

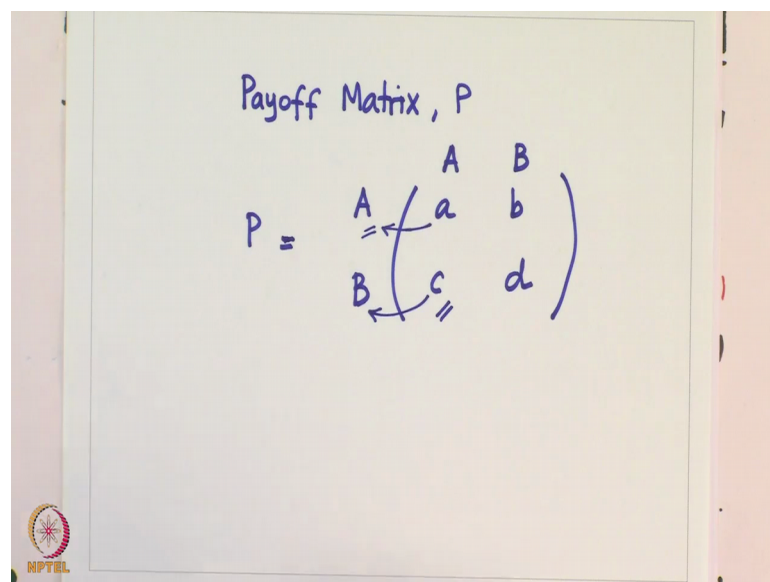
**Introduction to Evolutionary Dynamics**  
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**Lecture - 36**  
**Evolutionary game theory - 3**

Welcome back everybody. We will continue our discussion on game theory and borrow concepts from that field and apply them to growing microbial populations to come up with a framework where we represent where fitness is a function of the composition of the an population, fitness is dependent on the frequencies associated with the different genotypes which are present in the environment.

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Payoff Matrix, P

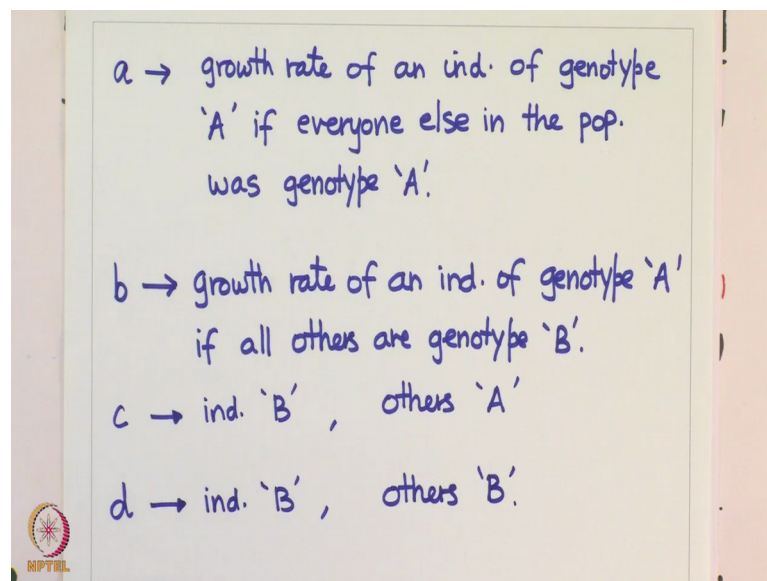
$$P = \begin{array}{c|cc} & A & B \\ \hline A & a & b \\ \hline B & c & d \end{array}$$


So, just to pick up from where we left off last time; we are defining a payoff matrix P, where P represents of the two strategies that are available A B. And when these strategies are competed against the two strategies A and B, what is the payoff that a player gets when strategy A is competed against strategy A. In that case the payoff associated with what the player who is playing with strategy A gets a small a, when strategy B is competing against strategy a the payoff for the player playing with strategy b is given by this number c.

