Introduction to Evolutionary Dynamics
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Lecture - 37
Evolutionary game theory - 4

Hi. We will continue our discussion on Evolutionary Game Theory associated with microbial populations. And in the last lecture we had finished our case 1, which was represented in terms of our payoff matrix as the one where a is greater than c, and b is greater than d.

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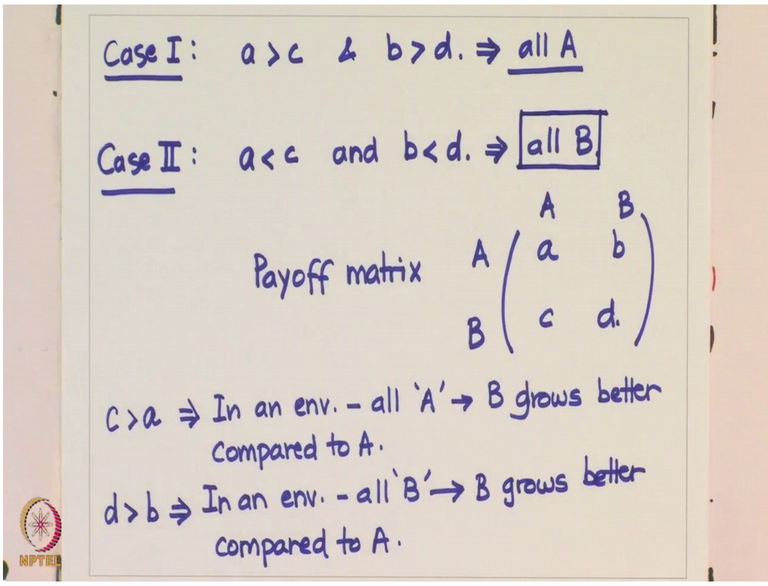

And we saw a couple of reasons why this why this particular set of relationship suggests that this corresponds to all A type of a outcome associated with population growth. Let us take a look at another one which is case two and this is defined by a as less than c and b as less than d. And since, the relationships that that we are defining in case one are exactly the opposite associated with 1. I am sorry, the relationships where that were defining in case two are exactly the opposite associated with those in case one you would expect that this corresponds to the case all B.

One of the ways to think about this its useful to think about this in terms of our payoff matrix, where we are saying that when genotype A and B grow in the presence of genotype A and B the associated growth rates are a b c and d and what we are saying when we say that c is more than a, what we are implying there is that in an environment.

Where there are all A s in this particular environment B grows better compared to A. So, this is an environment where everybody else is an a genotype and to this particular environment if you add an individual of genotype b that individual growth grows at growth rate c and of to the same environment you add an individual of genotype A that individual grows at growth rate a, and if c is more than a is essentially you are applying that in this particular environment B grows better compared to A.

The other condition is that d is bigger than b which implies that in an environment where there are all B s in this environment if you were to add an individual of genotype B that would grow at growth rate d and in this environment if you were to add an individual of genotype a that individual will grow at growth rate b, and since d is bigger than b you are saying in this particular environment B grows better compared to A. And again what this what these two conditions imply is that irrespective of the environment that we are talking of genotype b is doing better as compared to genotype a and hence we converge to a situation where in this particular environment b dominates a and the system move towards all B.

So, so we have recreated sort of that two of the four scenarios that we started with in our analysis all B and all a let us see if we can get an estimate if we can sort of somehow imagine conditions on our payoff matrix such that we can recreate conditions which would lead us to scenario three which was coexistence and scenario four which was by stability.

