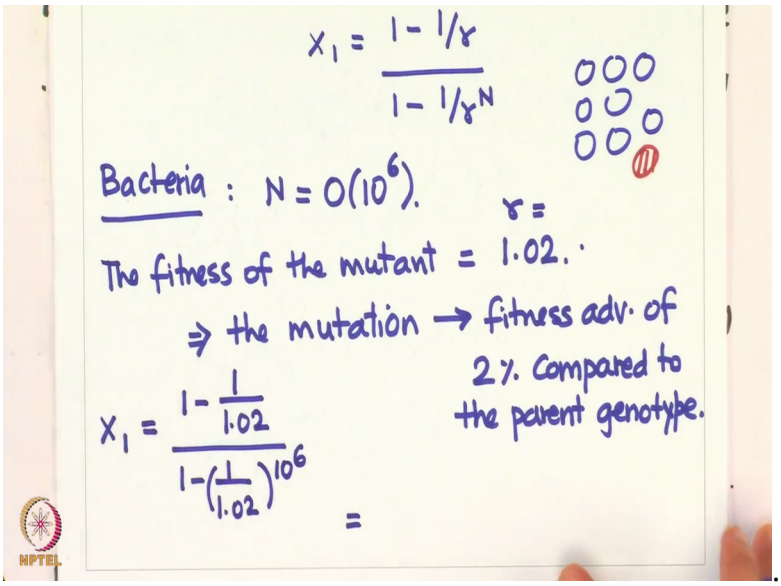

When we write the equation so we have that write from the first x 1 is just equal to 1 minus 1 by r divided by 1 minus 1 upon r to the power N. Now we are interested in doing this in bacteria where N is often going to be very very large. So, N will be of the order of let us say 10 to the power 6. So, N is a very large number, and we can just take N to be equal to 10 power 6.

Now what this tells us is that what is the probability that this one mutation; one mutant which is going faster than the others is able to eliminate all the slow growing individuals in the population. Let us say that the fitness of the mutant is equal to 1.02 which implies that the mutation this is r that I am defining this implies that the mutation that has

happened has incorporated a fitness advantage of 2 percent compared to the parent genotype.

Now, we are talking of an actual setting where there are 10 power 6 bacteria growing in a constrained environment where the number of individuals cannot exceed 10 power 6. We have 10 to the power 6 minus 1 individuals which are going at rate 1. We have 1 individual which is growing at rate 1.02. And now the growth dynamics is being modeled according to the Moran process where there is a birth and death event each taking place randomly. And we are interested in the probability that this individual mutant which is growing at rate 1.02 is able to replace all individuals which are growing at rate 1 only.

And that quantity is just given by 1 minus 1 divided by 1.02 divided by 1 minus 1 divided by 1.02 to the power 10 power 6. So, what is this quantity equal to? Let me do that on the next sheet.

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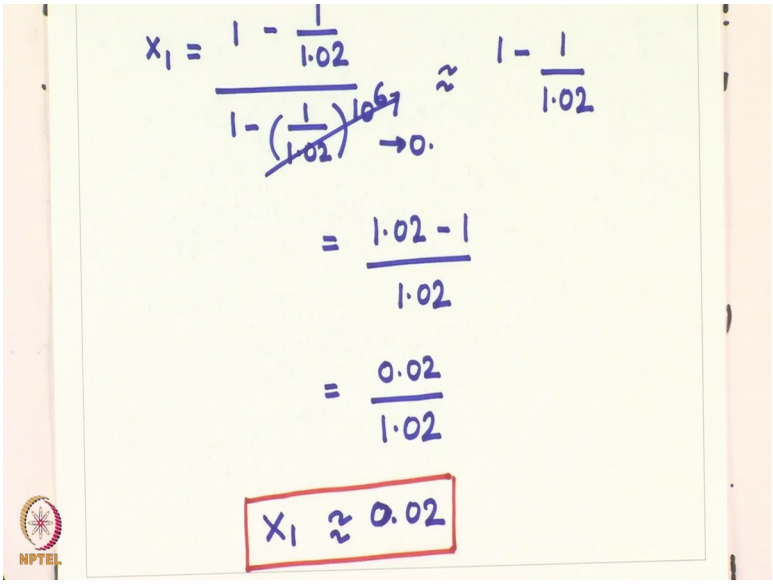

So, x 1 is equal to 1 by 1 minus. When you plug in these numbers in your calculator you will notice that this quantity 1 divided by 1.02 to the 10 power 6 is approaching 0. So, the denominator is approximately equal to just 1, so this is approximately equal to 1 minus 1 divided by 1.02 which is equal to 1.02 minus 1 divided by 1.02 which is equal to 0.02 divided by 1.02: which is roughly equal to 0.02. This is slightly less than 0.02

because the denominator is slightly more than 1. So, for all practical purposes it is roughly equal to 0.02.