So, how do we extend this logic to microbial populations? And the way we are going to do that is the following. Imagine two populations which are coexisting in this

environment and again we will call them genotypes a and genotype B. Now what we are going to do is define a growth rate associated with any individual of genotype a, if it was growing in an environment which contained only individuals of genotype A also we will define another growth rate associated with a with a individual of genotype A assuming that this individual is growing in a population where everybody else in the environment belongs to genotype B, ok.

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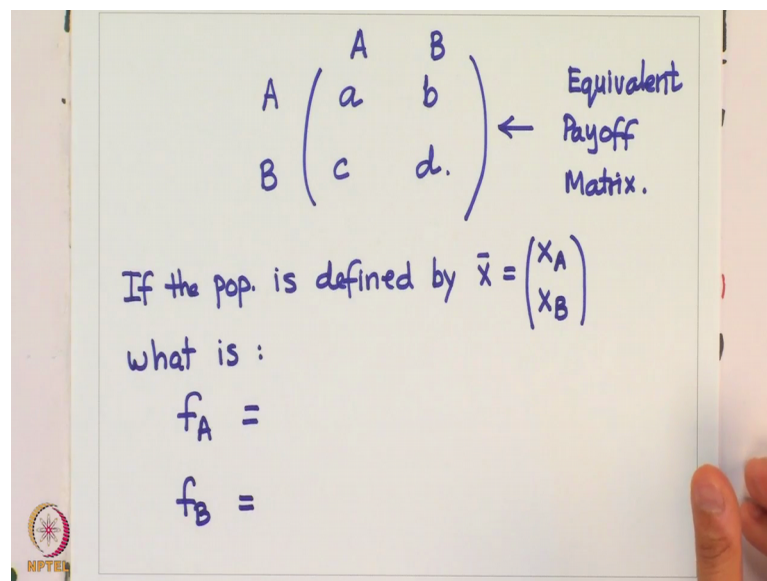


So, let us define these quantities let  $a$  be the growth rate of an individual of genotype A, if everyone else in the population was genotype A. So, this corresponds to talking of a case where there is only one particular genotype which is present in the environment which is genotype A, and in that case what is the growth rate associated with a individual in this environment. Compare this to the second quantity we want to define as  $b$  which is growth rate of an individual of genotype A, if all others are genotype B.

And this corresponds to a situation that we are talking of growth rate associated with one particular individual belonging to genotype A which is growing in an environment where everybody else is of genotype B. So, this can be thought of as an environment where every other where everyone was genotype B, and this one particular mutant has arisen which is of genotype A and how does this mutant grow in terms of every in the presence of everybody else which is of a different genotype is represented by number  $b$ .

Similarly, we define c and d, c represents to individual of genotype B when all others are of genotype A, and b refers to growth rate of individual of genotype B given that all others are of genotype B. So, we define these four quantities and what this should tell you is that, this looks very similar to the payoff matrix that we defined and in fact, we are going to use these definitions of small a b c d to define our own payoff matrix in terms of microbial growth rates associated in very specific environment.

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Handwritten notes on a whiteboard:

$$\begin{array}{cc} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \leftarrow \begin{array}{l} \text{Equivalent} \\ \text{Payoff} \\ \text{Matrix.} \end{array}$$

If the pop. is defined by  $\bar{x} = \begin{pmatrix} x_A \\ x_B \end{pmatrix}$

what is :