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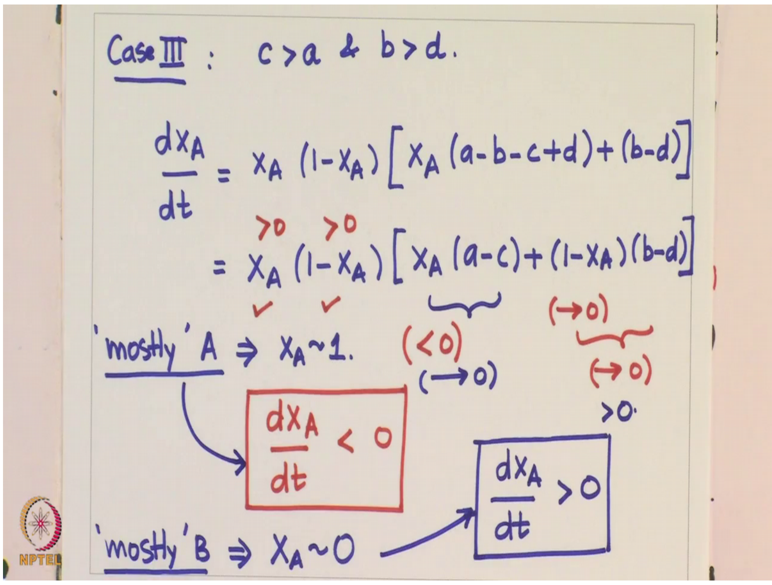

So, our next case is this case 3, which is defined by the conditions on the payoff matrix as c is more than a and b is more than d. Now what this tells us is that if we look at this in terms of our dynamical equation d x A by d t equals x A times 1 minus x A times x A into a minus b minus c plus d plus b minus d that is the dynamical equation that I have and I can write this as x A times 1 minus x A times x A into a minus c plus 1 minus x A into b minus d that is essentially what we are talking about here. So, what does this tell me about dynamics of the system what this tells me is that when I am when the population is mostly A using the word mostly in quotes here.

Which implies that x A is approaching one is not quite one, but is approaching one most individuals in the population belong to genotype a and there are only a very few type of very few individuals which actually belong to genotype b in this scenario that is the scenario we are calling mostly A here. So, if we have mostly A that means, x A is slightly less than 1 because x A cannot exceed one in that scenario let us look at this what this dynamical expression is telling me in that case this is greater than 0 this is greater than 0.

So, these two are no problem in that scenario 1 minus x A approaches, because x A is approaching one hence 1 minus x A is approaching is approaching 0. So, I can ignore this particular expression as almost 0 and then I am left with x A into a minus c, but under the conditions that I have been given c is bigger than a hence this is less than 0. What that implies is that as x A approaches one d x A by d t is less than 0 that is what this relationship is telling us here. On the other hand if you are dealing with a scenario if the system is present in a state where its mostly B, what that implies is that x A approaches 0 and x B in turn approaches one in that case what happens to this expression, in that case x A would still be greater than 0, 1 minus x A would still be greater than 0, but of the two contributions that are coming here from this term x A which is approaching 0 this quantity now can be ignored because that is almost approaching 0.

Whereas, 1 minus x A is multiplying with b minus d, and b minus d in the given set of conditions is greater than 0 hence this this expression in the bracket in this condition is greater than 0 which implies d x A by d t is greater than 0 for this condition whereas, for this condition d x A by d t is less than 0 what does that mean? What that means, is let us try to sketch this graphically what the result that we have derived says that when the system is in a state where its mostly a s and very few b s d x A by d t is less than 0 which means if it is mostly a s d x A by d t is less than 0 hence as t increases x A decreases; that means, the system wants to move away from a situation where there is only all A s and no b.

On the other hand when the system is present in a state when there are a very few a individuals and its mostly B d x A by d t is greater than zero; that means, the system wants to move to a state where the frequency of a individuals is actually increased bit type ok.

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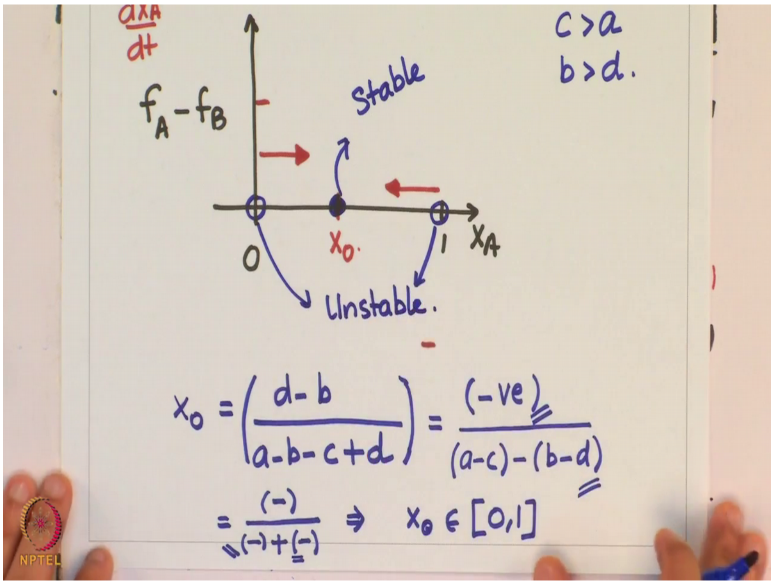

