Introduction to Evolutionary Dynamics
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Lecture – 07
Modelling selection – 2: Two species

Hi. Welcome to the next lecture of the course and we will continue our discussion from the last lecture and start and keep talking about selection in an environment. So, we had started our first model for selection between two competing genotypes; A and B of a bacterial species and we have noted that if the growth rate of the mutant that has arisen in the population is more than that of the parent or the original genotype. Then it is likely that the mutant is going to take over the entire population and eliminate the parent from the population. On the other hand if the mutant that has a reason is follower fitness then the original parents genotype in which the mutant has occurred in which the mutation has occurred then the mutation itself is likely to get eliminated from the population.

But one thing that we did not account for in our first selection model is the fact that population could still increase exponentially for an unlimited time and approach infinity that we have already seen is not a representative of how growth occurs in liquid media for bacterial specie or for any specie for that matter. I am going to try and address that issue by building slightly more advanced models of selection which are much more representative of biology and population growth. So, how do we approach this? We approach this by assuming an environment, let us think of an environment which has a carrying capacity K.

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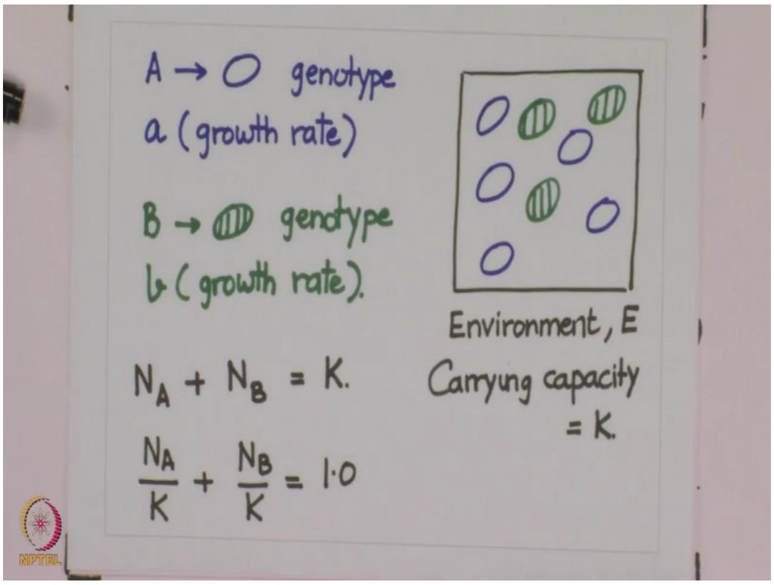

This is my environment E and the carrying capacity of this environment is equal to K and we have already seeing that the carrying capacity of an environment means what is the total number of bacteria for individuals in this case we are talking bacteria that can survive in this particular environment and now let us imagine scenario where in this environment E at any given point in time at any given point even point of time.

We have 2 distinct genotypes which are coexistent and let us say that is genotype A which are represented by the blue bacteria, the growth rate associated with this genotype will be small a, we will just continue the same terminology as what we used in the last lecture. So, a is the growth rate of this particular genotype and b and this population this environment is co inhabited by another type which is genotype B which are these green shaded circles this is genotype B represented by these bacteria with these shades this is genotype B and the growth rate associated with this particular genotype is b so that is the scenario that we are going to be looking at and we are going to make one more change in the model compared to how we did it last time.

What we going to start with assuming is that the system is operating at a situation at the particular instant on way at which we started monitoring the system does the number of individuals in the environment taken A and B together is equal to K the system is operating at its carrying capacity. That means, number of A individuals N A plus and N B is equal to K and selection basically takes place the basic tenet of selection is based on competition that there is resource limitation and individuals are wine with themselves for the limited amount of resources which are available in the environment and those which are better adapted to the environment take more advantage and grow further their numbers increase further in the environment and those individuals which are less suited to survive in that environment get left behind and are eventually eliminated.

And what we are interested in monitoring is that in a system like this where N A and plus N B is equal to K; that means, the system is already operating at its carrying capacity how do N A N and be change with time while the total population in the environment is maintained at K that is the question that we are trying to address why are this model and to do that in this framework we are going to not talk about numbers of bacteria, but we are going to define 2 speak 2 variables which is N A by K plus N B by K equal to 1. So, we have just taken K from here to the other side and arrived at this relationship.