$$f_A =$$

$$f_B =$$

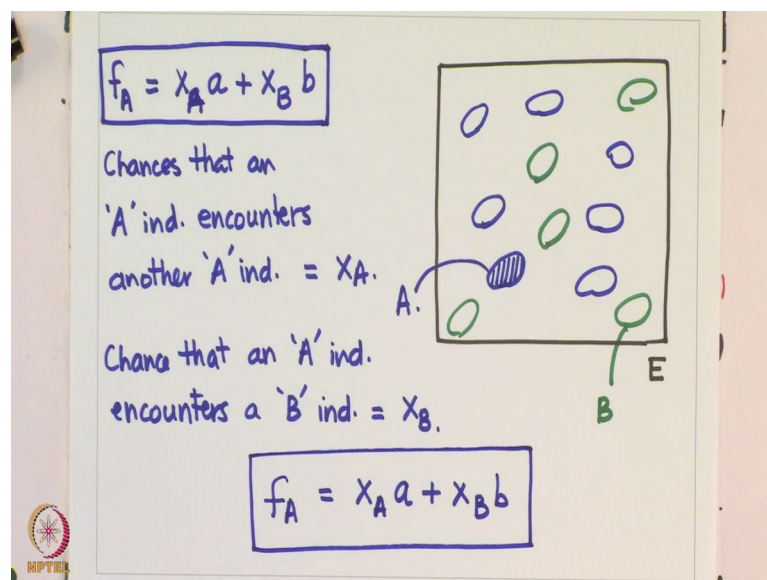
So, now payoff matrix for my environment is just A and B, and now A and B are now not strategies, but genotypes and I know when genotype A is growing in the presence of genotype A the growth rate is a when genotype A is growing in presence of in an environment where everybody else is genotype B its growth rate is B and c and d complete the matrix.

So, these are the growth rates associated with these two particular genotypes, when they are growing in environments which have these two particular genotypes. So, that is my equivalent payoff matrix, now the next thing that we want to define is what would be the fitness of an individual if the composition of the population at any given point is defined by  $x_A$  and  $x_B$ . So, if the population at any given point is defined by the vector  $x$ , then what is fitness of A and fitness of B. This is what we are interested in at this point and we want to make use of payoff matrix to help ourselves this question. But remember the payoff

matrix only talks about fitnesses when one particular genotype is growing in the presence of everybody else which could be genotype A or B.

So, it does not talk of it does not talk of cases where there are finite compositions of  $x_A$   $x_B$  associated with the population, it talks of it talks only about the case where one particular individual is one particular individual is growing in an environment where everybody else either belongs to its own genotype or everybody else is of a different genotype that is the context in which payoff matrix is defined. But if the population is defined by this particular vector then how would you come up with an expression for  $f_A$  and  $f_B$ . And the answer to that can be taught in terms of probability. So, let us imagine our environment to the images draw this.

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Let us imagine our environment like this and this environment now has individuals of genotype A and also individuals of genotype B. Let this be B and let this be A these two coexist and now what we are interested in is at this particular instant at this composition of the population what is  $f$  of A, and we know that if an individual was growing in all a individuals then its fitness was a small  $a$ , and if an individual was growing in all b then its fitness was defined by small  $b$ .

But we do not know what would be the fitness  $f_A$  if it was growing in a population whose composition was defined by something like this where  $x$  where the fraction of individuals of genotype A and are  $x_A$  fraction of individuals of genotype B are  $x_B$ . Of

course, we are not going to get a very exact answer in terms of what exactly is the growth rate associated in a case like this, but what we are going to assume is that if  $x_A$  is the fraction of population which belong to genotype A in this setting then the chances that this.

So, if you are talking in the context of this particular individual and finding out its growth rate in this composition, then the chances that this particular individual encounters another a type are  $x_A$ . So, before we develop this expression chances that an genotype A individual encounters another A individual are equal to  $x_A$ . The probability that this individual interacts with another individual of genotype A are  $x_A$ , and the chance that an A individual encounters a B individual are given by  $x_B$ . Now if an A individual was always encountering an A individual, then the growth rate we have already found to be equal to A.

