

## **An Introduction to Evolutionary Biology**

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**Week 8 Lecture 39**

### **Kin Selection and Hamilton's Rule**

Hi. So, in our last discussion, we said that although sexual evolution explains a large number of things in biology, there are certain patterns that even sexual selection or sexual evolution cannot explain. And I said one of those things is the phenomenon of honey bees. Now, all of you have seen honeybees, wasps, or ants, and as you know, they make these very nice, intricate nests. So, I am here showing you the hive of a honeybee and the nest of the harvester ants, which you can find quite a bit of in India. But the reason these organisms are important or enigmatic to biology is not that they can make such intricate nests, Many other organisms can do the same.

But the reason these are very important is that they exhibit a certain phenomenon known as eusociality. Now, what exactly is eusociality? So, there are four major characters, and in order for an organism to be called eusocial, All four characters need to be present together. So, the first characteristic is that the adults must be living in groups. Of course, you know that many other organisms also do that.

For example, zebras and wildebeests also live in groups. But the next character, which is very important, is that there has to be cooperative childcare. So, individuals should take care even of those children who are not always their own. And this is perhaps the most important one: there has to be a reproductive division of labor. Which means that not all individuals will get to reproduce.

And finally, there has to be an overlap of generations at the same nest or the same nesting place. Now, individually, many organisms will show either one character or the other, which is why in order for something to be called eusocial, all four characters need to be present together. And, as you know, prime examples are honeybees, wasps, termites, ants, naked mole rats, and so on. Now, there are two major things about these eusocial animals, which actually led to a lot of, you know, explanations that are needed from evolutionary biologists.

The first thing is that, as we said, in many of these organisms, only a small fraction of the total colony breeds. So, for example, here I am showing you the honeybee queen, the one that has a green marking on its body. You can see that it is much larger than all the other workers, and all these workers are sterile. An even bigger size disparity exists in terms of the queens of the leaf cutter ants, *Atta colombica*. So, here you see the queen and these small things over here; these are the workers.

Now, the interesting thing here, as I said, is that the workers do not reproduce and therefore their fitness is 0. That entire colony, the hive, represents only the offspring of the queens, and they have all the fitness. All the millions of workers have zero fitness. The other very interesting thing in the context of eusocial animals often is. That they will often end up sacrificing themselves for the sake of the colony or the hive.

So, for example, here is a honey bee, and you know that honey bees, when they sting, really hurt, and more importantly, when they sting and go away, the sting actually remains in the body of the organism, particularly if it is a vertebrate. And this is because the skin has barbs in it. And the problem is that when the sting is left in the body, the sting actually continues to pump venom into the you know body of the victim. But on the other hand, when the sting is left inside the body of the victim, as you can see over here, you know this white part that you are seeing; that white part is actually the inner organs of the bee. So, the sting actually when it is detached from the body, it takes much of the organs of the worker's body with it.

And therefore, the honeybee that stings actually dies within 15 to 20 minutes. So, it is a suicide mission on which you know it ends up stinging an intruder. Similarly, if you look at an ant colony, the soldier ants often just end up dying. You know, in the process of defending its colony. And both these aspects, you know, obviously, are leading to zero fitness for the worker or the soldier.

And this is what has been a massive headache for biologists, even since the time of Darwin: why is it that the workers or the soldiers give up their fitness for the sake of the mother or for the sake of their colony mates. Now, although I am talking about eusocial organisms here, if you look at it closely, even in non-eusocial organisms, there are many that behave in such a way that they end up reducing their fitness while benefiting another organism. Now, in biology, this phenomenon whereby the action of an organism ends up reducing the fitness of the actor, but ends up enhancing the fitness of somebody else, this is what is known as an altruistic act, and the phenomenon is known as altruism. Now, this is a bit different from how we use the word "altruism" or an "altruistic act" in regular English usage. So, let us say in a human society, suppose somebody comes and asks me for a few rupees, and I give that person a few rupees.

Then the reason that I am giving it probably has some kind of moral angle to it, and under many situations, I actually incur no major costs, no major disadvantages by giving those few rupees. So, in the context of regular social usage, an altruistic act does not necessarily have to be an expensive thing for the actor. Basically, it is defined in moral terms. Whereas, in the context of biology, an act is altruistic if and only if it reduces the fitness of the person or the organism who is. Committing the act also enhances the fitness of another organism toward whom the act is being done.

So, this is a very crucial difference that one has to keep in mind. Now, the whole problem here is that natural selection is always trying to enhance the fitness of the individual. Anything that reduces the fitness of the individual under normal situations should not be selected for. But if that is the case, how can these kinds of things that I am telling you

about the honey bees and the ants, where, The actors are giving up on their fitness; how can such a thing be selected for? and, how can such a thing even exist in the presence of natural selection. So, that is the crucial question here, and of course, this is a question that did not escape Darwin's notice.

