Introduction to Evolutionary Dynamics
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Lecture – 38
Evolutionary game theory applied to Moran process

Hi and welcome everybody to the next lecture of the course Evolutionary Dynamics. And in the last couple of lectures what we had started with was a discussion on evolutionary game theory, and how we can visualize evolution in a microbial population when we have two different genotypes competing against each other in a game theoretic framework.

But the assumption and we had ended the last lecture by our discussion on stability of these strategies in a game theoretic framework, or in our context of bacterial populations stability associated with the particular genotype. But the assumption that we had made in that particular analysis was that the population size was infinite. And that assumption was paid when we were discussing and defining an evolutionary stable strategy an e s s. When we had defined the fitness of a particular mutant which was competing which had just arise in a population of strategy a and the mutant is playing with strategy b. We had said that strategy a which is the population strategy is a stable one, if its fitness is more than the fitness associated with that of the mutant strategy that has just arisen in the population.

And the condition that we had imposed on the while type or the parent strategy or the parent genotype to be stable was that the fitness at that particular instant where N minus 1 individuals are of strategy a and one individual is of strategy b. A is said to be a stable strategy if its fitness, if the fitness of an individual belonging to genotype A is more than that of the mutant which was just arisen.

And when we did that we put the frequency associated with the mutant genotype as epsilon, and the next step that we had made in that derivation was that this epsilon is a negligible number is a very very small number and hence we dropped all terms which contained the factor epsilon in them and that (Refer Time: 02:29) was a result in terms of the elements of the payoff matrix, which told us whether strategy a is stable or not. However, the assumption that we can drop the terms with epsilon is based on the fact that population size is very very large, but what, but populations maybe very large, but it is a fact that populations are always going to be finite, and on top of that if population sizes are not very large then the relationship that you get for a strategy a to be an e s s is in terms of the elements of the payoff matrix and also the number of individuals which are there in that environment.

It is a interplay between the elements of payoff matrix and the number of individuals present in the environment that allows you to comment on whether strategy a is an e s s or not and that is what we are going to do in today's lecture, is look at how does a finite population size and specially if that finite number is not very large if the n associated with the environment is very small, how does that dictate the condition whether strategy a is an e s s or not. So, that is the goal that we will be working towards today analysis of effect of finite small populations on whether strategy a is an e s s or not.

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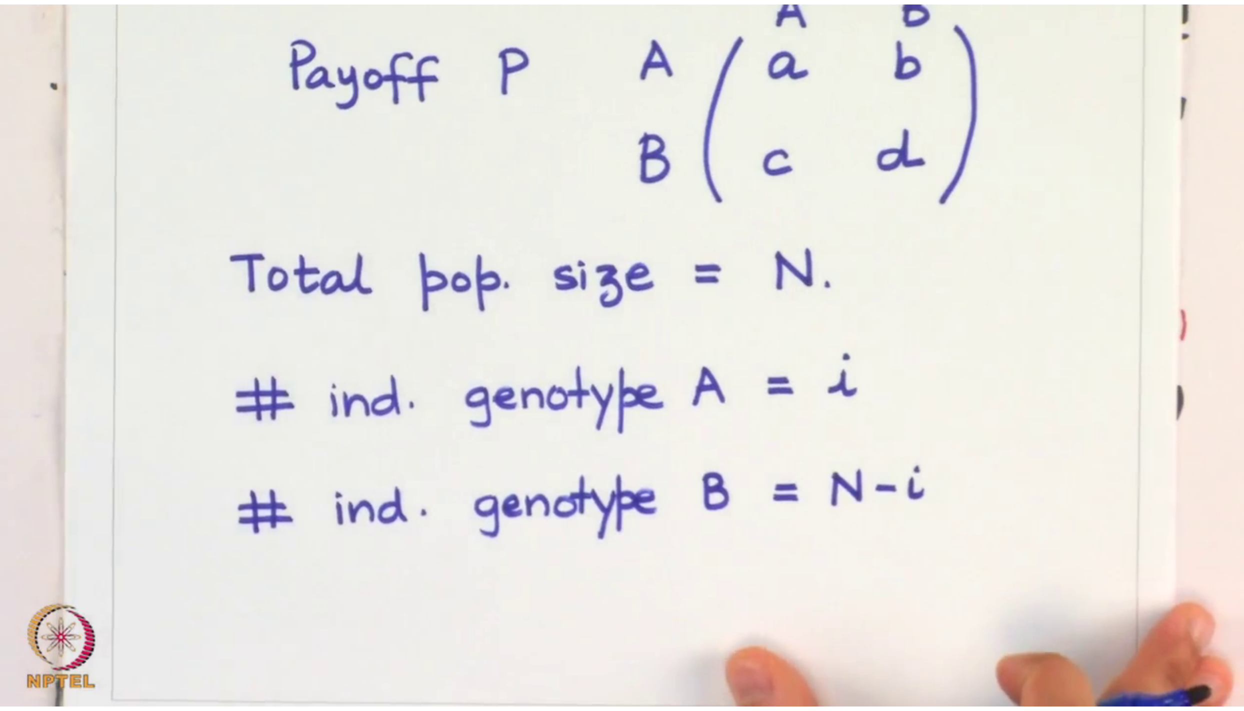

So, we will begin our analysis by defining a payoff matrix just in the minor that we have been doing so far.

