Introduction to Evolutionary Dynamics
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Lecture – 06
Modelling selection – 1

Hi, and welcome to the next lecture of Evolutionary Dynamics. We will continue our discussion on stability of stable points associated with systems. So, last time in the last lecture we had talked about the stability associated with logistic equation which gives us 2 steady states N equal to 0 and N is equal to K. We found out that N is equal to 0 is an unstable steady state and N is equal to K is a stable steady states and we could relate the math that we get graph that we got graphically from our analysis of the logistic equation with the simple example of bacterial growth in a test tube.

Within that the stability analysis associated with the first equation that of growth that we started with where resource limitation was not taken into account and was easy to see graphically that N is equal to 0 was the only steady state of the system and the nature of that steady state was unstable. Once we introduce the disturbance to go from N equal to 0 to N equal to 1 in the simplest model that we started with the bacterial population showed unconstrained growth towards N equal to infinity.

So, we can correlate our understanding of biology with these very simple mathematical models. So, while we have only done this stability analysis for these 2 models that we started with what I want to do is present a very general framework and demonstrate that these can be extended to any system that you have for a first order differential equation that you might be looking at in any context.

So, to do at let us let us generalize the problem and let our differential equation be dX by dt equal to f of X.

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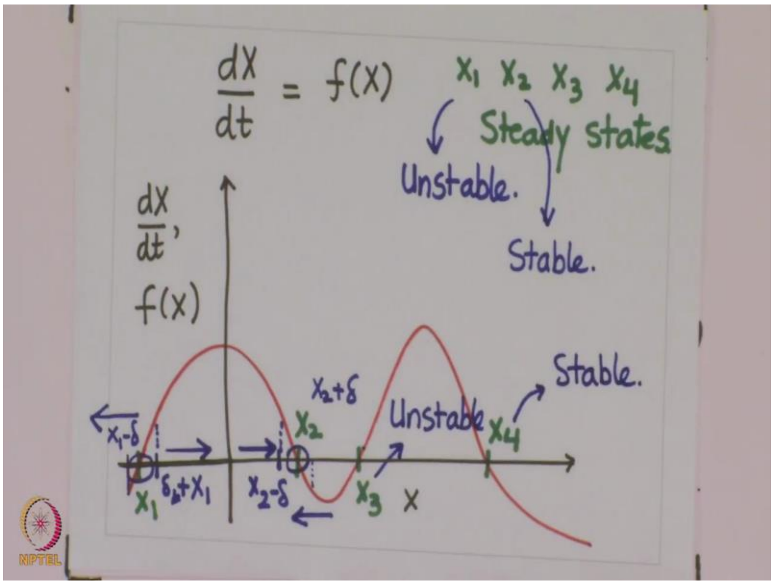

Now, this need not be biology these need not be bacteria this could be any system that we are talking about the steps in the process of analysis of steady states analysis of nature of steady states associated with the system are simply to draw X versus f X or dX by dt these 2 quantities are equivalent whether you write dX by dt or f X because they are in the same quantity in the context of biology where often interested in numbers of individuals of a particular species. So, X might represent how many bacteria are there or how many human beings are there in a population, but in a different context you might also be interested in negative values of X.

Of course in biology when we are talking of number of individuals of a specie negative X does not make any sense, but they might be cases where you are interested in negative one and those negative values of the variable X also have a meaning associated with them. So, you want to draw the graph between X and f X and let us imagine that you have a graph which looks like this, let us imagine that you plot this and this is the graph that you get and now the first thing to do is how many times does this graph cross the X axis because those are your steady states. So, you have X 1, X 2, X 3 and X 4 and X 1, X 2, X 3, X 4, are my 4 steady states of this system.

So, the first thing that you want to do when your analyzing stability of our dynamical system and its steady states is identify these steady states and now all you have to do is take up to one steady state at a time and comment on the stability of that particular steady state by introducing disturbance by introducing disturbance, we mean this, we mean exactly the way we did it the last time around we introduced the disturbance once to the left of that steady state and ones to the right of the steady state and analyze what is the sign of dX by dt variable at that particular moment if at that particular if the sign of dX by dt is such that the X value moves back towards the steady state from where the disturbance was introduced then that steady state is called stable in nature. And if this value of dX if the sign of dX by dt is such that the value of X wants to move away from the steady state value that we introduce the disturbance from then the steady state is said to be unstable.