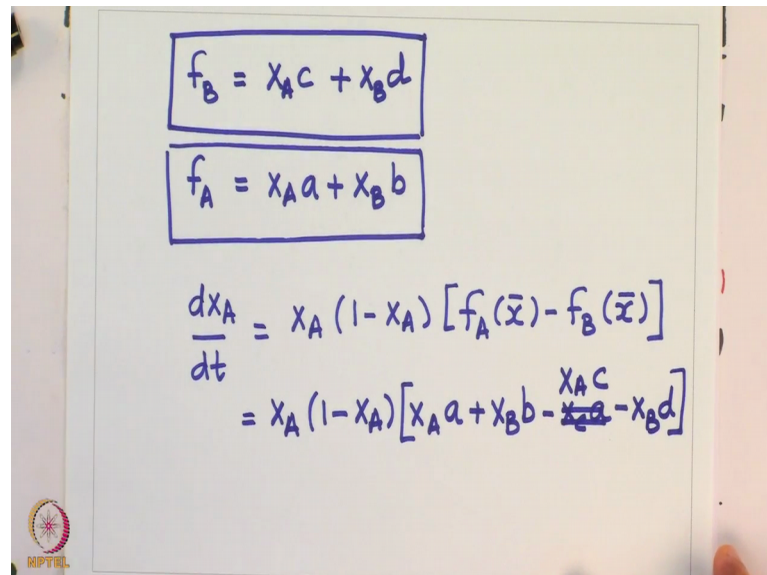
On the other hand if an A individual was always encountering a B individual then the growth rate would have been B hence we write  $f_A$  as just waited sums of these two probabilities.  $f_A$  is just given by  $x_A$  times a plus  $x_B$  times B, and what this represents is that the if A was always growing with A type individuals then its growth rate would be one. So, if you plug in  $x_A$  equal to one here that automatically means  $x_B$  equal to 0 and  $f_A$  just comes out to be equal to A.

If you plus  $x_B$  equal to 1 which means  $x_A$  equal to 0,  $f_A$  automatically comes out to be equal to B, and hence this is a linear interpolation between these two extremes and what you are saying is that at any composition  $x_A$  and  $x_B$  of the population, the fitness of the individual can be given as weighted mean of the two growth rates if they were growing with all a s and all b s and weights here the weights who assigned to each of these growth rates are equal to the frequency of the particular genotype that we are interested in here. So, that sort of allows us to define  $f_A$  and for the first time what we are able to do is define fitness where fitness is actually a function of the composition of the population.

Now, this of course, is  $x_A$  let me just rewrite that  $f_A$  is just equal to  $x_A$  times a plus  $x_B$  times b. So, this is sort of the first representation that we have, where fitness is are a function of the composition of the population all right. So, if this is equal to  $f_A$  what

would  $f_B$  be equal to. You should perhaps pause the video for thirty seconds and try to do this yourself this is just an extension of what we have been talking about so far.

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$$f_B = x_A c + x_B d$$

$$f_A = x_A a + x_B b$$

$$\frac{dx_A}{dt} = x_A(1-x_A)[f_A(\bar{x}) - f_B(\bar{x})]$$

$$= x_A(1-x_A)[x_A a + x_B b - x_A c - x_B d]$$

So, again if a b individual was always growing with an a individual, then if a b individual was growing in an environment where everybody else was an a was a genotype then its growth rate was c, but if a b individual was growing in an environment where everybody else was a b genotype, then the growth rate associated with that particular individual was d.

Hence we just weight these two numbers by the two genotypes associated and we get we get fitness of B as the following function. And on the previous page we had just derived that  $f_A$  is equal to  $x_A$  times a plus  $x_B$  times b. So, in terms of our payoff matrix these are the fitnesses of the two genotypes at any given composition of the population, whether composition is defined by number of individuals which belong to a particular genotype. So, what does this tell us in terms of where the population is going to move if I were to start at from any random mixture of a and b individuals, what does this tell me about the dynamics of the system and in the last lecture we have already seen that for a case where frequency where fitness is dependent on frequency of individuals of a particular genotype, the dynamics of the system are defined by the following relationships, which is  $\frac{dx_A}{dt}$  is equal to  $x_A$  times 1 minus  $x_A$  times  $f_A$  dependent on composition, minus  $f_B$  dependent on composition. We can write this similar equation



for  $\frac{dx_B}{dt}$  and all we have to do to understand dynamics of this particular system now is plug in these expressions for  $f_A$  and  $f_B$  into this term here and that would give me  $x_A$  times  $1 - x_A$  times  $x_A$  times  $a$  plus  $x_B$  times  $b$  minus  $x_C$  times  $a$  minus.