So, payoff matrix P is just strategy A and B or genotypes A and B, and the payoff associated with the rows strategy when competing against the column strategy is given by a b c d this is what we have been doing so far.

Now, we will assume that we need to assume a finite population size. So, we will say that the population size associated with this environment is equal to, and at any particular instant that we are interested in talking about here the number of individuals which belong to genotype A or strategy A is equal to i, and that automatically leans that number of individuals which belong to genotype B or strategy B is equal to N minus i.

And next, what we want to do is we want to calculate that what probability does an individual of type a have of meeting another individual of type a what probability does an individual of genotype A have of meeting another individual of genotype B. And for that we are just going to do we are just going to make a very simple assumption that the probability of meeting an individual of a particular genotype is just proportional to number of individuals which are present in the environment which belong to that particular environment.

So, if of all the other individuals which are present in the environment half are of genotype a, and half are of genotype B my probability that i will meet someone from genotype A is just equal to half and this is just in proportional to the number of individuals which are present which belong to a particular genotype. So, for this for our analysis; since the population size is N and we are talking in the context of what probability does one individual have of meeting another individual of genotype a, then from the context of that individual there are N minus 1 other individuals.

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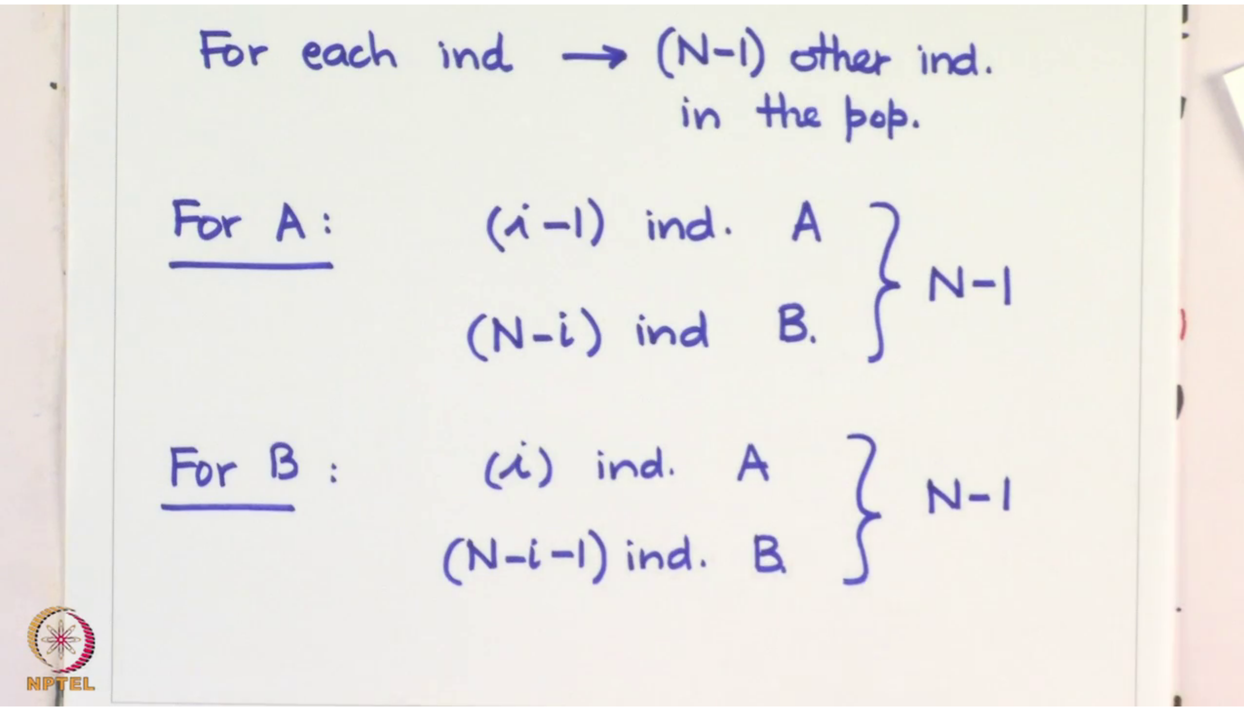

So, the total population size from the context of one individual is not n, but there are N minus 1 other individuals that this individual sees. So, we will just put the term that for each individual there are N minus 1 other individuals in the population. So, for an individual with genotype A there are i minus 1 individuals with genotype A, and there are N minus i individuals with genotype B, because in all there are i individuals with genotype A.