So, that is what this analysis is telling us graphic analytically graphically what that means, is that if this is x A this is essentially f A minus f B that we analyzed this is 0 what this is telling us is that the sign of f A minus f B which is the same as the sign of d x A minus d t you should commence yourself of that is that when x A is small this quantity is positive and when x A is large this quantity is negative.

That means, starting from small values of x A the system wants to move towards higher values of x A and starting from larger values of x A the system wants to move towards smaller values of x A. Now ideally these two values should convert somewhere at a value called x naught and that take us back to the third steady state that we had derived for this type of analysis and let us see what that steady state is telling us for this condition here. And the value associated with that steady state x naught was d minus b divided by a minus b minus c plus d, that was the expression we derived in the last lecture and let us see if this value does lie does end up lying between 0 and 1 for the conditions that we are discussing.

So, what does the numerator tell us? Remember the conditions we are working under are c is greater than a and b is greater than d that those are the conditions that we are working under now if that is the case b is greater than d; that means, the numerator is negative because d is less than b, but what about the denominator I can write the denominator in the following fashion, I can write this as a minus c minus b minus d. If I write it like this then what this is telling me is that the whole expression is a negative number divided by a minus c is again a negative number. So, this is again a negative number minus b minus d.

B minus d is a positive number which is the b minus d is a positive number, but these are my negative sign here. So, this is plus another negative number I can rewrite this as negative of a positive or positive of a negative. So, what this tells me is that X 0 is actually a negative number divided by two negative numbers and the magnitude of the denominator is more than the magnitude of the numerator because in the numerator here is d minus b and in the numerator this term is essentially also d minus b, and to this d minus b we are also adding another negative number hence the magnitude of denominator is more than that of the numerator.

What this implies is that x naught under these conditions will always belong to the range 0 and 1, which means that this particular steady state does exist and our stability analysis here shows that that particular steady state not only does it exist, but it is also stable in nature. So, this X 0 is the stable steady state associated with the system and these two are the unstable steady states associated with the system. So, that covers the third case associated with our analysis in terms of payoff matrix, where we have shown conditions that constrain the behavior of payoff matrix which would lead us to coexistence of the two genotypes associated with the environment.

Let us look at the final case and see if we can also find conditions which would lead us to bi stability associated with the system.

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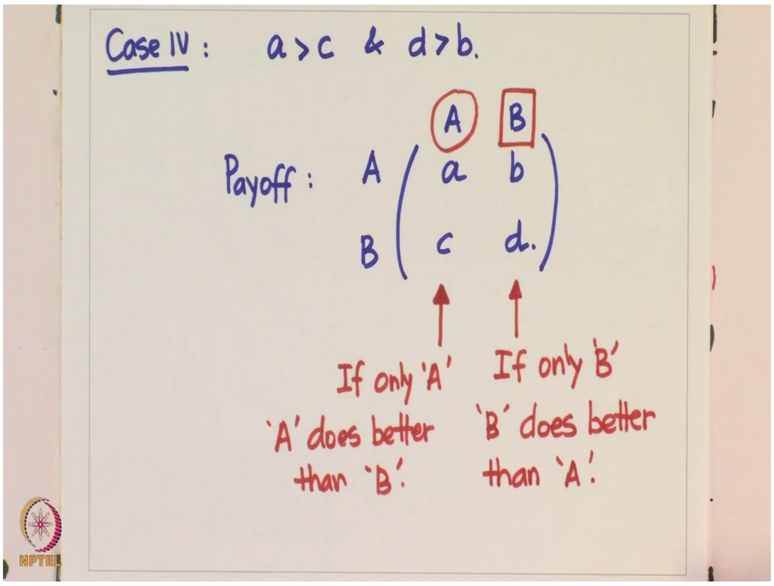