He himself was quite puzzled about it, and there have been many other people who have thought about it later on. So, I will give you a quick answer: the main thing, the main story, I will give you straight away. So, the quick answer to this conundrum is that if you have an action that reduces the lifetime direct fitness of an individual, What do I mean by direct fitness? I mean the number of individuals, the offspring that this particular organism produces, that is the direct fitness. Now, if there is an action that ends up reducing the direct fitness of the individual but enhances its lifetime inclusive fitness, What do I mean by lifetime inclusive fitness? So, inclusive fitness is the direct fitness of an organism plus the fitness of the relatives of that organism. So, that is this sum: my fitness plus my relatives' fitness; this sum is what is known as inclusive fitness.

We need to look at the lifetime inclusive fitness, which means over the entire lifetime of both my relatives and me. So, if there is something that reduces direct fitness but increases inclusive fitness, then under certain circumstances, This is very critical over here; under certain circumstances, the trait can actually be favored by selection. And this phenomenon wherein it is the inclusive fitness that is being selected for rather than the direct fitness, This phenomenon is what is known as kin selection. Now, of course, much of today's discussion is trying to figure out what this under certain circumstances means. But we will get there over the next few minutes.

Now, as I said, this problem of eusocial organisms committing suicide is Essentially doing things that do nothing for their fitness, this problem was spotted by Darwin himself. He thought a lot about it; he, you know, came up with this kin selection answer in some ways. Echoes of this can be found in the work of Ronald Fisher.

In 1955, J. B. S. Haldane very famously, you know, gave some back-of-the-envelope

calculations for this. But the person who actually formalized this relationship and kind of made it. You know, coming to the consciousness of most evolutionary biologists is the British evolutionary biologist William D. Hamilton. So, in order to understand what Hamilton said exactly, we have to understand the concept of inclusive fitness.

And in order to understand the concept of inclusive fitness, We first need to understand what exactly is meant by a relative and who is a relative of an organism. But before we go there, we need to understand one concept—just one—and that concept is the concept of identity by descent. Why do we need this? It will become clear as soon as I tell you what it is. So, suppose you have a diploid organism, and let us assume that there are two identical alleles at a given locus in a given individual. So, when I say identical, I mean that, let us say, both of them are AA.

And so, the genotype of the individual is AA; the individual is homozygous for the A allele. One way is when these two A alleles are copies of an ancestral allele. The single ancestral allele has led to both of these alleles in this focal individual. When you have a scenario like this, then you say that these two alleles are identical by descent. So, by definition, that means that they are copies of the same ancestral allele.

What is another way in which the same thing can happen? The other way the same thing can happen is that sure the organism has two AA alleles, but the origins of these alleles are different. They are not copies of the same ancestral alleles. And if you have a situation like this, that is what is known as identical in state. Now, why do we need this concept? What is the meaning of this concept? Suppose you have two individuals. So, let us say this is one individual, and let us say this is another individual.

And let us say, inside this individual, you have this allele and you have that allele. Now, if you can show that both these alleles are actually copies of an ancestral allele, that is, they are identical by descent, Then you can say that these two individuals are related to each other, right? And the greater the probability that these two alleles are identical by descent, The greater the probability, the closer their relatedness to each other. That thing

will become clear in the very next slide, but essentially, if these two are copies of the same ancestral allele, You can say that these two individuals are related to each other. On the other hand, let us say this allele has come from one source; this allele has come from a completely different source. Then, even if they are the same allele, you can say that they are probably coming from, you know, different sources which means that they are not related to each other or the chances of their being related to each other are much, much lower. So, this concept of identical identity by descent actually allows us to evaluate how closely two organisms are related to each other. How exactly does it do that? Let us figure it out. So, in order to do that, you need the second concept, which is known as relatedness. So, relatedness is the probability that two individuals share an allele that is identical by descent.

That is it. Now, it is very easy to express, and it is actually not at all complicated. But there are several people who end up getting slightly confused by this one. That is why I am going to spend a little bit of time with you, you know. Spell it out in detail what this means and how exactly one can calculate it. Now, let me confess here, I am one of the people who have always been very confused by You know the calculation of relatedness, which is why I am kind of going out of my way to spell it out in a little bit of detail.

If you are one of those people who are very good with probability, then you might think that, ah, this is too easy. But trust me, there are many people; the majority of the people are actually like me; they find it difficult to get the calculation. Which is why it might be a good idea, even if you understand it well, to pay some attention to how to get this done. Now, let us assume an autosomal one-locus scenario in a diploid organism. And let us assume that at that locus, I mean you do not have to assume if it is a deployed organism.