So, for an A individual there are only i minus 1 individuals which have this genotype. Similarly for an individual with genotype B there are i individuals with genotype A, and N minus i minus 1 individuals with genotype B. And in both these cases the number of other individuals that are there both these quantities add up to N minus 1 and N minus 1 that s to be expected because this takes care of everybody in the population who is not that particular individual.

So, now, if we have this the next step is just defining probabilities that what is then chance that an individual has that an a type individual or a b type individual has of meeting another a type or a b type individual and that s done that s going to be done in proportional to the frequency associated with individuals belonging to that particular genotype. So, we will just extend this number to probabilities.

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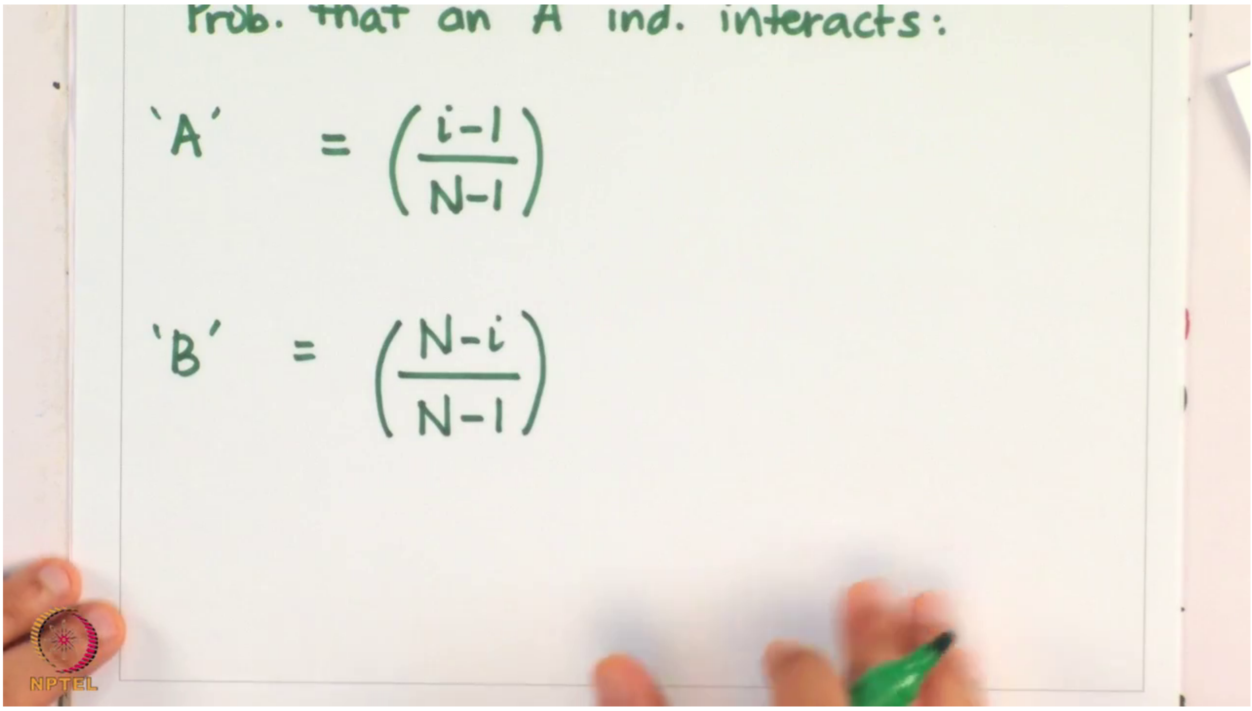

Now, and we will say that the probability that an A individual the an individual genotype A interacts or meets, an A individual is this probability is just equal to i minus 1 divided by N minus 1. Because of all the other individuals that are present in the environment which is N minus 1 there are i minus 1 which belong to this particular genotype and the probability that an A individual interacts with genotype B is just going to be equal to N minus i divided by N minus 1 and similarly we can define equivalent probabilities for genotype B and again this is in the context.