So, this is case 4 and this says that a is greater than c and d is greater than b, and I am not going to do the complete analysis of this system, but we are just going to make some intuitive arguments about what s happening in this system. And if we look at we are going to make those intuitive arguments by looking at the payoff matrix. The payoff matrix here suggests that competing strategies and then the payoff is just a b c d what this is telling me is I am going to look at this in terms of columns. So, when an individual is playing when an individual is playing or in this case a particular individual is growing in an environment where there are only a s in that particular case a is bigger than c.

So, if only A environment A does better than b that is what this payoff matrix is telling us that if you are growing an environment which is mostly A and you happen to be a b individual then you are going to grow with a growth rate a, but if you happen to be an individual of genotype a you are going to grow with A growth rate a. And since a is greater than c in this particular environment an a does better than b. But on the other hand if you are growing in an environment where there is all B s, then the converse holds true that if you are growing in only B then B does better than A and that is because d is now more than B.

So, what does that tell us what that tell us is that if I am growing in an a environment and there are a handful of b type individuals, those b type individuals are likely to get eliminated from the environment, because in that particular environment where most of the individual belong to genotype a, a does better than b type and hence those few b type individuals are going to get eliminated and we are going to move to a situation where there is all A and no B. On the other hand if I am growing in an environment where most individuals are of genotype b and there are a handful of a type individuals in such a scenario, the b type individuals are actually growing better than the a type individuals and hence selection is going to eliminate the a type individuals and you are going to end up with all b s and no a. That is what this payoff matrix is telling us and that leads us to the case of bi stability that now whether you end up in a state where there are all a s or all b s is actually dependent on what was the starting composition of the population that you began your experiment with.

A within a within one confines of the population you are going to end up eliminating b, and if you are starting to close to all b s and only a handful of a s then you are going to end up eliminating the genotype a from the population and you will end up with only B s. So, that sort of also tells us about what are the conditions on the payoff matrix which would imply that there exists a scenario where you can have this bi stable sort of a behavior. What I leave as an exercise for you is analysis of the dynamics of the system and what I would like you to show is that in this particular scenario case four that we just discussed if we have x A.

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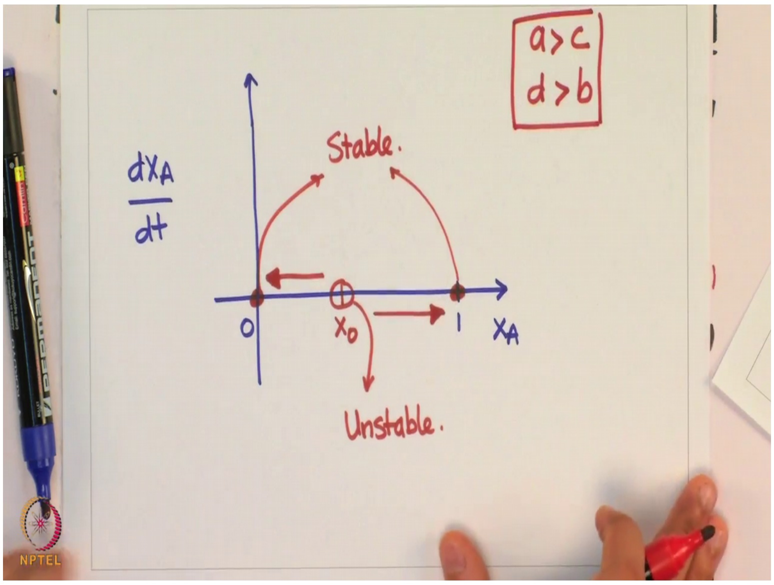

Going from 0 to one and those two particular conditions hold and this is the sign of d x A by d t what I would like you to show is that there exists an x naught the third stable steady the third steady state for this system does exist, and that this is unstable in nature. Moreover, if there is any deviation to the left of this system you move towards x A equal to 0 which means all B and if there is any disturbance from this steady state towards the right you move towards this scenario which is all a and elimination of b. So, in that sense these two steady states are my stable steady states under these conditions this is a greater than c and d greater than b I will leave this particular analysis as an exercise for you all right.