Then, at that locus, the individual can have only two alleles, nothing else, right? Now, we will deal with four or five cases one after another. So, the first case is what an individual's relatedness is with itself. Now, suppose you have the individual, and let us say the individual's alleles are A1 and A2. So, all that I am showing you here is that these two alleles are not identical by descent. So, in terms of their, you know, actual state, they can

be AA, they can be Aa, whatever the case. But here, 1 and 2 are simply showing that they are not IBD. Now, suppose I have picked one allele from these two, right? Let us say, just by chance, I have picked this A1 allele. Now, what is the probability that I am going to find a copy of the A1 allele in this individual? And the probability of that, obviously, is 1 because I know that the individual's genotype is A1A2. So, whichever allele I pick, A1 or A2, the probability that I will find that allele in the organism itself is certain, right? Which is why an individual's relatedness to itself is always counted as 1. So, now we go to case 2: parent-offspring relatedness.

So, suppose you have a parent, and let us say from that parent we have got an offspring. What is the relationship between these two? Now, again let us assume that the parent's genotype is A1A2. Again, all I am showing is that these two are not identical by descent; that is it. Now suppose I pick any one allele from the parent, let us say by chance I pick this one. Now we know that in a diploid organism, a parent is going to pass either of these alleles to its offspring or it will pass this allele to its offspring, and assuming normal meiosis, everything. The probability of passing this allele is 50 percent. Therefore, if I pick up any allele at random from the parent, The probability that the parent has passed on that allele to the offspring is going to be 50 percent, right? Because I will either pick A1 or A2, and the probability that whichever The one that I pick is the one that has been inherited to that offspring is 50 percent. Therefore, parent-offspring relatedness is equal to 50 percent, which is equal to  $1/2$  and equal to 0.5. So, if you just remember this thing that parent-offspring relatedness is  $1/2$ , Then all the further calculations actually become extremely simple. Let us now look at the third case, where we are talking about the relatedness between full siblings. So, let us assume that this is the male parent, the circle is the female parent, and let us say that they have given birth to You know two kids, one male and one female, and we want to know what the relatedness is between these two, C and D. So, let us assume that we have two alleles here, and let us say we pick one of the alleles at random. Now, we know that the probability that this kid has inherited this allele from the father is 50 percent, or  $1/2$ , right? So, the probability that this allele it got from its father is 50 percent.

Now, what is the probability that whichever allele I picked over here is the allele that the father has passed to this child? Remember, both alleles have an equal probability of being passed. Therefore, the probability that the father has passed that one to his daughter is again  $1/2$ . So, the probability that this allele is shared between C and D, two full siblings, is  $(1/2)*(1/2) = 1/4$ . But this does not complete the calculation; why? Because remember, there are two alleles at that locus, right? So, it is entirely possible that I could have picked up an allele in the first case that this C actually received from the mother B. So, in other words, I could have gotten the allele received from its mother B with a probability of  $1/2$ .

And what is the probability that the mother had passed that same allele to D? That probability is again  $1/2$ . So, this is D over here, this is D over here, this is  $1/2$ . So, the product of these two, that is, the same allele, has been passed from the parent from C via B. Or rather, from B to both C and D is  $(1/2) * (1/2) = 1/4$ . Therefore, The total probability of finding an allele that is identical by descent in both this and the full sibs is equal to  $(1/4) + (1/4) = 1/2$ .

So, the relatedness between full siblings is equal to  $1/2$ . So, you can see that there is a simple way of doing this, which is to simply figure out the parent-offspring relationship. And for each parent-offspring transition, just put  $1/2$  because there are two alleles. And  $1/2$  is the probability of one allele going to that parent or the other, and then simply multiply these probabilities. So, this multiplication is going to give you the probability of sharing one allele from this parent between this individual and this individual.

And similarly, this is going to give you the probability of sharing that allele with the other parent. So, all you have to do for cases like this is to figure out these paths. For every transition, put  $1/2$ , then take the multiplication along any path, and sum it up for all the paths. So, I will just show you what I mean in one more situation. So, let us assume that we have a situation like this in which D and E are what are known as half-sibs.

What does that mean? They have one parent, which is common. So, in this case, the common parent is mother B, and B has mated with two separate individuals. When she

has mated with A, D is born, and when she has mated with C, E is born. Now, in this case, remember that whatever alleles A has, A cannot pass those alleles to E. Similarly, whatever alleles C has, C cannot pass those alleles to D, right? Because you know that you can see it from the genetics, right from the pedigree.