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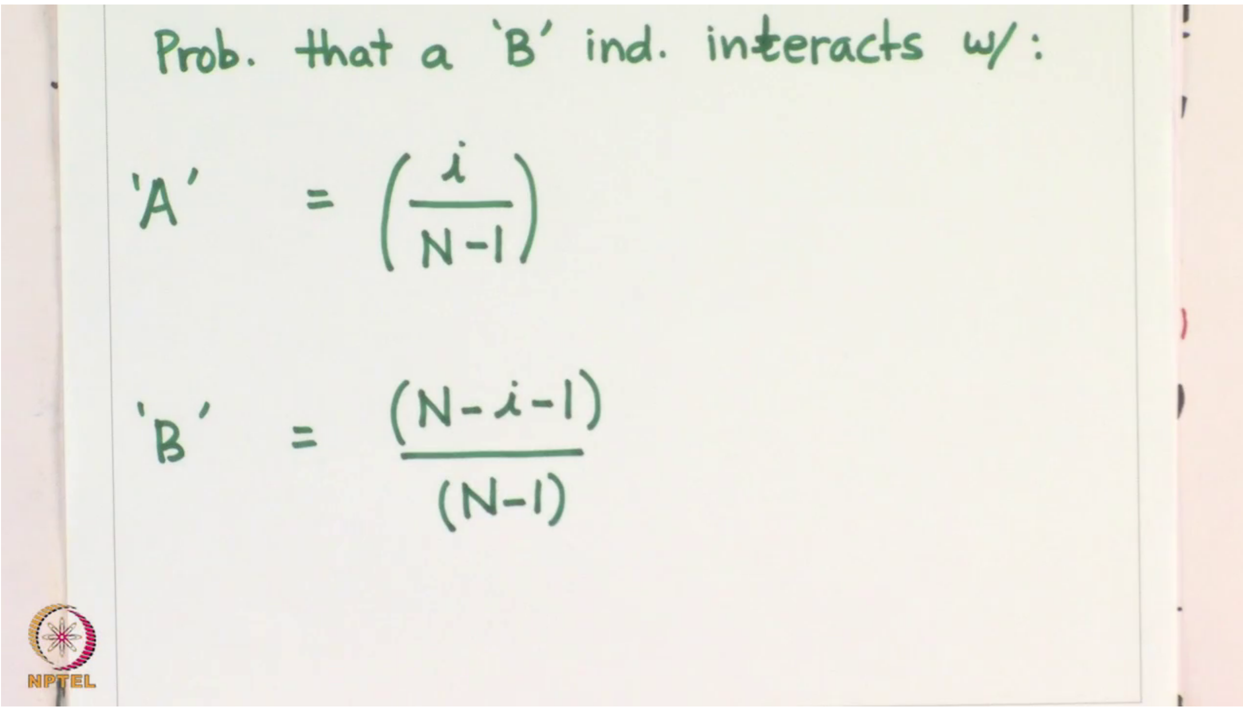

This is from the context of an individual which belongs to genotype B and we are going to put down the probabilities associated that this individual sees an individual of genotype A or genotype B. So, just as we did for an A type individual, probability that a B individual interacts with an a type individual.

is just equal to i divided by N minus 1 and this B type individual the probability that it interacts with the B type individual is just going to be equal to N minus i minus 1 divided by N minus 1. So, we have these we have these probabilities associated with both the genotypes of meeting an individual of type A and type B, and the next thing that we are going to do is calculate the associated payoffs for each of these type of individuals.

So, what is the average payoff depending on taking into account that likelihood that this individual encounters a genotype A and genotype B at the given instant where the structure of the population is defined by variable i in the sense that there are i individuals and N minus i b individuals, what is the payoff associated with these two genotypes going to b given that these are the likelihoods of them meeting individuals of these two genotypes and given the fact that the payoff matrix has a structure as given. So, that payoff again is just an extension of what we had done in the last lecture except for the fact that now we take into account that population size is finite.

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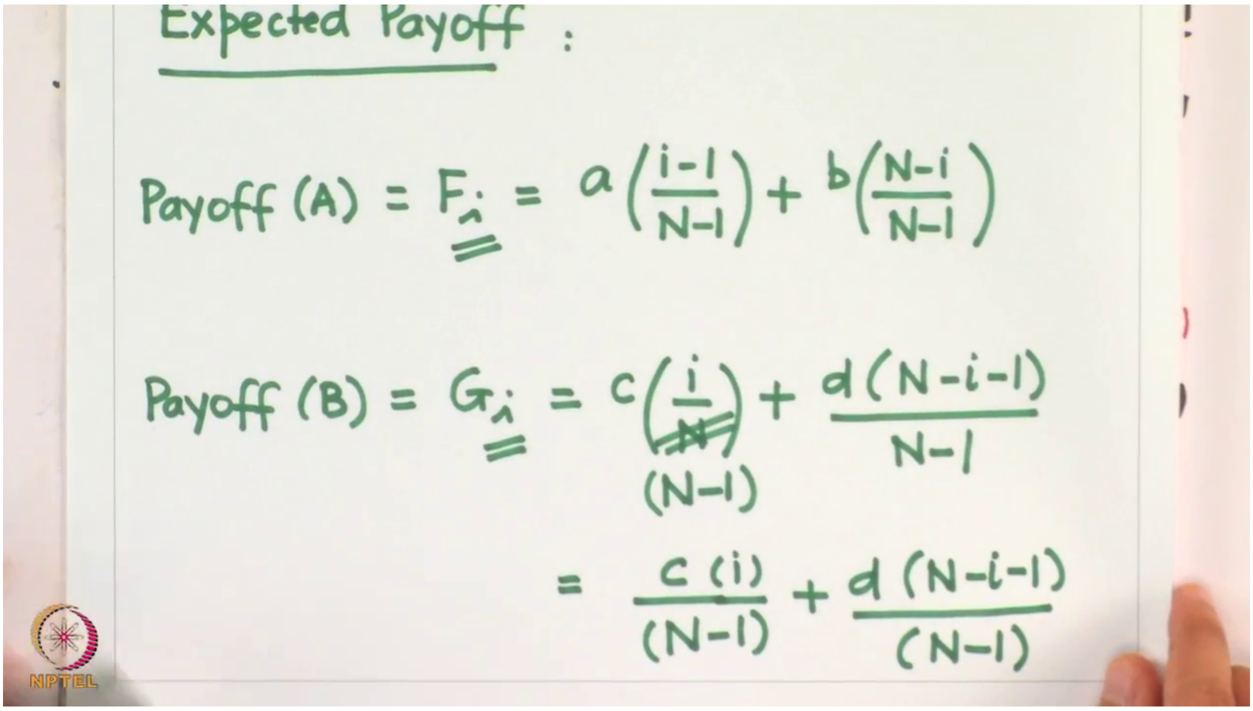

