PROFESSOR: I decided that we won't have a quiz today. There will be one more quiz in the class. It will cover discoveries of sociobiology, which we've been talking about, and we'll still talk about today and Friday. And then we're also going to finish going over some of the notes I've made on EO Wilson's book *Sociobiology.* And I'll try to do that in class next time. Then we'll have that quiz.

Could easily have been two quizzes. But instead we'll have one more homework, and that homework will be for you to find topics for your reports. And I'm going to ask for at least two. You could decide later that you didn't really like those two well enough, but I want you to describe two topics. I'll decide just how long a description we want. But it means I want you to be searching.

But to do that, you've got to read that assignment. It's posted near the syllabus up there. So you will find that online there, near at the beginning of the Stellar site. I'm much more specific this year about the way I want you to do these reports. So study that in preparation for looking for topics. Otherwise you will get topics that just won't be acceptable.

And so the points you get on this homework is going to be based on how well you read that and can come up with some topics, even if you decide it's not your final topic. Because then you have to start working. We will ask for a final decision about your topic later, and then you'd better get busy on the reports. Yes?

AUDIENCE: When is the quiz? Is that next week?

PROFESSOR: The quiz, I think, will be next Wednesday.

As you've probably realized already from what I've said about sociobiology and from your reading of Alcock, sociobiology has led to a lot of changes in the reports occurring in the literature, and the number of people studying animal behavior, and the topics they're working on. So that's the first thing I want to talk about. We've mentioned it already.

And then we'll be talking about more examples of things that could be considered Darwinian puzzles-- things that probably wouldn't have been worked on-- nobody would have even have thought to work on without the ideas of sociobiology.

So what were the big changes in animal behavior research after about 1970? This was all after the publication of this book *Adaptation and Natural Selection* by George C Williams. In other words, the changes started before the publication of the book *Sociobiology* by EO Willson. It was really George Williams that got that all started. And the stress was on adaptation. Why is this behavior adaptive? In other words, ultimate questions about the behavior, not just proximate questions about the sensory processes, the hormonal changes that cause it, details of fixed-action patterns, and so forth.

And according to Alcock, the change was so dramatic that he looked at articles that appeared in the year 1970 and the year 1995 in the journal *Animal Behavior*. And he's got his table there. Here's page 95 there. 72% of the articles were on proximate questions in animal behavior in 1970. Only 16% in 1995. Pretty dramatic shift. Dealing with sensory and hormonal, if you just limit yourself to those kinds of proximate questions, 44% of them were on those topics in 1970. None of them in 1995. Whereas articles dealing with the adaptive basis of mate choice-- just that one topic, which was one of the big topics in sociobiology-- one article-- 4%-- in 1970. Went up to 54%-- 20 articles-- in '95.

Now was the change really so extremely dramatic? Well, remember, they're just looking at the journal *Animal Behavior*. Proximate questions have continued to be very important in studies of animal behavior. But some of that has shifted more towards neuroethology. People in this department work on bird behavior and on mouse and rat behavior. But of course they're studying brain mechanisms, and their biggest interest is in brain mechanisms. But they also contribute to the study of behavior.

All right what was the view of evolution presented by Konrad Lorenz? And especially in this earlier book, *On Aggression*? That was a book that became very popular and very controversial. And it was a mistaken view, and this is the way I describe it. He wrote about species benefits very much against George C Williams in '66, who had argued for the dominance and evolution of individual benefits-- survival and propagation of the specific genes carried by the individual.

So the question is, why didn't that mistake impede Konrad Lorenz? And of course, the reason is that he was focusing on the proximate questions. So it didn't matter what his view of evolution was. He had a-- you could call it a group selectionist approach to evolution in that book *On Aggression.* And he cites some of it in the book we've been reading, the *Foundations of Ethology,* his later book. On page 29 he says its explicit function was selected because of its species-preserving value.

But when he writes about genetic variation-- which he knows is very important in evolution-- he does discuss the survival of individuals. You can find that early in the book, page 26. And he has this interesting quote from Eigen-- a quote from 1975-- "Life is a game in which nothing is stipulated but the rules." Well, when people make statements about life that way, they're being philosophers, and they can have very different things in mind.

But that was the way Lorenz did realize that evolution was about rules. It's just followed rules-- coldly and without regard to things that often human societies value. And this really wasn't so dissimilar to EO Wilson's book when he discusses the morality of the gene, which we've gone over before. He says that in a Darwinian sense, the organism does not live for itself. Its primary function is not even to reproduce with other organisms. It reproduces genes. We're just temporary carriers of genes. It's the genes that are evolving.