Therefore, in this pedigree, A and C do not really matter for calculating the relatedness between D and E. So, here all that we have is D to B and B to E, and D to B is  $1/2$  while B to E is another  $1/2$ . So, the total is equal to  $1/4$ , and that is it. Remember A cannot contribute to E, and C cannot contribute to D. That is why there is no second path as we had for the full siblings, and therefore, the relatedness between half-sibs is equal to  $1/4$ .

We will do one more case; this is a little bit of a complicated case, but if you do the path thing, it becomes very, very simple. So, this is a case of first cousins. So, A and B are the ancestors; they had two kids, C and D. C married F, and D married E; F and E are from outside the family.

And now C and F have a kid, G; D and E have a kid, H. So, G and H are first cousins; what is the relatedness between G and H? So, again remember F cannot contribute to H, E cannot contribute to G. So, in some sense, all that is gone; you do not really need to think about it. So, what are the paths? So, G to C to A to D to H. This is one path, right?  $1/2, 1/2, 1/2, 1/2$ . This is through the father, correct? You can have one more path that goes from G to C to B, the grandmother, to D to H.

So, G to C to B to D to H again  $1/2, 1/2, 1/2, 1/2$ . So, for this path,  $1/2, 1/4, 1/8, 1/16$ , this is  $1/16$ :  $1/2, 1/4, 1/8, 1/16$ . So, the sum of this is equal to  $2/16 = 1/8$ . Therefore, the relatedness between first cousins is  $1/8$ . So, this method that I am showing you can be used for pretty much any pedigree that you have.

All you have to do is figure out all the paths. which connect the two individuals between whom you want to calculate the relatedness. And for each one of the parent-offspring pairs, just put it as  $1/2, 1/2, 1/2$  and multiply all of them. For each path, you will get one

value; sum all those values up. So, obviously, the greater the value of the relatedness, the more closely they are related to each other. I mean, an individual is related to itself perfectly, which means you cannot get anything better than that.

Similarly, an individual is related to its clone by a relatedness of 1. Now, given all this backdrop, when exactly is altruism favored by natural selection? Now, in order to understand this, we have to start with a derivation. So, let us assume that we have a one-locus system in which the A1 allele is extremely rare. That means the number of A1A1 individuals is so small that they can be neglected.

This is an assumption. So, we are assuming that you know the system is just starting, and A1A1 individuals are very, very small or almost nonexistent. This should not be too hard to assume because remember when we were reading about the Hardy-Weinberg equilibrium? We saw that when an allele is extremely rare in the population, then most of the copies of that allele are actually in the heterozygotes, right? So, similar things here. Now, also assume that all the genotypes produce an equal number of babies, which means their fitness is equal. Now, let us assume that our focal individual is one who has the genotype A1A2. Now, since the allele A1 is extremely rare in the population, you can assume that the probability of an A1A2 individual interacting is.

This is not mating; interacting with another A1A2 individual is equal to the relatedness of the two individuals, which is equal to  $r$ . This is an assumption that you have to make. Now, we are going to look at two cases. So, the first case is where you have no altruism, and I am going to call it  $n_a$ . So, let us assume that we have a focal individual, and I am going to call this focal individual "the person" as an actor and let us assume that we have an interacting individual whom I am going to call a recipient. So, this is the first case in which there is no altruism. So, there is actually no difference between the focal individual and the interacting individual, except in one way. What is that? So, by our very assumption, the probability that the recipient is also an A1A2 is smaller. So, we start by assuming that the fitnesses are equal for both, which means the fitnesses of both are equal to  $w$ .

Now, what will be the number of A1 alleles that are coming out of this interaction? That total number is going to be  $P_{na}$  (na means no altruism) =  $w/2 + \dots$ , why  $w/2$ ? Because each A1A2 individual is producing  $w$  babies, half of those are going to carry the A1 allele. Therefore,  $P_{na} = (w/2 + r(w/2))$  divided by 2 is because of the half; why? Because we know that you know these two are going to interact with each other with a probability that is equal to  $r$ .

So,  $P_{na} = w/2 + r(w/2) = ?$

You take the  $w/2$  common outside. So,  $P_{na} = w(1 + r)/2$ . This is my  $P_{na}$ . Now, we introduce altruism. We start exactly the same. You have the focal individual, the actor, the interacting individual, the recipient, and the probability that the recipient is also an A1A2, which is  $r$ .

So, now we have altruism in the mix. What does that mean? That means that the fitness of the actor is reduced by some amount when it interacts with the recipient. And that reduction, we are going to call it  $c$ . So, the fitness over here becomes  $w - c$ . Now, what happens to the fitness of the recipient? Remember, in the absence of altruism, the fitness of the recipient is  $w/2$ . But now what is going to happen is, I am sorry, the fitness of the recipient in the absence of altruism is  $w$ .