So, let us put that payoff down and that s going to be. So, expected payoffs for the two strategies or two genotypes is just going to be equal to let us say payoff for A is equal to F of i which is just going to be equal to times i minus 1 divided by N minus 1 plus b times N minus i divided by N minus 1.

So, we are we are calling payoff of a as just a into probability that this a individual meets another a type individual, plus b into probability that this a individual meets a b type individual and we are using the word F here this is represented this is a variable that we are choosing to represent expected payoff, the subscript i here represents this is the payoff when the population structure is defined by the variable i. When the population is at a stage where there are i a individuals and N minus i b individuals.

So, we do this and similarly we get a payoff for B, which we are going to write as G of i again payoff G is just a variable we are using to represent payoff of B, and the subscript i again denotes that this is the payoff which is given when the population structure is given by the variable i which is the number of a individuals, and this just comes out to be c into i by N plus d into N minus i minus 1 divided by N minus 1, there is a small mistake here this is not N this should be N minus 1 because from the context of this particular individual there are only N minus 1 individuals N minus 1 other individuals which are present. So, this is just let me just write this again this is c times i divided by N minus 1 plus d into N minus i minus 1 divided by N minus 1 alright.

So, we have these payoffs now we have payoffs associated with genotype A and genotype B when the population structure is given by this variable i, and this also incorporates the payoff matrix elements a b c and d. Now we want to connect this payoff with fitnesses.

Now payoff and fitnesses we have often since the start of this discussion on evolutionary game theory we will be seeing that we will be using payoff and fitness somewhat interchangeably, but what we want to incorporate is that payoff could payoff from this particular matrix this particular difference between genotype A and b could influence their fitnesses the rate at which they are growing in a different manner. There might be some genotypes there might be some differences between genotype A and B where payoff is very closely linked to fitnesses, but A and B could also have genotypic differences where payoff is not very closely or very strongly dictating the fitness associated with these two genotypes.

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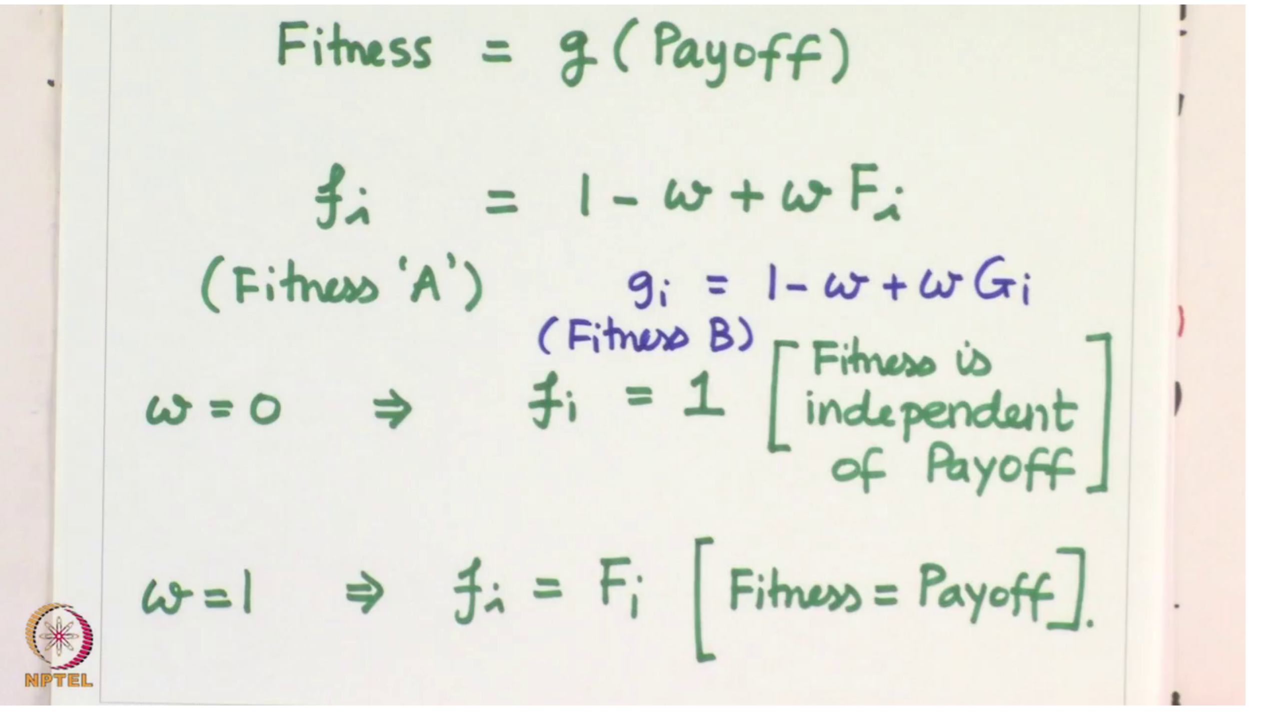