I am sorry I wrote this wrong this is  $x_A$  times  $c$  minus  $x_B$  times  $d$ , that's the expression that we have for the dynamics of  $\frac{dx_A}{dt}$ .

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The image shows a whiteboard with handwritten mathematical work. At the top, the equation  $\frac{dx_A}{dt} = x_A(1-x_A)[x_A a + (1-x_A)b - x_A c - (1-x_A)d]$  is written. Below it, the equation is simplified to  $\frac{dx_A}{dt} = x_A(1-x_A)[x_A(a-b-c+d) + b-d]$ , which is enclosed in a green rectangular box. Underneath the boxed equation, the text "Steady states:" is written in red. To the right of this, a note says "depends on particular values in P." with an arrow pointing towards the steady state equations. Three steady states are listed:  $x_A = 0$ ,  $x_A = 1$ , and  $x_A = \frac{d-b}{a-b-c+d}$ . A blue arrow points from the third equation to the interval  $[0, 1]$  written in blue.

We can simplify this further by substituting for  $x_B$  equal to  $1 - x_A$  because we know that at any given point, and time  $x_A$  plus  $x_B$  is just equal to 1 and if we do that we get  $\frac{dx_A}{dt}$  equals  $x_A$  times  $1 - x_A$  times  $x_A$  into  $a$  plus  $1 - x_A$  into  $b$  minus  $x_A$  into  $c$  minus  $1 - x_A$  into  $d$ . So, we have this longest expression which defines the dynamics associated with the system, but we can simplify this a little bit more and we can do that by bringing together all the terms that contain  $x_A$  we can bring together all the terms that contain  $x_A$  here. So, if I write  $x_A$  this is the first term which contains  $x_A$ . So, this is the second term, but it has a minus sign here. So, minus  $b$ , this is the third term also has a minus sign minus  $c$ , this is the fourth term it has two minuses here. So, this becomes positive and we write whatever is left now. So, one of the things that left is this  $1$  times  $b$  plus  $b$  and the second thing that's left is this  $-1$  into  $d$  which is  $b - d$ .

So, that is the expression that we have for  $\frac{dx_A}{dt}$  we can derive a similar expression for  $\frac{dx_B}{dt}$ , I just (Refer Time: 18:18) mirror image of this. So, that is not going to

tell us anything new about the system all right. So, that's the relationship that we have which defines the dynamics associated with the system, and now what we are going to try and do is try and imagine scenarios depending on the values that  $a$ ,  $b$ ,  $c$ ,  $d$  are able to take, we can create let us try and see if we can create the four scenarios that we discussed when we started our discussion on evolutionary game theory. So, the four scenarios that we were talking about were all  $a$ , all  $b$ , coexistence and bi stability. And what we want to see here is that are we able to create those scenarios here by choosing particular values of  $a$ ,  $b$ ,  $c$ ,  $d$  small  $a$ ,  $b$ ,  $c$ ,  $d$  the our payoff matrix, such that the system dynamics automatically takes us towards those four cases.

Before we do that we just we should just take a look and identify the four steady states associated with the system, I am sorry the three steady states associated with the system and those are this would give me just  $x_A$  equal to 0. So, again I am looking at all values of  $x_A$  such that  $\frac{dx_A}{dt}$  is equal to 0 and this is the first one the second one is if I equate this term equal to 0 which gives me  $x_A$  equal to 1, and both these are sort of intuitive and away because this represents the case where there is no  $a$  but all  $b$  and this represents the case where there is all  $a$  and no  $b$ . So, this these two cases essentially.