So, the fitness in the presence of altruism is  $w + b$ , right? Now, please appreciate that  $c$  and  $b$  do not need to be equal to one another. Just because I am paying 10 units of cost does not necessarily mean that the recipient is also reaping 10 units of benefit. So, that is why  $c$  and  $b$  do not necessarily need to be the same thing. So, the fitness of this is  $w - c$ , and the fitness of this is  $w + b$ . Now, what is the number of A1 alleles that are coming out of this interaction? So, this is what I am going to call  $P_a$ : A is for altruism.

So,  $P_a = (w - c) / 2 + \dots$ , right? Because this is the fitness of  $w$ , the actor, and half of the alleles that it produces are going to be the A1 allele.

Therefore,  $P_a = (w - c)/2 + r(w + b)/2$ , right,

because the probability that this interaction happens at all,  $r(w + b)$ , and then you divide it by 2. Because half the alleles that are being produced are going to be A1, let us just finish off the derivation here. So, we said that we will just go back here,

$$P_a = (w-c)/2 + r(w+b)/2 = ?$$

Take the 2 below:

$$P_a = (w - c + rw + rb) / 2 = ?$$

We can take w common over here; we take w common,

$$P_a = [w(1+r) + rb - c] / 2 = ?$$

I can simply write this as

$$P_a = [w(1 + r)]/2 + [rb - c]/2.$$

This is my  $P_a$ , and if you remember, my  $P_{na} = w(1+r)/2$ . Now, for the A1 allele, which is the altruism allele, to increase in the population,  $P_a$  (P altruism) >  $P_{na}$  (P no altruism). The fitness increase of the A1 allele in the altruism scenario has to be greater than that in the no altruism scenario. So,  $P_a$  has to be greater than  $P_{na}$ .

In other words, what is my

$$P_a = [w(1+r)]/2 + [rb - c]/2 > P_{na} = w(1+r)/2?$$

So, I have a  $w(1+r)/2$  on both sides; I get rid of it.

$$\text{So, } (rb-c)/2 > 0, \text{ or } rb-c > 0, \text{ or } rb > c.$$

This is the condition that we are deriving. What does that mean? That means that the A1 allele, which you know in this particular case as we saw under the condition of altruism, is the altruism allele. It is going to be favored by selection if the product  $rb > C$ , which can also be stated as genes spreading via kin selection. Relatedness  $r$  of a recipient to an

altruistic actor multiplied by the fitness benefit  $b$  received outweighs the fitness cost  $c$  to the actor. So, the relatedness  $r$  of a recipient to an altruistic actor is multiplied by the fitness benefit  $b$  received outweighs the fitness cost  $C$  to the actor. So, this relationship is what is known as Hamilton's rule, which was proposed in two back-to-back papers by W. D. Hamilton. Now this sounds great, but why does this explain? Why honeybees are eusocial, or why does this explain why you know wasps or anything else is eusocial? So it turns out that honeybees, wasps, and ants are all what are known as hymenopterans. This is a particular order of insects, and these insects have a very peculiar system of sex determination known as haplodiploidy.

What is haplodiploidy? So, in haplodiploidy, the males are haploid and the females are diploid, which means that The female gametes are formed through meiosis by reduction division; the male gametes are not formed by meiosis. Now in a honeybee society, the females, which means the queens and the workers, They arise when there is fertilization of the male and female gametes. However, the male gametes, or the males, also known as the drones, arise parthenogenetically from haploid female gametes. Now this actually leads to a very peculiar scenario. What is the scenario? So this is the male, this is the female, this is basically the queen, and these are, let us say, two females who are sisters.

So, let us say these are two workers. Now, what is the relatedness between the mother, let us say B, and her daughter? So what I mean is, what is the relatedness between B and, say, C or B and D? So we know that the parent-offspring relationship in a deployed situation is  $1/2$ . So this is  $1/2$ . But what is the relationship between C and D? Now let us assume, if you are talking about C and D, let us do our path. So you have an allele; let us say C inherits it from B, and then B passes the same allele to D. So, what is the probability that C will inherit a particular allele from B? That probability is  $1/2$ . What is the probability that B will pass on the same allele to D? The probability is again  $1/2$ . So  $(1/2) * (1/2) = 1/4$ , no problem, but you also have one more root via A, the father. So C to A, right? Now, remember this is a female, so she has two alleles. So if I pick an allele at random, the probability that it has that allele from its father is  $1/2$ . So the probability that it got that from its father is half, no issues. But if C has that allele from father A, what is

the probability that A has passed that allele to D? The probability from A to D in this particular case is actually 1.