This is an extremely important calculation that we have just completed, which shows us the role of randomness associated with growth dynamics. What this tells me is that should there be a mutation that occurs in the environment and this mutation confers a 2 percent advantage to this mutant individual that has arisen, that mutant is only able to survive the probability that that mutant is able to survive and take over the population is only about 2 percent.

Which means, that if 100 such beneficial mutations which each conferring and fitness advantage of 2 percent were to happen in an environment then 98 out of those 100 mutations would actually get lost because of randomness associated with the process of birth and death; and only 2 out of these 100 mutations will be able to eliminate the genotypes which are growing slower than their these particular mutant genotypes. It shows you the remarkable effect that these random effects have on population growths.

Another question we should ask ourselves is that what does 2 percent growth advantage mean in case of an actual growth experiment. Is the mutation that confers a 2 percent growth advantage a very large mutation, a very small mutation, how frequently do we encounter mutations which confer and fitness advantage of 2 percent. So, what we know from experimental side of evolutionary microbiology is that mutations which confer very large fitness advantages; mutations with such a large beneficial effect that they are particularly hard to find its only once in a while that you will see mutations of such large magnitude take place in an experiment.

These very large beneficial mutations only confer and a fitness advantage of about 4 to 5 percent. So, 2 percent fitness advantage is a very realistic value of a beneficial mutation that we are talking about then this case.

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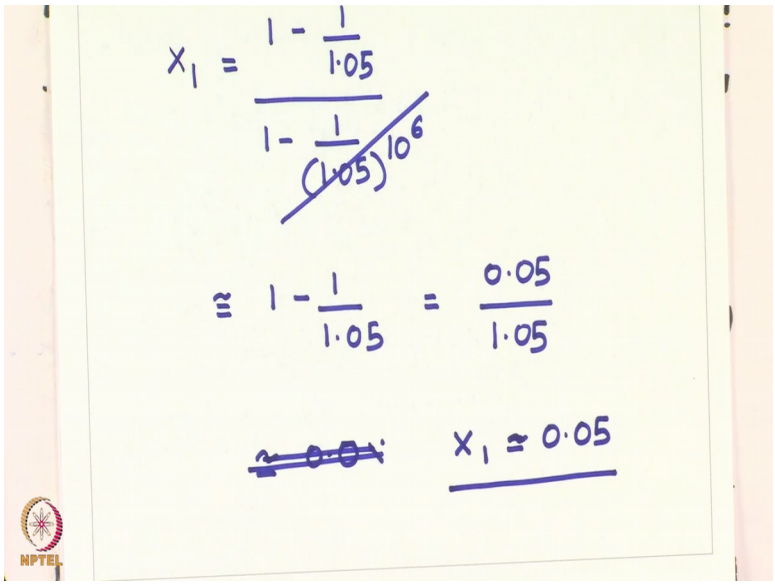

And even if we were to take about, even if we were to talk about a 5 percent beneficial advantage let us; if you were to quickly do that calculation the probability that that mutation survives is just equal to 1 minus 1 divided by 1.05 divided by 1 minus 1 divided by 1.05 to the power 10 power 6. Again this quantity goes to zero we get this is roughly equal to 1 minus 1 divided by 1.05 which is equal to 0.05 divided by 1.05 which is approximately equal to 0.05. Sorry, we write that again: this implies that x 1 is approximately equal to 0.05.

Again, what that tells us is that even if we are talking of beneficial mutations which are very large in magnitude these are strong beneficial mutations which confer a fitness advantage of up to 5 percent to the individual that are conferred upon even those mutations have a survival chance of only about 5 percent. That means, if 20 such mutations were to occur 19 times out of those 20 these mutations would be lost because of randomness associated with growth and death, and only one of them would go on to establish itself and lead to elimination of the genotype which is associated with a lower fitness.

So, in this lecture what we have try to do is sort of emphasize the role of randomness associated with these growth and death processes, and what we have eventually arrived that is a result which shows that these random processes associated with bacterial growth

are exceptionally important in determining the dynamics of evolution that are taking place in a population such as this.

We will continue our discussion on these topics in the next class onwards.

Thank you.