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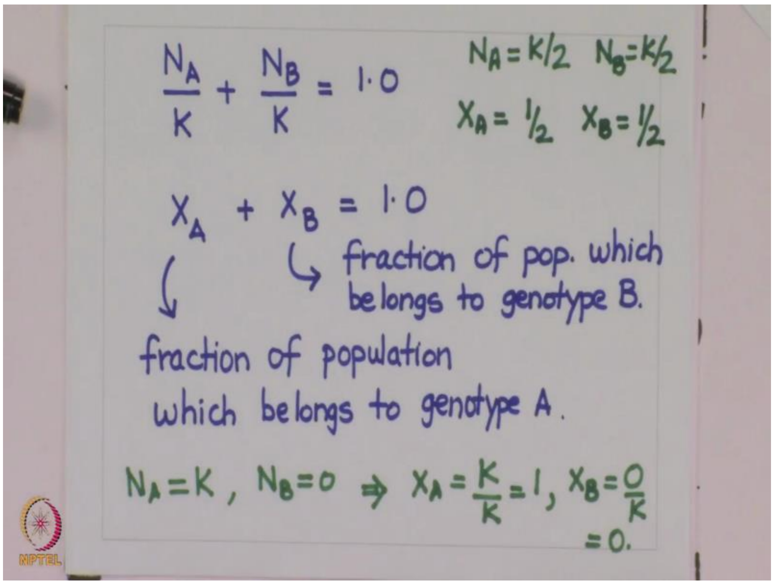

So, any just rewrite that equation again and we have these relationships that in this 2 bacterial system, the number of individuals were added up for the both types equals K and I can write we write that equation as N A by K plus N B by K equals 1.

And I am going to write this as X A plus X B equals 1 where X A represents fraction of population which belongs to genotype A. Similarly, X B represents fraction of population which belongs to genotype B this is a very simple, but a very important statement imagine that we are operating at a scenario when where N A is equal to K and

N B is equal to 0 which has to be true, because we know that at any instant of time and N A plus N B is equal to K for the system in such a situation X A will be K upon K remember X A is being defined as N A divided by K. So, X A is equal to K by K which is 1 and X B will be 0 by K which is 0.

So, the fraction of population which belongs to genotype A in such a scenario is equal to 1 and the fraction of population which belongs to genotype B in such a scenario is equal to 0 if N A let us take one more simple example if N A was K by 2 and N B was K by 2 then you simply have X A equals half and X B equals half a value, but at all points N time no matter what are the individual numbers that these 2 species are operating at we have the fraction of individuals fraction of the population which belongs to type A plus fraction of the population which belongs to type b. When these 2 are added together you get a sum constant equals to 1 and which is because of the fact that the total population size is equal to K at all instance of time if that is true and restart with this relationship.

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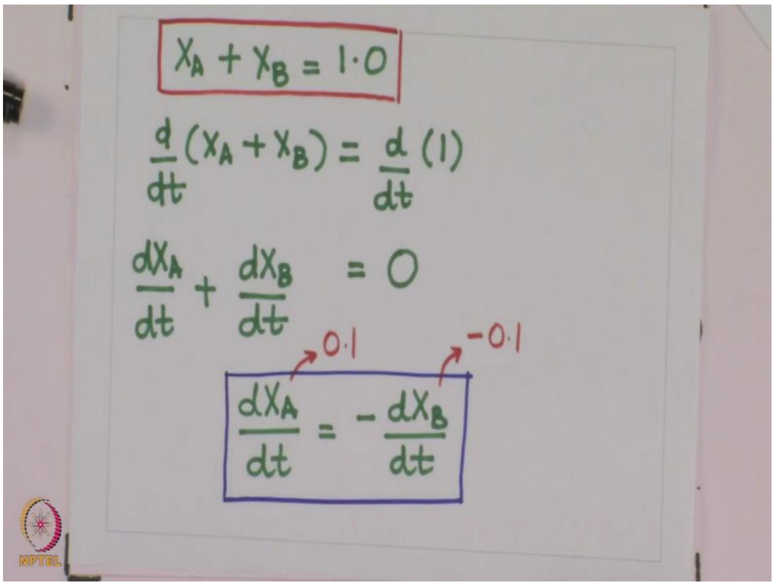

We have X A plus X B equal to 1, I want to understand how does X A and X B change with time because that is the basic quantity that I am interested in that should I have a and b genotypes coexist in a similar environment.

How do these fractions X A and X B change as time progresses forward; that is the basic idea that I want to understand when selection adds how do these frequencies change or how do these fractions change. So, the rate of change of X A and X B with time is the quantity that I am interested in. So, I am going to differentiate this simple equation that I have with respect to time. So, I get d by dt of X A plus X B and I differentiate the right hand side with respect to time as well d by dt of one now derivative of a constant is just 0. So, I get 0 on the right hand side and the left hand side gives me d X A by dt plus d X B by dt equal to 0 the second is a very important result because what this tells me is that rate of change of X A with time plus rate of change of X B with time is equal to 0.