Why? That is because A, the father, is passing its entire genome to the daughter. Therefore, anything that A has given to C is the same thing that A is also going to give to D. Therefore, this thing over here is not  $1/2$ ; this thing over here is 1, and therefore, this multiplication is going to be half. And therefore, the total relatedness between C and D is actually  $(1/2) + (1/4) = 3/4 = 0.75$ . Here, this is equal to 0.5. Now, note that I am making a simplifying assumption here that C and D have the same father and the same mother. Now, in the context of a honeybee hive, this is fine because there is only one mother for all the workers. but this mother actually can and does mate multiple times. So, theoretically speaking, it is possible that the fathers of the two workers are different.

In which case, this calculation is not going to work; the relatedness is going to be lower. But as long as the fathers are the same, the two workers are going to be related to each other by 0.75. Which is greater than the relatedness between the mother and her offspring. Now, how does this explain why honeybees are altruistic? So, this explains why honeybees are altruistic due to a very interesting point.

What is that point? See, because the relatedness between the father, the mother, and the offspring is 0.5, If suppose this particular worker hypothetically were to reproduce, The relatedness between her and her offspring is going to be 0.5 again, right? But her relationship with her sister is actually greater than that. Therefore, she is going to be evolutionarily favored; she is going to pass on a greater fraction of her genes if she ends up. Helping her sisters rather than helping her own daughter or even creating her own daughter.

And that is why it is better for us, better in the sense of evolution. better in the sense of having a greater fitness than this daughter over here, She ends up helping her mother raise the mother's babies, who are her sisters. and if necessary, sacrifice herself than produce daughters of her own. This is entirely due to the fact that you have this very

peculiar haplodiploidy kind of sex determination in the hymenopterans. Now, this explains the altruistic behavior.

Now, this Hamilton's rule was actually a massive, massive conceptual leap. It predicted that haplodiploidy as a kind of sex determination is what will lead to eusociality. And in the 60s and 70s, when people were studying eusocial organisms, an overwhelming majority of those organisms they were actually hymenopterans: the ants, the bees, the wasps, etc., all of which were haplodiploid. And therefore, people thought that yes, this is a mega mega thing that is, you know, explaining so much of biological phenomena.

More importantly, this provided a general condition for when there should be cooperation. Of course, it explains eusociality in hymenopterans, but even if you do not have hymenopterans, let us say you have human beings; this explains why human beings typically end up being more partial or favorable to people who are their relatives than to others, let us say who are not related to them, or why they are more partial to people who are closely related to them, you know their own sons or daughters, etcetera, rather than, let us say, a third cousin or a fourth cousin or something else.

So, people obviously thought that this was a very, very big deal until the counterexamples started to emerge. So, as I said during the 60s and the 70s, many of the eusocial animals or an overwhelming majority of them. They were all hymenopterans that were haplodiploid. But then people started seeing situations where you do not have haplodiploidy, yet there are eusocial animals. So, for example, there are these gall-making aphids; these are the only exceptions.

But apart from that, no clonally reproducing animal has evolved eusociality. Now, this is very problematic because clonally reproducing animals. As I told you, all clones are related to each other by one right, which is the highest form of relatedness that you can have. So, by the logic that we made, those clonally reproducing animals should be much bigger candidates for evolving eusociality, yet except for one species, one group nobody else had.

Then, if haplodiploidy is the primary driver of eusociality, then most hymenopterans should be eusocial. But it turns out that hymenopterans are actually a huge group, and in fact, most of them are solitary. So, for example, many, many bees are all solitary. So, only the honey bees and a few others have evolved eusociality. The numbers that have not evolved eusociality in hymenopterans are actually probably larger and Other hugely successful eusocial groups are the termites, and they are diploid.

And so are the naked mole rats, which are mammals and diploid. So, and obviously you know exhibit eusociality. So, it turns out that haplodiploidy is equal to eusociality; that logic was not really making sense. Now, while this was happening on the empirical front, right from the time when the whole theory was propounded by Hamilton, The theoreticians were actually saying that, look, things probably need to be taken with a pinch of salt. So, if you remember when we were deriving the whole thing, we saw that it works. Only when the altruistic allele has a very, very low frequency such that we can completely ignore the A1A1 homozygotes. Now that is okay during the initial stages, but if the altruistic allele is going to be successful, Altruism is going to spread in the population; then, very soon, the frequency of the A1 allele is going to go up.

And at that point, you cannot really neglect the frequency of the altruistic heterozygote allele, right? I am sorry altruistic homozygous genotype. Secondly, this derivation, if you saw it, I simply added the, you know, costs and the benefits to get hold of the fitness. But in many cases, the costs and the benefits are not going to be additive; they are going to be non-additive. If that happens, one can show that this entire thing can fail.