So, let us look at these 4 and see what do this tell us about the system is hypothetical system that we are talking about. So, let us start with X 1 if you introduce a disturbance to the left which means I have I am operating at X 1 minus delta where delta is the magnitude of the disturbance that I have introduced. Now again I want to look at the sign of dX by dt at this value X 1 minus delta and I can clearly see that at this value the sign of dX by dt is less than 0 if it is less than 0 if dX by dt is less than 0 it means as t increases X decreases which means as I go forward in time from this point onwards X decreases moves in this direction. So, you can see that the system is moving away from the steady state from where we introduced the disturbance and hence it seems to be unstable in this direction what about the other direction.

Now, we introduce a disturbance to the right which is X 1 plus delta and now again we look at the sign associated with the X by dt at X 1; X 1 plus delta and we see that it is a positive number and positive number implies that as t increases X also increases and hence as we move forward N time the value of X moves towards a right. So, upon introduction of a disturbance in either direction at the steady state X equal to X 1 we see that the system wants to move away from the steady state.

And hence this particular steady state X 1 is unstable what about X 2 let us have a disturbance here which brings me to X 2 minus delta and the sign of dX by dt at this point is positive sign means that as t increases X increases and hence the system wants to move in this direction which is towards X 2 and on the other side we introduce a disturbance which brings us to the point X 2 plus delta and the sign of dX by dt at X 2 plus delta is negative which means as t increases X decreases and the system wants to move in this direction and hence we can see that for point X equal to X 2.

Irrespective of which direction we introduce the disturbance the system wants to move back towards X 2 if the disturbance is on the lower side the system he wants to increase the value of X if the disturbance is on the higher side the system wants to decrease the value of X and hence X equal to X 2 is a stable steady state and I leave this has an exercise to show that X equal to X 3 X equal to X 3 should be unstable while X equal to X 4 should be stable. So, using this if we have a first order differential equation represent dynamics of any system and the differential equation might be very complicated such that an analytical solution might not be possible. We can simply draw we can simply do this graphic and analysis which tells us a lot about the system it tells us about the steady states associated the nature of those steady states.

But the next thing when you want to ask is can we get some more information from this type of analysis and we want to go back to the logistic equation and see whether we can squeeze in some more information from this type of analysis about the system that we are interested in. So, let us go back to the logistic equation and analyze it one more time again.

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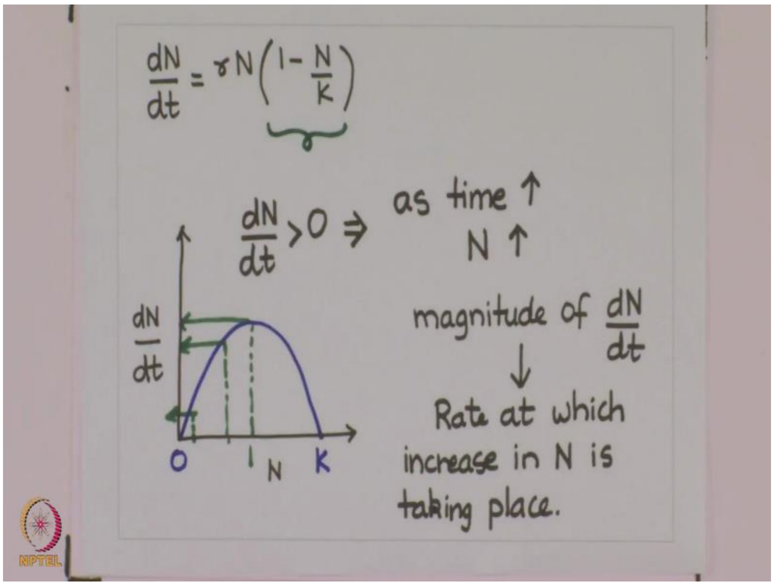

So, again our equation is d N by dt equals r N times one minus N upon K and when I did the step plot to analyze the stability of the system I plotted N against d N by dt and we saw that that graph looks something like this a parabola which meets the X axis at N equal to 0 and N equal to K. Now we want to see if this graph tells us anything more then what we already know about the system and one thing that you should realize is that between N is equal to 0 and N is equal to K for simplicity sake will constrain our self to this region only.