Now since, we have talked structure of payoff matrix and the associated dynamics that result from it what we want to discuss is the is the appropriate condition for stability in terms of my payoff matrices. We have stalked the equivalent definition of stability associated with steady states and dynamical systems and we have been doing that from the course we want to discuss stability in terms of these payoff matrices that we are defining and the most widely applied definition that is used in this context is what is called a Nash equilibrium and let me define that here. So, Nash equilibrium is defined as the following.

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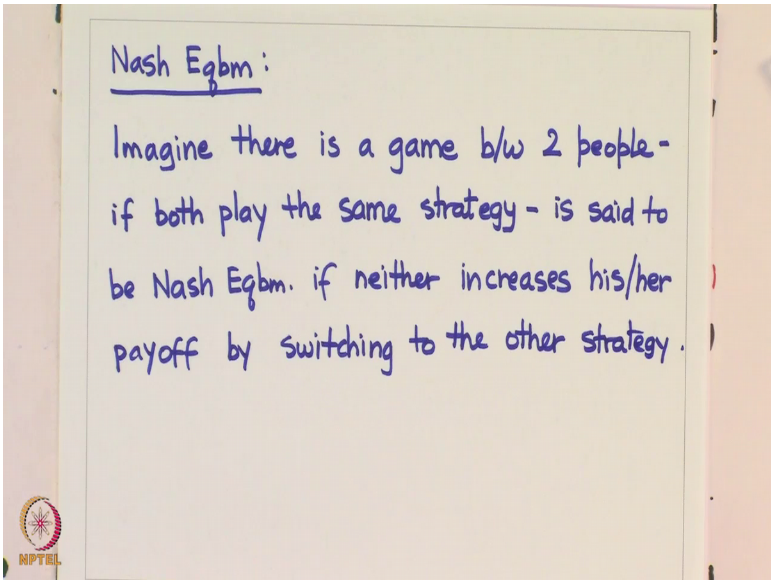

Imagine there is a game between two people game between two people in our context we are going to replace this people with the two genotypes, and it goes on that if both play the same strategy, in our context the strategy is replaced by the particular genotype. So, if two bacteria are both of the same genotype, this strategy the definition goes on is set to be Nash equilibrium, if neither of the two players increases his or her payoff by switching to the other strategy.

What does this mean? What this means is that if in the context of game theory if there are two individuals which are both playing with strategy a with each other, and the other available strategy is called strategy b. Now if I am playing my opponent with strategy a and if there is an incentive for me in switching from strategy a to strategy b, my opponents sticks with strategy a, but if on switching with strategy b I increase my payoff.

If there is an increase in my payoff; that means, that a is not a Nash equilibrium because there is no incentive for the two agents or two players which are competing here to remain with strategy a. Switching to strategy b increases payoff and hence the agents are not going to stick with strategy a, and hence this is not an equilibrium strategy. On the other hand both of us are playing with strategy a and on switching to strategy b my payoff actually decreases then a is said to be an Nash equilibrium because on switching strategies now my payoff decreases and hence I will never do that. In terms of the bacterial example that we have been talking about imagine that that we are all a genotypes existing in this environment and all of us are growing at a small growth rate a.

Now if there is a b particular if there is a genotype b individual that arises because of a mutation, this b individual is present in a pool of a individuals and this particular b individual is going to grow at a growth rate c. Now if c is less than a and a remember is the is the growth rate of an a individual which is surrounded by a individuals. If c the growth rate of the mutant that has arisen is less than the growth rate of the individuals belonging to the parent genotype.

Then this particular new individual is not going to be able to penetrate into the parent population and increase its frequency, and in that context genotype a here is going to be said to be as a Nash equilibrium associated with that problem. So, that is the definition of Nash equilibrium let us just do a quick example matrix to sort of make this complete and let us imagine that if my payoff matrix P is given as the following 3 5 0 1.