Similarly, you know the way we did the derivation; we saw that it is only in the context of pairwise interactions. But many interactions in real life are not pairwise interactions. They are 1:many, many:1, or many-to-many kinds of interactions. And finally, it is shown that in many cases, you know our derivation was in the context of one locus. The moment you increase the number of loci from 1 to 2 or anything higher, in many cases, the entire thing actually fails.

Now, to be fair, these things were not said in the '90s or so. These things people started talking about in 74, 78, and so on. In spite of that, many people were completely, you know, taken over by the elegance of that cute little relationship until things came to a head in the year 2010. So, in that year, three very famous biologists, Martin Nowak, Corina Tarnita, and E. O. Wilson, they published an analysis paper in Nature called "The Evolution of Eusociality. And Martin Nowak is, of course, a big name. E.O. Wilson is like the father of the subject called sociobiology. His book, called Sociobiology, launches the study of, you know, social organisms in many ways. I mean not entirely, but he is one of those people who did an enormous amount of work in making sociobiology a big deal. So, when E.O. Wilson says something, you have to take it a little seriously. And what E.O. Wilson and others were saying, I am just quoting from that paper. Inclusive fitness theory is an alternative accounting method that works in a very limited domain. Even in the limited domain of inclusive fitness theory, Hamilton's rule does not hold in general, and there are no predictions that are specific to inclusive fitness theory. These were very, very bold claims, and essentially, the rest of the paper was trying to come up with a slightly different formulation which does not even need to use inclusive fitness or kin selection to explain the evolution of eusociality. Now the reaction to this paper was absolute electric. So there was a massive uproar in the field, and people started writing rebuttals left, right, and center. Nature itself, one year later, published a few of those rebuttals. I mean, they published multiple rebuttals; however, none of the rebuttals even got into Nature because they did not have space. So, many of those rebuttals got published in other journals and in particular one of those rebuttals was signed by 103 researchers. Many of those people are, you know, almost as famous as the authors of the original paper, Nowak and Wilson.

So this tells you that there was a serious upheaval in the field. In this paper, the Abbot et al. paper argued that Noak et al.'s arguments are based upon a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature. I mean this is as strongly worded a criticism as one can make. However, I mean, at the same time, the other papers that came out were equally scathing.

And basically, everybody was saying the same thing: these people have completely lost it. However, Nowak et al. stuck to their points. and stated that it was the other people who hadn't really understood what they were trying to say. So, the period between 2010 and 2025 has been an extremely fertile period in this context, and it has seen a lot of work on this topic. I mean when you have something that is like dividing the field into two opposing camps and both camps are claiming. That the other camp is getting it completely wrong, you realize that there is something very fundamental happening.

And over these 15 years, people have really tried to figure out what those fundamental differences are. because of which the two sides are talking past each other. So, as I said, they have carefully examined both positions, scientists and philosophers. Tried to figure out where the negative, you know, was coming from. So, for example, in 2014, Birch argued that there are actually two versions of Hamilton's rule, not one.

And he called them, you know, like the general theory of relativity, the special theory of relativity. He called them General Hamilton's Rule and Special Hamilton's Rule. And he showed that much of the debate is actually arising. Because people are not distinguishing between the two when they are arguing with each other. Similarly, in the same year, 2014, there was a nice review paper by Bourke where He examined the empirical examples in favor of Hamilton's rule.

Now appreciate one thing: although Hamilton's rule is very easy to express, Figuring out the exact value of  $b$  and  $c$  is an empirical nightmare. Why? Because  $b$  is the benefit over the entire lifetime,  $c$  is the cost over the entire lifetime. So, how are you going to figure out the cost and the benefit of You know what particular action of an individual organism is going to lead to. So, in spite of that problem, Bourke actually identified 12 papers that, in his way of thinking, Actually led to or has actually quantified  $b$ ,  $c$ , and  $r$  properly, or various aspects of it properly. And after examining those papers in some detail, Burke comes to the conclusion that The focus studies strongly confirm the predictions of Hamilton's rule regarding the conditions for social evolution and their causes. So, if the

papas and the mamas in the field have not figured out what it is, what can we do? Where does that leave us at this moment? Of course, over time, people will sort it out, and eventually, this will come into the textbooks, but as of this moment, what do we do? So, what we are going to do is take this advice from Joe Felsenstein, a very famous theoretical evolutionary geneticist.

So, this is from his book, *Theoretical Evolutionary Genetics* where he says that there is no single canonical model of the evolution of social behavior. This one, which is Hamilton's rule, is useful primarily for its simplicity and nothing more. So, in other words, as of now, we should perhaps use Hamilton's rule more as a way of thinking. So, obviously, for altruism to evolve, the benefit that the actor gets somewhere has to be greater than the cost.