Are talking about a single species just existing by itself and there being no other genotype, but the second, but the third case is obtained when I equate this expression equal to 0, and that gives me my third steady state associated with the system which is  $\frac{d - b}{a - b - c + d}$ . So, these are the three steady states which are associated with the system as we have just defined.

Now one of the things that you should note here is this third steady state is not guaranteed to exist all the time, because depending on the values of  $a$ ,  $b$  and  $c$  and  $d$  that you end up choosing or you may have for a particular system, those particular values when you plug those in here could might as well could give you  $x_A$ ; for instance which is less than 0.

So, whether this exists as a stable whether this value of  $x_A$  exists as a steady state or not depends on particular values in your payoff matrix  $P$ , because a choice of  $a$ ,  $b$ ,  $c$ ,  $d$  could very well exist such that  $x_A$  comes out to be negative. And in that sense that's not a representative of physiology of the case that we are discussing, and that's the irrelevant steady state for us and we just throw that out that one does not help us in any way and



that is a stable state that does not exist in the system as we have described it. So, in those cases we are only left with two steady states  $x_A$  equal to 0, and  $x_A$  equal to 1, ok.

So, every time we pick a b c d we need to check whether  $x_A$  this define this particular way lies between 0 and 1 or does it lie outside this window if it lies outside of this window this steady state does not exist as far as our particular system is concerned all right. So, we have these three steady states: one of them we need to check for its existence with every particular set of a b c d that we take. So, how do we look at this?

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Case I:  $a > c$  and  $b > d$ .

$$\frac{dx_A}{dt} = x_A(1-x_A)[x_A(a-b-c+d) + b-d]$$

$\downarrow$   $\downarrow$   $\downarrow$   $\downarrow$   
 $(>0)$   $(>0)$   $x_A(a-c) + (b-d) - x_A(b-d)$

$$= x_A(a-c) + (1-x_A)(b-d)$$

$>0$   $=$   $>0$

$\frac{dx_A}{dt} > 0$

 $\Rightarrow$ 

$\text{all } A$

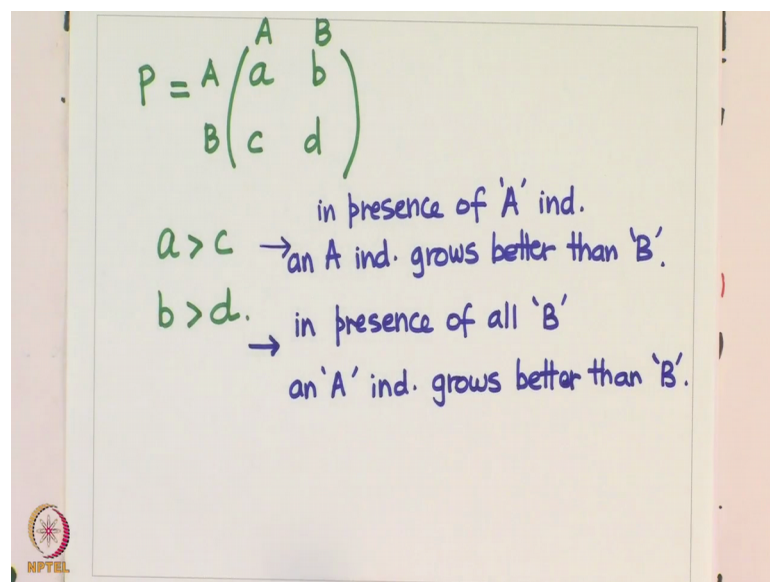
let us imagine a case where so, let us say this is case one, let us imagine a case where a is greater than c and b is greater than d, and now let us try and understand that what a case like this would try and tell us. First let us look at we can do this a few different ways and we are going to do that, but first let us look at this via our equation remember our equation said  $\frac{dx_A}{dt}$  equals  $x_A$  times one minus  $x_A$  times  $x_A$  into a minus b minus c plus d plus b minus d, and we are saying that for a particular scenario these are the conditions on a b c d that we are working this system, that we are looking at this system at. Now let us take a look that what does this mean what this means is that  $x_A$  of course, is always greater than 0 it could be equal to 0, but that is a steady state  $x_A$  equal to 0. So, we are ignoring  $x_A$  equal to 1 and  $x_A$  equal to 0 and talking for any other composition of the population other than  $x_A$  equal to 0 and  $x_A$  equal to 1.