In other words I can write this as d X A by dt equals minus d X B by dt, this is an important result here because the total number of individuals in the population is conserved to K and the total number of individuals does not change with time at any given point and time we have K individuals some of them belonging to type A some of them belonging to type B. Now we are interested in understanding how do these numbers belonging to type A and type B change with time, but because the population size total is constrained to be equals to K d X A by dt which is how do numbers of type A change with time is equal to and opposite in sign to d X by dt.

So, if you look back if you look at the equation again what this means is that a fraction of type A goes up by 0.1: let us imagine that X A goes up from 0.5 to 0.6 what all of this analysis means that if this ratio changes by 0.1, this has to change by minus 0.1. So, as to ensure that the total number of individuals remains equal to K if during selection number of 10 individuals belonging to genotype A are eliminated; that means, 10 individuals belonging to genotype B must have arisen to make sure that the total population size is held constant at K hence the rate of change of the 2 genotypes is related via this relationship.

So, where does this take us we have this relationship between the rate of changes of the frequencies of the 2 genotypes and we also have the relationship that X A plus X B is equal to 1, we are going to take these forward and try and develop our model for selection.

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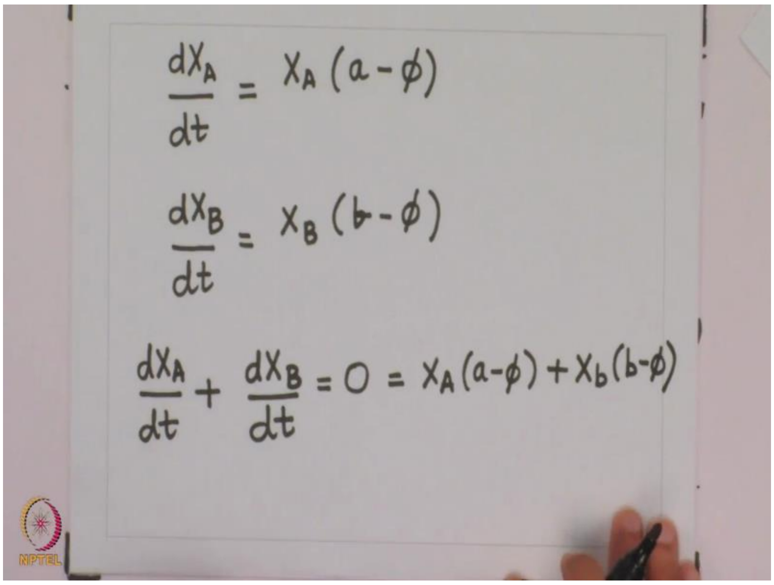

So, now I am interested in d X A by dt equals X A times a minus phi and d X B by dt equals X B; B minus phi; phi is an unknown that I am not sure about at this point what is it, but I want to find that out and I want to introduce phi to impose some sort of resource limitation on the modeled because I know I am working for a model where the population size cannot exceed K even when both the genotypes are added together. In fact, when all the individuals are counted belonging to both genotypes the population size in this model has to be equal to K.

But I am not sure, what is that variable phi that I should introduce in my model. So, as to ensure that the population size does not exceed K in the last lecture we had developed the both simplest selection model we had put phi equal to 0 and that would give me d X A by dt equal to a times X A and d X B by dt equal to p times X B that model had meant that the numbers of individuals belonging to each specie could go to infinity and that is the particular scenario that exactly the scenario that we want to avoid here and constraint the population size do not go beyond K and for that reason where introducing this variable phi which we do not know at this point what is it.

So, how do you find phi? Remember this result that we just obtained that d X A by dt plus d X B by dt is equal to 0 and we are going to make use of this to make use of this in the model that we have we are going to add the 2, we know d X A by dt we already have an expression for that and to that we are going to add d X B by dt and we know from the analysis that we just completed that these 2 differential derivatives were added together must be equal to 0. So, this is equal to 0 this we know from the previous slide, but we what we have done here is derived expressions for these derivatives and this gives me X A times a minus phi plus X B times B minus phi.