One thing as you should know is one that you should realize upon looking at this graph is that d N by dt in this window is always positive. So, in this window between N equal to 0 and N equal to K d N by dt is always positive what that implies as we have already seen is that as time increases N also increases, but there is one more thing that we should realize that we have been looking at only the sign associated with d N by dt does the magnitude of d N by dt also tell us something and if you look at the magnitude of d N by dt tells me about the rate at which this increases happening. For instance if we look at this point if I look at very small values of N if I look at small values of N d N by dt has a value has a value which is lower as compared to the value at somewhat higher values of N.

What; that means, is what that tells me is that at smaller values of N the rate at which the population is increasing is smaller as compared to this point where the rate at which the population is changing with time is higher from this graph I can see that there is a peak value which occurs somewhere between 0 and N at which the rate of increase of population with N is maximum and after that as N numbers increase further the rate of increase of N with time decreases and eventually the system wants to stop at N equal to K. Hence when the number of bacteria in the population reaches K d N by dt is equal to 0 and the population is no longer increasing with time. So, this is the rate of increase of N with time is first increasing it reaches a maximum somewhere between 0 and K and then it starts to decrease and come back to 0 as N approaches K.

Now, what does this tell us about the biology of the problem if you think about it what is happening I am starting with a fresh tube where I have only added one bacteria after one generation time that one bacteria divides and I have 2 bacteria. So, the rate of increase which is at this moment is I have added one additional bacteria in one generation time as I wait another generation time which in rich culture equal which we saw a couple of lectures pack is 20 minutes if I wait another 20 minutes those 2 bacteria. Now divide to give me 4 bacteria next 20 minute window the number of increase that has happened place in terms of number of bacteria is not 2.

As I wait the next 20 minutes those 4 bacteria divide and I have 8 bacteria. So, the increase that has taken place in the next 20 minute window is now 4 bacteria and so on and so forth and that is what is taking place in this window of the graph between N equal to 0 and the point where d N by d dt reaches its maximum because division is happening for higher number of cells the number of new progenies being produced is increasing and hence d N by dt increases with time. But why does it slow down if N is continuously increasing because that is where this factor of the equation comes into picture the resource limitation associated with this.

Now, as you cross this point now resources are becoming increasingly is cares and not every individual in the population is able to divide freely and as a result in that one generation time the 20 minute window that we have been talking about not every cell gets a chance to reproduce because to be able to reproduce you need to produce all the cellular machinery you need to replicate the entire genome associated with the organism and then divide into 2.

But now because resources are becoming scares and you are beginning and their numbers have gone up that there is competition for those resources 20 minutes is not sufficient time for every individual present in the population to divide. And hence division rate the rate at which N is increasing with time slows down. And eventually when you reach N equal to K there can be the environment is completely saturated with individuals and there can be no more growth unless there is a death in the in the culture media which leave some scope for addition for an additional individual to exist in that population.

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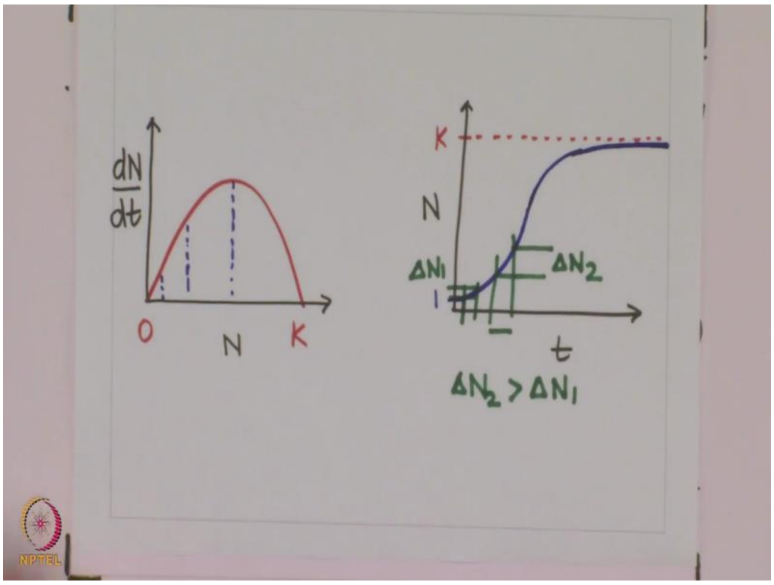