So, to incorporate this we want to establish a relationship between payoff and fitness and we will do that via a tunable factor omega and the way we do this is we say that first we realize that the fitness the rate at which these populations are growing is equal to some function g of payoff; and we do not know what this function is, but we make an assumption that fitness F of i this is fitness of genotype A, is just going to be equal to 1 minus omega plus omega into F i and F i is the payoff associated with the population structure and the given payoff matrix as defined in the previous slide.

So, this is capital F i and what we are saying is that the fitness of a small f i is just equal to this where omega is the parameter associated with this definition. So, let us see what happens when omega is equal to 0, if omega is equal to 0 what you are saying that F of i is equal to one and the and the payoff associated from the fitness payoff associated with the evolutionary game that we are talking about here has actually no impact on the fitness associated with the genotype. So, payoff and fitness in this case are not linked at all and what we have we have a case here where we are saying that fitness is independent of payoff.

So, this would be a case where if you have two genotypes coexisting in an environment and they are interacting via the via the payoff matrix as we have defined then no matter what the return to a particular genotype is from that payoff matrix, that return does not in any way impact the growth rate associated with those two genotypes. So, growth rate the variable growth rate is independent of the returns that the particular genotype derived from the payoff matrix that s the case that s represented by omega equals 0. On the other extreme we can have omega equals one which would imply at f of i is equal to capital F of i.

Because when we plus omega equal to one these two will cancel each other this is just equal to one. So, we get small f i equal to capital F i which implies that fitness is equal to payoff. So, this would a case where the return that a particular genotype is deriving from the payoff matrix is very very strongly related to the fitness or the growth rate associated with that genotype. So, we call omega equal to one as the case where there is very strong selection in terms of the payoff matrix that we have defined and we call the case when omega is equal to 0 as there being no selection because the returns from the payoff matrix do not in any way dictate what is the growth rate associated with that genotype.

So, when we are defining these models we tune the variable omega between 0 and 1, and that takes us from one extreme where there is no selection in terms of the game being played in the game being played in terms of the payoff matrix that we have defined two omega equal to one where the payoff the return from the payoff matrix actually very strongly dictates the rate at which these species are going to grow. So, depending on what value of omega we choose between 0 and one we get the corresponding growth rates associated with any particular individual genotype and of course, this is F i similarly g i which is the fitness of B will be correspondingly defined as 1 minus omega plus omega into G i, where G i is the payoff return from the matrix that we defined in the previous slide this gives us G i.

And we when we plus G i here that gives me the equivalent growth rate for genotype B alright. So, omega for any case is just going to be the same value somewhere between 0 and 1 depending on the exact phenotype which is associated or the exact relationship that s associated N terms of the physiology of the organism when I am looking at strategies a and b, but it is going to be a variable between 0 and 1.

Now, when we have this suppose we have a population at a structure i whose where there are i a individuals and N minus i b individuals, now we want to calculate what is the chance that if we were to apply the Moran model to this process that the system transitions from state i to i plus 1 and remember morns process was discovered was discussed earlier in the course, where we said that in each step there are two processes that happened in the Moran process that you choose an individual for birth and you choose an individual for death hence depending on if you choose an a type individual for birth. That means, the number of a type individual goes up by 1 and if you end up choosing a b type individual for death; that means, the number of a b type individuals goes down by 1.

The consequence being that you move from a state of the system where there are i a individuals and N minus i b individuals you move to a state where there i plus 1 a individuals and N minus i minus 1 b type individuals. So, that is the transition we said that the system goes from i to i plus 1. So, we do that similar kind of a thing and the idea being that we want to incorporate population size N is a variable that s associated with all our fitness definitions here. So, we want to incorporate that effect and calculate this transition probability. So, if we apply that Moran formula Moran process formula here.