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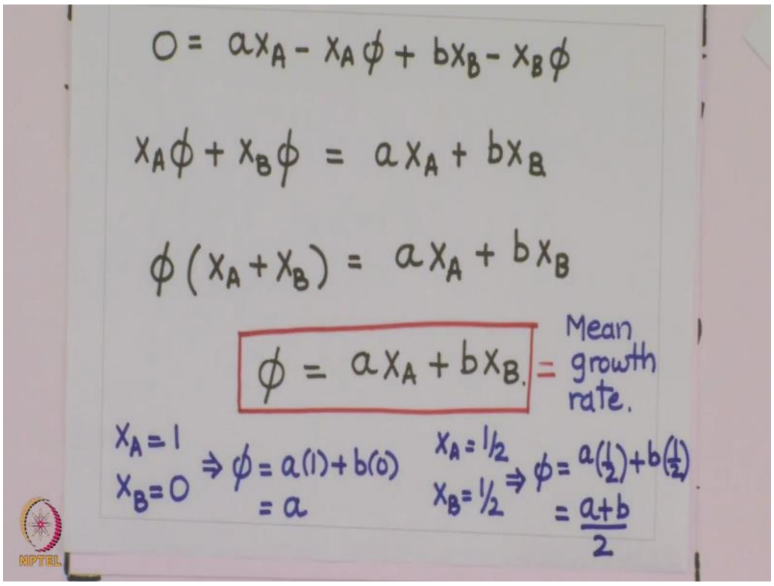

I solve these together and we do that on the next slide I get 0 equals a times X A minus X A times phi plus B times X B minus X B times phi I am just going to do some rearranging I will take the phi terms over to the left hand side and that gives me X A times phi plus X B times phi equals a X A plus b X B and this can be re written as I take phi common and I write X A plus X B equals a X A plus b X B, but again let us go back to the 2 results that we derived 2 slides back I know that X A plus X B is equal to 1 and I am going to use that result here.

Because, this is X A plus X B and I have already shown that this sum is equal to 1 and hence phi is equal to a times X A plus b times X B. So, using the model that we started with within unknown phi which we did not know how to explain, but having imposed the constraint on the model that the population size of both genotypes put together has to be equal to K at all times I have obtain an expression for phi. Now what does this phi mean this phi has a very important biological meaning associated with it this is the expression that I have for phi just look at this expression carefully what is a? A is the growth rate associated with genotype A and B is the growth rate associated with genotype B X A is the fraction of population which belongs to genotype A X B is the fraction of population belonging to genotype B.

So, what this tells me is that growth rate of a multiplied with fraction of population belonging to genotype A plus growth rate of b times fraction of population belonging to genotype B this means that this is just equal to the mean fitness of the culture what this means is that this is the mean growth rate of the culture when I have my population has X A fraction belonging to type A and X B fraction belonging to type b let me illustrate that with a couple of examples.

Suppose X A is equal to 1 and X B is equal to 0 what does that mean; that means, that all individuals in the population are of type A what that implies is if all individuals are of type A the average growth rate should be equal to just a because there is no individual of type B and what does phi give me that gives me A times 1 plus B times 0 which is a on the other hand if X A is equal to half and X B is equal to half, because their sum has to be equal to 1. We have already derive that then what is the mean growth rate that you associate with this culture which has half the cells growing at rate a half the cells growing at rate B and intuition tells us that growth rate should be the average of the 2 growth rates A and B.

And if you plug the values in this relationship we get a into half plus b into half which is just equal to a plus b phi 2 again this goes to illustrate that phi has a very real biological meaning which is the mean growth rate of the culture when the culture is existing at frequencies or fractions X A and X B. So, let us go back to our equation and use this meaning of phi in the selection model that we have developed.

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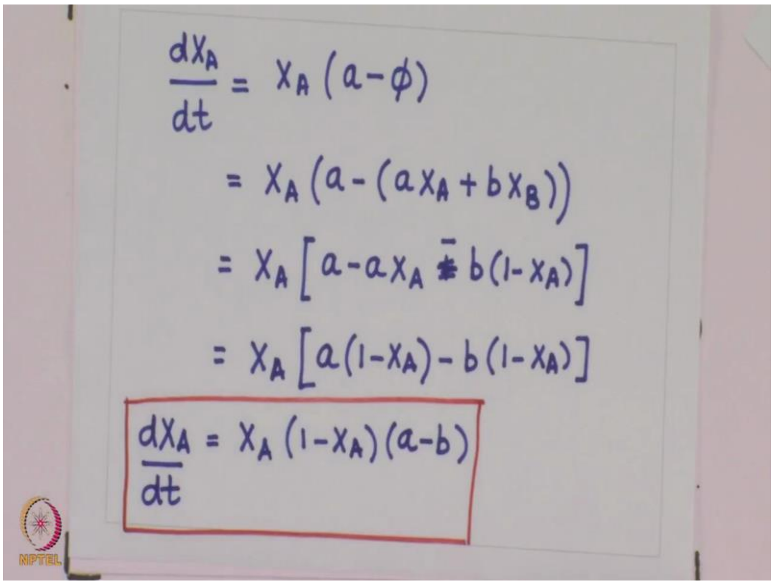