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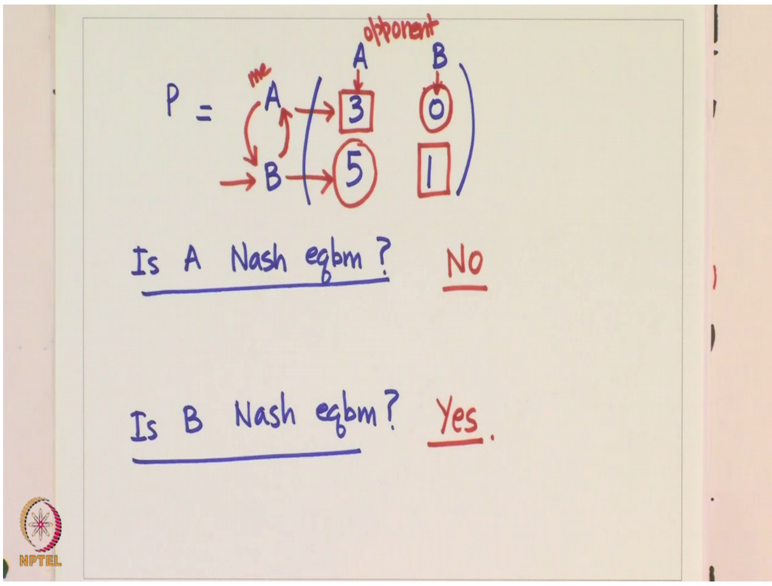

Now what we want to comment on is whether is A Nash equilibrium, and the other question is B a Nash equilibrium. So, you should pause the video for 30 seconds or so, and think about these two questions according to the definition that we have just laid out and try to answer these yourselves. Now if a was an Nash equilibrium what that means, is that both the agents both the players are playing with strategy A. So, A is playing a and the payoff associated is equal to 3.Now if this is me and this is my opponent then if I switch my strategy to B my opponent sticks to strategy A if that happens then my strategy is b opponent strategy is a.

And hence, I increase my payoff from 3 to 5 Nash equilibrium says that if you can increase your payoff by switching then that particular strategy is not a Nash equilibrium hence a is not a Nash equilibrium on the other hand if both the agents are playing with strategy b this is their payoff one both of them are getting payoff one and now if I decide to switch from strategy b to strategy a then my opponent of course, is still playing with strategy b then in that case my payoff when I am playing a and the opponent is playing b my payoff is actually equal to 0.

Hence there is no incentive for me in switching from strategy B to strategy A, hence B is A Nash equilibrium. So, looking at your payoff matrices in terms of the biological example that we have been talking about you can comment on whether a particular strategy is going to be an equilibrium strategy in terms of should a mutant of the other genotype arise in the population, would that mutant be able to grow faster than the parent individuals or grow slower. If the mutant is able to grow faster than the individuals of the genotype that already exist in the environment then that strategy is not going to be Nash equilibrium because then the mutant frequency is going to increase and eventually and it might get eliminated from the environment.

Another way to define stability is something called an evolutionary stable strategy.

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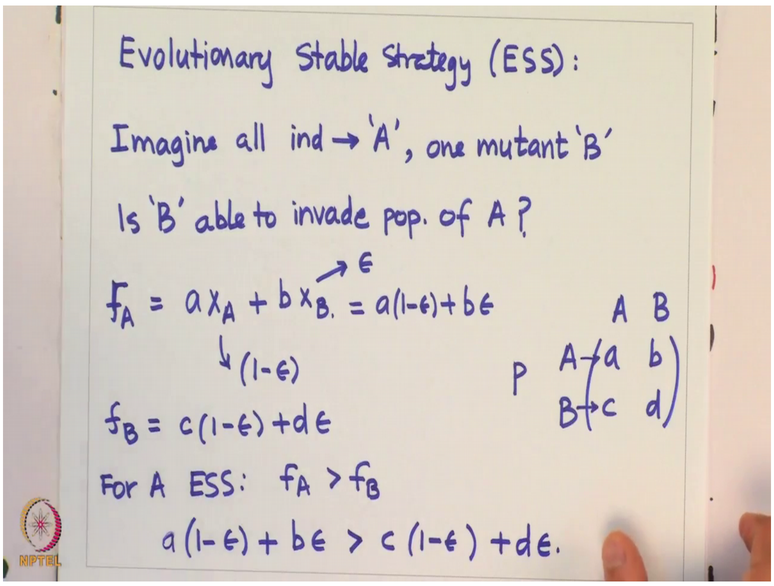