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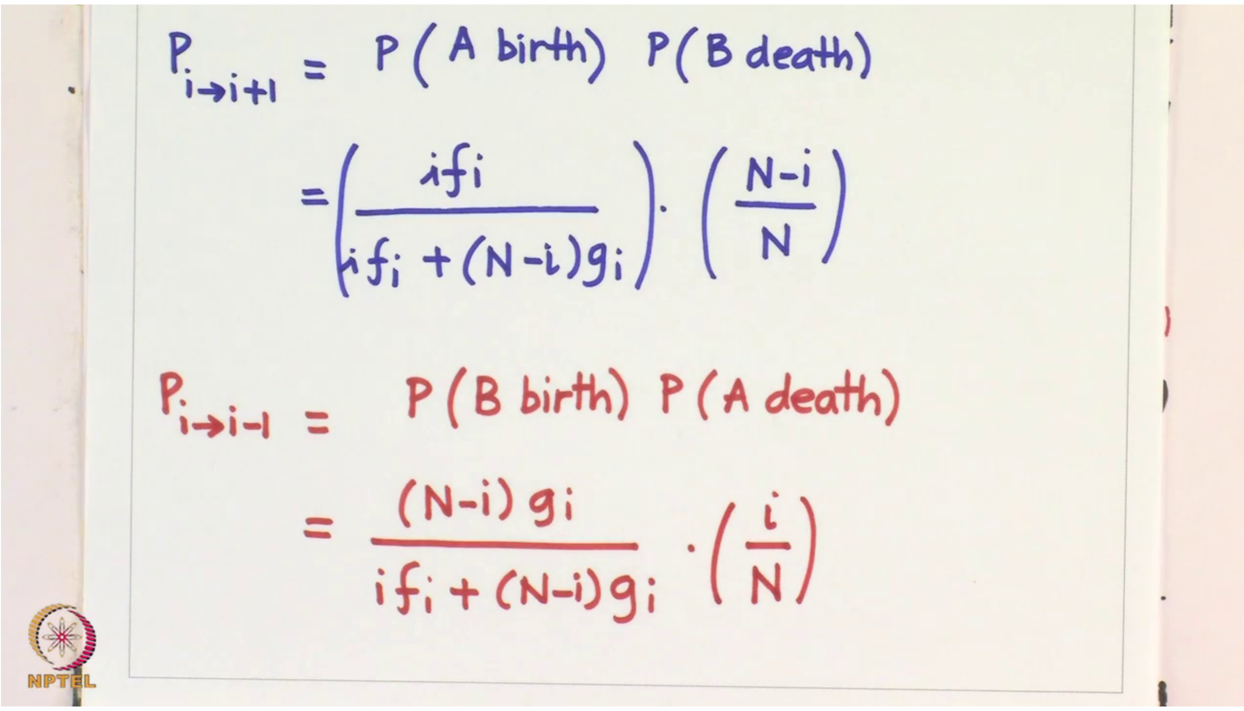

And we want to compute P i to i plus 1, now this transition can only happen when you are selecting an A type individual for birth and B type individual for death. So, this happens when probability A birth times probability that a B type individual gets selected for death, and as we have done before the probability that an a type individual get selected for birth is in proportion to the fitness associated with the A genotype and that fitness we have already seen is equal to f of i.

And since there are i number of individuals which belong to this genotype, that total fitness associated with a type individual is i times f i and the total fitness with all individuals in the population will just be i times f i plus N minus i times g i. Where g i is the fitness of the N minus 1 b type individuals in the population and the probability that b gets selected for death is just going to be equal to N minus i divided by N. And the way we had defined this we had said that its only the birth processes which are selected weighted in proportion to weighted by their fitnesses the death processes are selected totally randomly without any weight associated with fitness.

So, that s the probability that the system transitions from state i to i plus 1, similarly we can have another probability that the system transitions from state i to state i minus 1 and that is will happen when you select a B individual for birth and an A individual for death.

And using the same logic as above this will happen when this will happen with the probability N minus i divided by g i times g i divided by i times f i plus N minus i times g i and the probability of choosing an a individual for death is just going to be equal to i divided by N. So, our transition probabilities now incorporate N as one of the variables which has common to be, but of course, there are two more transitions two more events that can happen, that you select an a type individual for birth an a type individual for death.

So, selecting an a type individual for birth increases the number of a type individuals for one by 1, and selecting a a type individual for death decreases the number of a type individuals for death hence the total number of individuals belonging to a type remain constant at i. Remain the same as the previous step which is equal to i and similarly you can have a b selection of b for birth and b for death which would also ensure that the structure of the population does not change and it remains at i, and in both these cases the structure of the population does not change.