If we do that we get d X A by dt equals X A times a minus phi, now phi we have already derived is X A times a minus a times X A plus b times X B which can be re written as X A; a minus a X A plus b, I am going to write X B as 1 minus X A because I know X A plus X B is equal to 1, hence this can be written like this and I get this equation as X A from these 2 terms I can take a common I get 1 minus X A. This should be a negative here, because when I open the bracket there is a negative sign outside a; I take a common and I will I am left with a times 1 minus X A minus b into 1 minus X A. And now from these 2 terms I take this common factor 1 minus X A out and I get X A time 1 minus X A into a minus b that is my first model for selection which tells me how does frequency of a change with time when it is competing with another genotype B which is growing at growth rate b.

So, we will spend the next few minutes analyzing the dynamical properties associated with this particular equation using some of the concepts from 2 lectures back we will be talking about stability of these systems.

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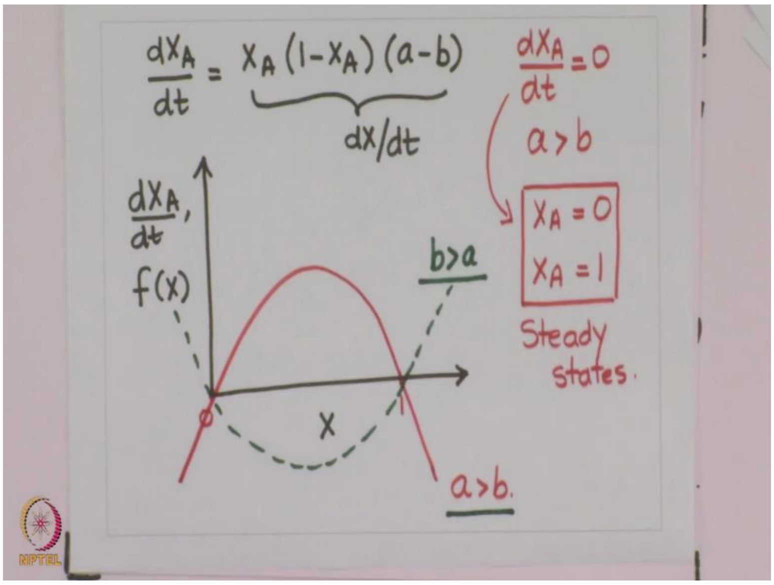

So, how do we do that again we have our differential equation d X A by dt equals X A times 1 minus X A times a minus b, now remember from how we did this in the previous class the first thing that we need to do is plot the curve between X and f of X where f of X is just the expression that d X A by dt is equal to. But the nature of this graph that we have for this situation is actually going to depend on the parameters associated with this model which are the individual growth rates of the 2 species a and b if a is greater than b then I am going to have one particular shape of the curve, but f b is greater than a I am going to have a different shape associated with the curve.

So, I need to analyze the system differently depending on whether a is less than b or a is more than b. So, what we are going to do is for the case a greater than b, the steady states of this system are d whenever we to calculate the steady states we put d X A by dt equal to 0 and that tells me that this is true when I put this entire expression equal to 0 this is true whenever X A is equal to 0 or X A is equal to 1 these are my 2 steady states associated with the system which ensure that either this quantity is 0 or this quantity within the brackets is equal to 0 a minus b does not come into picture when I am computing the steady states of the system.

Now, we discussed that the plots are going to look different when I am trying to plot f X and that will depend on whether a is bigger than the b or b is bigger than a if is a bigger than b; that means, this quantity here a positive quantity if b is bigger than a; that means, this factor is a negative factor. So, and my 2 steady states are 0 and one if a is bigger than b the plot looks something like this; this is for a bigger than b and if b is bigger than a the plot changes its nature and it looks like this.

So, the green curve is for when b is bigger than a and the red curve is for the case where a is bigger than b. So, I leave this as an exercise and we will begin the next lecture by solving the stability of this system using these 2 scenarios and see what that tells us about the biology.

But, before we do that I would like you to try these 2 scenarios yourselves and comment on the stability of the 2 steady states. We have in either cases when a is greater than b what can you say about the stability of the 2 steady states X A equals 0 and 1 and what can you stay about the stability of the same steady states when b is big bigger than a and more importantly what do they tell you about the biology of the problem that we are talking about 2 competing genotypes a and b in the environment we are population size is constraint to be equal to K at all points. So, we will pick that up when we start the next lecture.

Thank you.