Evolutionary stable strategy its referred to as an ESS, and what this says is that imagine all individuals are playing strategy A or are of genotype A in our context and one mutant is introduced or you have one agent which is playing with strategy B, then the question that arises is that is B at that point able to invade population of this A type individuals that is the question and if B is able to invade into the population of these a type individuals then a is said to be a strategy which is not an ESS on the other hand if b is not able to invade into the population of a type individuals in that case this a strategy is an ESS. So, if my payoff matrix looks like this how can we comment if a particular strategy is an ESS. So, all individuals are of type capital A and now we have one b type individual.

So, at when this B type individual is introduced what is fitness of a type individual what is f A. f A is just going to be equal to a times x A plus b times x B, but since x b is only x b corresponds to the frequency which is obtained when you have only one individual of type b and everybody else of type a, I am going to say that x B is a very small number epsilon and x A consequently is a number 1 minus epsilon, this is because epsilon is the frequency which is associated with one individual of genotype b and everybody else of genotype a. So, this is f A which is a times 1 minus epsilon plus b epsilon.

Consequently the fitness of b at that point is just going to be c into 1 minus epsilon plus d into epsilon and the condition for a to be ESS the condition is at f A at this instant should be greater than f B which is a times 1 minus epsilon plus b epsilon should be greater than c into 1 minus epsilon plus d epsilon. So, let us finish this in the next couple of steps. So, the condition for a to be ESS as we have derived is a into 1 minus epsilon plus b epsilon should be greater than c into 1 minus epsilon plus d epsilon; since epsilon is a very small number.

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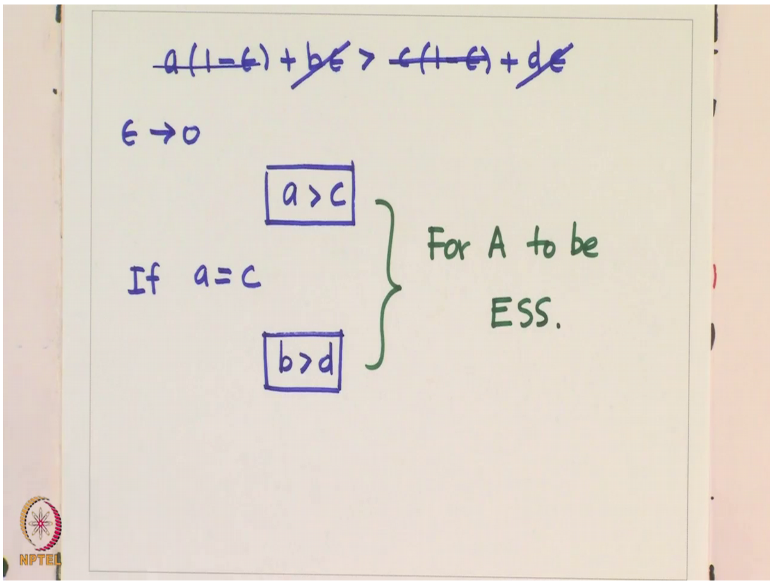

Next to 0 what I am going to do is drop these two terms their relative contribution to these terms is negligible and hence I drop them because typically in a bacterial environment I am saying that n is of the order of 10 to the power 6 7 8 9 and one mutant individuals contribution towards is epsilon is going to be very very small. If that is the case then the condition for a to be ESS is just a bigger than c that is the condition such that a is an ESS. On the other hand if a is equal to c then these two terms drop out because these exactly cancel each other out and then the condition for a to be ESS becomes b bigger than d.

So, these are the two conditions for a to be ESS. So, in this lecture we have talked about two conditions that we have for a strategy to be defined stable in one sense. One was the Nash equilibrium we can define a strategy to be whether it is a Nash equilibrium or not whether an agent has any incentive in switching from that particular strategy to another. And the second one is this evolutionary stable strategy via the definition that we just completed.

We will continue this discussion in the next lecture onwards.

Thank you.