And at first this seems ridiculous to me-- and I hope to you-- until you realize the purpose here from the standpoint of biological evolution is very restricted. Evolution follows a blind and simple rule. When we think about consciousness and the great ontological questions-- what are those? Why does anything exist? Why does consciousness exist? What is it? We're really placing ourselves outside the realm of that rule.

So anyway, then Wilson goes on. What's in blue there is what I'm saying. He talks about brain mechanisms as just engineered to perpetuate DNA. And he's right from the standpoint of biological evolution. That's why the brain has evolved the way it did. But I just want to point out that Wilson was also, like Lorenz, group selectionist in his view. But in a way it was very different, because he knew a lot about molecular genetics.

All right. So I've just highlighted from those quotes we saw before from *Sociobiology* that the ambivalences in organisms are due to these counteracting forces in evolution that have affected the way the brain is evolving. It didn't evolve to promote happiness and survival of the individual. It's just for maximum transmission of those controlling genes.

And he likes to stress that some of these result from differences in what's adaptive for the individual and what's adaptive for the family, and what's about adaptive for the tribe, and so forth. Because he thinks a lot more of the group, and there is certainly good evidence-- especially for small groups-- that small groups did evolve as groups-- not just as individuals.

William D Hamilton published another-- it wasn't just Williams that published these very influential papers that influenced the development of this field. William D Hamilton, again, before *Sociobiology* book was published, he published a very influential paper-- "The Genetical Evolution of Social Behavior" in the journal *Theoretical Biology.* And he had there an analysis of altruistic behavior of sterile workers in colonies of social insects.

So I'm asking there what knowledge that had been unavailable to Darwin did Hamilton apply to the problem? Because this was a big problem for Darwin, too. He knew it was. How could you explain sterile worker groups?

But what was the information that Hamilton had? Very simply, he knew about genes. Darwin didn't know about genes. He knew about inheritance. He knew it had to be something like that. But that field of genetics-- I mean what were the dates? He knew something about genetics, but very rudimentary. Nothing about individual genes. They couldn't count genes, nothing like that.

So unlike Darwin, Hamilton had a knowledge of genes. He focused on the genetic consequences of extreme altruism. And he pointed out that in a colony of social insects, males are haploid. They only have one copy-- one allele-- at each gene site. The females are diploid. So if a queen's eggs are all fertilized by one male-- so the male has just got that one allele at each gene site. So that's going to come together with the female's diploid.

So that will combine with the female's genes. And if the queen's eggs are fertilized by one male-- you have to assume that-- then sister offspring share 50% of the mother's genes, 100% of the father's genes-- and therefore, on average, 75% with each other. Sisters are 75% related to each other-- more related to their sisters than they are to their mother or their father.

This should promote altruistic behavior of female workers towards sisters who are future queens. At least some of those females. Many of the females, of course, will become workers. But some of them become future queens. And there, these are the workers are taking care of them.

Because if they do that, then it increases the chances of reproduction of their own genes, which is what genetic fitness is. So we can ask what the alternatives to Hamilton's theoretical analysis in explaining the evolution of sterile worker class. And for a long time, nobody talked about alternatives. But then this paper in 2010 appeared. Notice that EO Wilson was one of the authors. "The Evolution of Eusociality." Wilson and two associates published it in *Nature.* They present an alternative to the inclusive fitness theory of Williams and Hamilton and others.

And later Wilson and Wilson-- the other Wilson is not related to EO Wilson.

"Thinking the Theoretical Foundations of Sociobiology." So Wilson had worked on this issue of alternatives to the inclusive fitness theory, and these authors discuss the rejection of group selection. And they present their argument for a return to more consideration of group selection ideas.

And because of the importance of that, it's much harder to study. But anyway, I did post the article on Stellar, and to some of you, even in reports in the past I've had students that read that and find things related to it when they're trying to interpret social behavior.

My next question concern a mammal-- the naked mole rat. I'm asking how are they similar to the hymenoptera-- that is, the social insects-- in a way that leads sociobiologists to predict extreme altruistic behavior in these animals. And it has to do with their social organization. They have a queen with several male consorts, and the workers are siblings or half-siblings. But they're actually more related than that would indicate, because inbreeding is common, and it increases genetic relatedness. And that leads to the prediction of more extreme altruistic behavior than you would get otherwise.