So, that is why this graph drawn makes a lot of biological sense, but what we are going to try and do is try and plot the dynamics of the system with the help of this graph to do that let us let us redraw the graph that we started with one more time . So, that is why we are and using information from this graph we want to qualitatively comment on the nature of this graph we know that the bacterial population will not exceed K because as it approaches K the growth rate halls town and d N by dt is 0 and this is a stable steady state associated with the system. So, N equal to K is the peak value and the number of bacteria is not going to go pass this if you are starting from low values of N.

So, we start off with N naught which let us say is one we start with this one bacteria and let us try to draw the let us try to imagine the trajectory of this growth at the same time looking at this graph. So, right now we are at N equal to 1 which is very small value of n. So, we are somewhere here and as we go forward in time N increases, but as N increases the rate at which the change in the number of individuals is happening with time also increases which means as I go forward in time the change is happening more and more rapidly d N by dt at this point is much higher as compared to d N by dt at this point which means more number of individuals per unit time are being added here as compared to at a lower value of N which means that as I go forward in time the population growth speeds up this part is represented by the first half of this graph where on going towards higher values of N the rate of increase of N is increasing with time and that can be seen in this graph. If you just simply look at unit intervals of time or some constant intervals of time and analyze how many number of bacteria have you added.

So, in this interval you have added this many number of delta N 2 and in while in this interval you only added a very small number of individuals delta N 1 and it is clear from this graph that delta N 2 is bigger than delta N 1 which means that the rate of growth is speeding up as you go forward in time which is what increasing values of d N by dt represent as you go forward in n, but then you cross this threshold and the growth begins to slow down and that can be represented by this graph slowing down.

And eventually d N by dt approaches 0 d N by dt approaches 0 implies that N is no longer changing with time which is this population approaches K and it does not change with increasing time and no longer changes. So, what we have tried to demonstrate in this in this part here is that just without solving the differential equation we can analyze the steady states we can comment on the stability of these steady states and we can also estimate the dynamics of the equation with time just by looking at the steady state and its stability diagram.

We can picture qualitative we can we can plot a qualitative nature of the response of the variable that we are interested in with time right this is a thing that we will keep that we will keep coming back to the throughout this course. So, that concludes ours discussion on the first phenomena associated with the 3 tenets of a evolution that we started with reproduction. Next we are going to start discussion about the second one which is selection.

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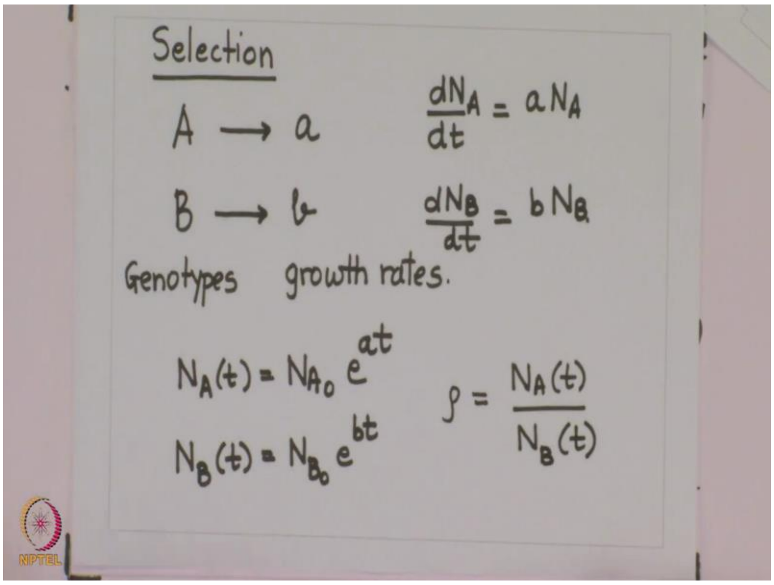

So, selection means that there is more than 1 genotype. So, we will call the genotypes A and B, we will say that the growths rate associated with genotype A is small a and the growth rate associated with genotype B is small b. So, these are genotypes and these are growth rates.