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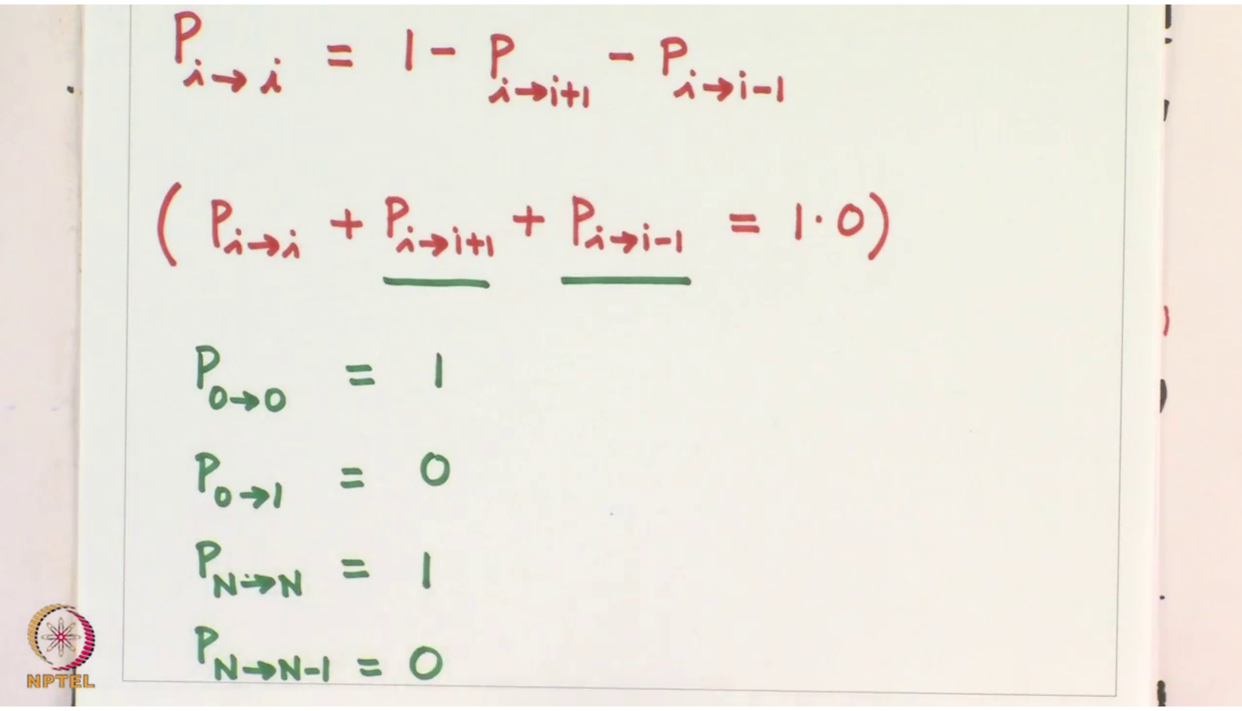

So, the probability associated with those steps are is the transition probability that the system remains from i at state i, and this can simply be written as 1 minus probability that the system transitions from i to i plus 1 minus probability of i to i minus 1, and this comes from the fact that we already know that the three transitions P i to i plus probability that system changes from i to i plus 1 plus probability that system transitions from i to i minus 1 is equal to 1. Because the way we apply Moran process these are the only three transitions that are possible with the population you cannot have any other transition other than these three hence the sum of these probabilities is 1. And I have already computed expressions for these for this probability and this probability.

So, the third one can simply be represented as a function of the other two before we go ahead just a few simple intuitive definitions of P i i applications of P i i, we have done this before, but you should just answer these four probabilities by pausing the video for maybe 30 seconds, and just answer that what are these probabilities. So, I am plugging specific values of I here we are plugging specific values of i which is the which is the state at which system starts and the second value here represents the state at which the system ends after one step of Moran process has been applied.

So, again the numbers here should be 1 0 1 0 and because this is true because we have to look at the first one P 0 0 means what is the transition probability that we start at a state where i is equal to 0; that means, there are no a individuals and end at i equal to 0 which is there is no a individual, because there were no individuals to begin with and there are no mutations permitted in the Moran model the probability of this happening is equal to 1 because this means that you are going to pick up b type individual for birth.

And pick up b type individual for death and if you do that this probability is just equal to 0 is equal to 1 and so on and so forth you can convince yourself of the other 3. So, so far in this lecture what we have done is derived an expression of this transition probabilities where the population size N has coming to be. What s critical to us or what we will be working towards in the next lecture is that the particular value of i that we are interested in is 1, which represents the physiological case that you have a genotypically identical population where all N individuals are of the same type and via mutation and a birth and a death process one mutant has arisen. So, that your population structure is now N minus 1 individuals of one type, and one individual of one particular type.

And in this scenario what we are interested in is the what is the probability that this one individual is going to be able to establish itself and spread through the population and eliminate all other N minus 1 individuals and specifically we want to study this relationship in the context of population size and how does the variable N the population N size dictate this probability; continue with that in our next lecture.

Thank you.