This has to be balanced, or this has to be weighted by the relatedness between the actor and the recipient. That is pretty much where we should leave it, and as of this moment, we should not go for a very rigorous formulation. Or rather, we should remember that Hamilton's rule, at least the way I showed you in this paper and in this discussion, It is not a mathematically rigorous formulation the way, let us say, Hardy-Weinberg is. Or, let us say that all those one-locus models of viability selection that we were dealing with are.

It is more of a thinking aid and nothing less. Now, obviously, there are two ways to look at it. One way of looking at it is that you know this field is still not settled. But the way I prefer to look at it is that this is an excellent time to be an evolutionary biologist. A fundamental problem that we thought was resolved in the 1970s, 40 years later, we now know that it has not been resolved. People are still working on it, and this means that the field is alive; the field is, you know, active.

And therefore, it again shows that it is a great time to be an evolutionary biologist. Now, until now, we have been dealing with the scenario where there was some kind of relatedness between the actor and the recipient. However, in biology, we have many situations where we find cooperation between unrelated individuals. So, obviously,

Hamilton's rule has that  $r$  in it, so that cannot explain any cooperation between unrelated individuals. Then what exactly can explain that? And one of the theories for that is what is known as reciprocal altruism, proposed by Trivers in 1971. So what exactly does reciprocal altruism say? So I will give you the formal statement in a minute, but prior to that, let me just tell you, you know, a way of thinking about it.

So here is a kind of flow chart. So suppose you and I, and suppose you do a favor for me, some kind of favor, and I notice the favor. I feel happy about it, and because I have received that favor, I feel obliged to you. That I have to return the favor because I really like you, and I want to return the favor to you. And returning the favor to you is what is known as reciprocation, or reciprocal altruism. Now, at some point later in the future, I will return the favor, and now you have received a favor from me, so now you will start liking me.

And then, you know, back and forth, back and forth, there is positive reinforcement. and therefore, you are now likely to do me favors assuming that you will end up getting a favor from me in the future. So, in some sense, you are doing something good for me not because you are getting a benefit right now, But because you are expecting to get a benefit later on. Now, this can also happen in the opposite direction. So, suppose you know you have done me a favor; I have noticed the favor, and I have felt happy about it, but I do not think that I am obliged to return the favor to you.

I do not want to do you a favor, and therefore, when the time comes, I actually do not return the favor to you. There is no reciprocation. Now, when there is no reciprocation, what happens? You notice it; you remember that you have done me a favor. But you are not getting a favor from me, and therefore you know not that you look at that as cheating. You did me a favor; I did not do a favor back to you. So, you do not like me and therefore, in the future, you are unlikely to do any favor for me. In other words, if I do something to you and you do something to me, there is positive feedback and After some time, I will do something for you simply because I expect to get something in the future.

But somewhere, if the chain gets broken, I do a favor, but you do not return the favor. Then I notice that, and after some point, I say that okay, done; I am not going to do any more favors for you. So, this kind of thing is what is known as reciprocal altruism, and formally it is a behavior where an individual sacrifices some of its own immediate fitness benefits another based on the expectation that the other will repay the help later on. So, there has to be an expectation of getting something in the future.

Now, does this work? Do we have evidence to believe that there are organisms that engage in this? So, it turns out that there are a few examples. Now, in this particular case, it is not very easy to empirically show reciprocal altruism either. But there are a few examples in the literature, and I will show you one such example. This is an example of an animal that looks a little scary: the vampire bat. So, you know vampire bats drink blood; that is their food, right? So, it turns out that every single day the vampire bats need to go and forage, and if they do not find food, if they do not get blood, then they can tolerate starvation for only up to 70 hours.

After that, they are going to die. Now, it is also true that not all foragers are successful on all days. There are days on which bats will not get food. Interestingly, it is seen that those who have found the food, they actually regurgitate some of the blood and feed to those which haven't got the food. Now, how do they know who has the food and who does not? It is thought that they just look at the belly, they see how much the belly is distended, and from that they can reasonably figure out. Now, since you know they can only stay without food for 70 hours, if you have a good meal, giving it to somebody else is, you know, going to be a huge cost to you, although it will also be of great benefit to the receiver. Now, the interesting bit is that it has been seen that all those individuals who end up helping somebody by giving them food, they are the ones who are more likely to be helped in the future when they do not have food.

Interestingly, individuals who have not helped others are the ones whom other people or other bats refuse to help. So, this is a direct example of the tit-for-tat kind of situation that is one of the ways in which reciprocal altruism can work. So, until this point, we have

been looking at how relatedness can lead to altruism or cooperation. But there are situations where relatedness can actually lead to conflicts. It can be the root of certain kinds of conflicts, and those situations are what we are going to discuss in our next meeting. See you then. Bye.