So, if we are not talking of  $x_A$  equal to 0 and  $x_A$  equal to 1 this is always greater than 0 this is also always greater than 0 what about this third term where  $a, b, c, d$  come into play and what I can write this as I could rearrange this and write this third expression as  $x_A$  times  $a$  minus  $c$ , am just pulling  $a$  and  $c$  from here and then write this as  $b$  minus  $d$  minus  $x_A$  into  $b$  minus  $d$  right. So, this  $b$  minus  $d$  comes from here and this minus  $x_A$   $b$  minus  $d$  are the two terms that I left out from this from this particular expression.

And if I simplify this further I get  $x_A$  into  $a$  minus  $c$  plus  $1$  minus  $x_A$  into  $b$  minus  $d$ , and if I do this then what I get is that  $x_A$  into  $a$  minus  $c$ , but I have been given that  $a$  is greater than  $c$ . So, this is always greater than 0 plus  $1$  minus  $x_A$  which is always greater than 0 times  $b$  minus  $d$  which under the given conditions is also always greater than 0. So, this is also greater than 0 what I end up getting under these conditions is that  $d \times A$  by  $dt$  is always positive under these conditions, which means this particular condition on my payoff matrix implies that I am talking of a case which is all  $A$ .

Because  $d \times A$  by  $dt$  as shown here is always increasing the population will keep on increasing and eventually  $b$  will be competed out  $h$  from the environment.

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Handwritten notes on a slide showing a payoff matrix  $P$  and its interpretation:

$$P = \begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{matrix}$$

$a > c$  → in presence of 'A' ind.  
 an 'A' ind. grows better than 'B'.  
 $b > d$  → in presence of all 'B'  
 an 'A' ind. grows better than 'B'.

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Another way to look at this is in terms of my payoff matrix, which is  $P$  equals  $a, b, c, d$  and what we are saying here is that  $a$  is greater than  $c$ , and  $b$  is greater than  $d$  and remember these correspond to the small  $a, b, c, d$  correspond to growth rates, they find in this particular fashion. If  $A$  is bigger than  $c$  what we are saying in that case is that in presence

of what we are saying there is that in presence of A type individuals, an A individual grows better than a B individual.

This can be seen from here because a is greater than c and a represents a scenario when a particular a individual is growing in an environment where everybody is genotype A whereas, C refers to the scenario, where a B type individual a single b type individual is growing in an environment that everybody else is of genotype A since a is greater than c we are saying that in presence of an environment where everybody else is a genotype an a individual does better than b individuals and similarly b greater than d implies that in presence of all B in presence of all b.

An A individual grows better than a B individual, and that's selling is the same thing that. So, what both of these put together are telling us is that- independent of what is the composition of the environment: if I am an individual in an particular environment independent of whether I am surrounded by individuals of genotype A or individuals of genotype B, an A individual is always going to do better than an individual of genotype B and if an individual of genotype A is always going to do better irrespective of the environment; that means, selection is just going to add straight up and just eliminate individuals which belong to genotype B from the environment. And we again go back to the scenario that this scenario these conditions on a b c d are going to leave me to a scenario where I get all a and no b in the environment.

We will continue this discussion in the next lecture onwards.

Thank you.