And now what we will try and do is understand how do their ratios change as we go forward in time if these 2 genotypes are co inhabiting an environment. So, if we go back to the differential equation model we have d N by d t; d N A by dt is equal to a times N A where N A represents the number of individuals of type A and we have d N by dt equals b times N B.

Now we have already seen the solutions to these equations and we know that N A with time is equal to N A naught e to the power 80 and N B t is equal to N B naught e to the power b t where N A naught is the number of a individuals that we start with at t equal to 0 and N B naught is the number of individuals of type b at time t naught not and what we are interested in is the ratio how does this quantity N A t by N B t change as time moves forward very often what is going to happen is that when growth is taking place you have an identical genotype.

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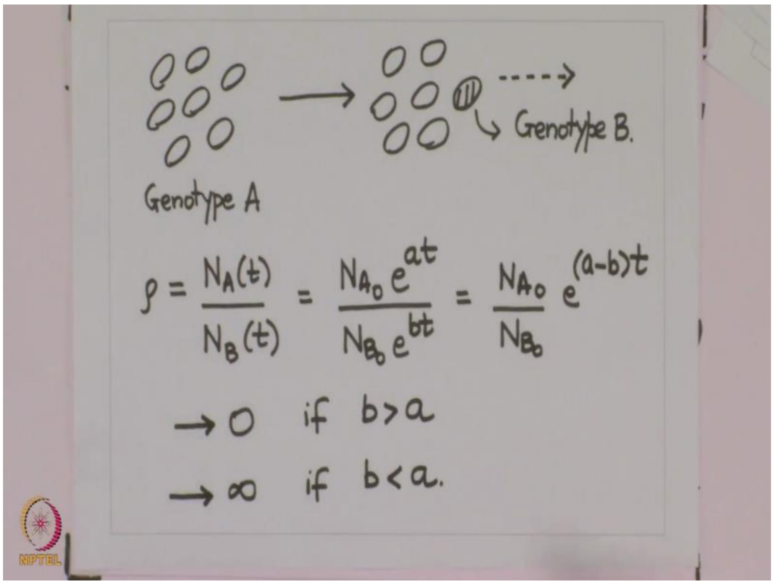

So, you have growth taking place and all cells are identical genotypes let us say this is genotype A, but our cells continue to grow and divide you have one mutation event take place and in your population you have a single mutant arise let say this mutant is genotype B. So, very often the number of mutants and an we want to monitor what happens to the system as this moves forward in time, but at the time when the mutant first arises the number of mutant cells in the system is only going to be one because that mutation was a singular event where as the rest of the population can be considered as at the parents genotype which is genotype A.

So, genotype A at this moment far out numbers that individuals associated with genotype B, but what we are interested in is what happens as we go forward in time to the ratio of individuals of type A to individuals of type B and to compute this ratio we are just going to take the expressions that we have already derived substitute them in the expression that we have and get an expression N A naught e to the power a t divided by N B naught e to the power b t which can be written as N A naught divided by N B naught e to the power a minus b into t. And what is interesting to note here is that this ratio always approaches 0 if b is more than a and always approaches infinity if b is less than a what; that means, is if the genotype that arose by mutation is growing at a rate faster than the original genotype which represents the scenario of b more than a this ratio number of individuals of type A divided by number of individuals of type B is going to go to 0, because the number of individuals of type B are replicating faster and hence they will populate the entire population and eliminate the individuals of type A.

On the other hand if the individual that arose via mutation is growing at growth rate b which is smaller than that of the original genotype then that individual is going to be eliminated via competition and you will have the entire population of genotype A and hence the ratio of individuals of type A divided by type B will move towards infinity because the denominator is being eliminated and is moving towards 0.

So, whether a mutant survives or not it is a very big factor towards which goes towards assigning that depends on the fitness associated with that particular mutant and how well does it grow in comparison with the parents genotype that the mutation has arsenal. But the model that we have just talked about right now does not yet solve the problem associated with numbers going towards infinity the numbers of individuals exploding as time goes forward. So, we again have to introduce some resource limitation associated.

With this, just as we done in the logistic section and that something that we will start within the next lecture.

Thank you.