And the studies of the naked mole rat have supported that. They will, to defend, their queen, defend each other, they will die in their tunnels preventing an intruder from getting in-- just one example of the extreme altruistic behavior that they show. This is an animal that humans can't help but think of as being ugly, but I'm sure to another mole rat they're not.

Let's go to some of these puzzles that sociobiologists have tackled, and sometimes they didn't even recognize because nobody had looked for them. Trivers and Hope Hare wrote an article in 1976 predicting that in colonies of social insects, workers would care more for future queens than for future drones-- and we talked just briefly about that-- because of these genetics we mentioned. Fertilized eggs produce females, unfertilized eggs produce males.

One result is that the female's more closely related to her sisters-- which we pointed out-- than she is to her daughters as well as to her brothers. Thus a female worker's genetic fitness benefits more if she raises sisters than if she raises brothers or daughters. And I just point out that it gives a reason why a sterile worker caste could evolve in the first place in social insects. It was because of this method of reproduction.

Then the other discoveries were made. Ant workers and other social insect. And I'm asking, why should it matter to the workers of the European wood ant whether their mother mates with one male or with several, just to make a point about the nature of this kind of reproduction. Because the ant workers behave very differently if their mother has just one mate or more than one mate. And that was very puzzling to people when it was discovered. So how do you solve the puzzle? It's a Darwinian puzzle.

And you solve it by gene calculations. The gene calculations are very different if she mates with one male or more than one. If there's just one male, then the female workers, as we said before, share up to 75% of genes with sisters, only 25% with brothers. If there's two males, then the workers, who are half-sisters, share only 25% of genes-- the same as with their brothers.

And somehow the workers know, because proportional investment in females by workers does depend on the mother's mating status. The sisters get more care only if the mother is monogamous-- not if she's got more than one mate. Alcock points out that no one would ever look for such a thing if they had not been educated by Hamilton and Williams. And these references are in the back of your book. They're two key articles-- the founding articles of this whole field that EO Wilson reviewed in his big book in '75.

And this is a paper in '96 that presented that discovery. Similar-- and I think even more surprising-- is behavior of red fire ant colonies if they have more than one queen. This one's even stranger. Only queens that are heterozygous for one particular gene are allowed to survive and reproduce. Well, of course it wouldn't matter if the ones that weren't heterozygous didn't survive. And that's true. This is the gene, GP9.

And if you call the two alleles big B and little b-- b is the more recessive gene-- you only find the heterozygous queens in a breeding pool. The ones with the double recess there, they don't survive to reproductive age. But what about the others? There are workers with BB-- big B-- with only that one gene.

There are workers like that, but you won't find queens like that. They're born, and they survive for a while, but they're attacked and killed by mobs of workers with the heterozygous genotype. And the workers that have that big B gene in double dose-- they don't participate in the mob. It's just the heterozygous ones.

It's not clear-- at least not to me at the moment-- I don't know of studies that have ever been able to figure out the proximate mechanisms of how they do that. Obviously they have to detect. There must be some behavioral signs of it. Or it could be olfactory. But the behavior could not be explained without this gene-counting of the sociobiologist. Yes.

AUDIENCE: Has a study been done if the homozygous dominance of allele-- or homozygous dominance queens had been preserved and had a colony of their own, what happens--

PROFESSOR: Exactly. That would be a good experiment. Now if you can find a paper on that, you've got a great report. But I haven't checked for that. But it's a very good question. It's an area that's sort of crying for more experimental work of that nature. And you're giving an experiment you could do without doing some of these proximate things that we're talking about, trying to look at how did they even know which of the females were like that.

Let's go to a simpler type of thing. And this is the explanation for why a male damselfly stays near a female he's mated, rather than just fly off in search of other females to mate with. He's perfectly capable of doing that. There are other females around. George Parker in 1970-- I started to call him George, because I know a famous George Parker much earlier century, but I'm not sure what his first name was, but Parker in 1970 called this phenomenon-- what?

He called it mate-guarding. Because that's what the male is doing. He's guarding his mate from other males, preventing her from copulating with other males. He stays with her right up to the point where she lays her eggs. She lays them in the water. And you will see the males following that female. You'll see them in the branches of trees over the water over the streams where they're laying eggs. And it's only after she's laid all her eggs that they would leave.

Would you expect it to be widespread across various species? And you'd have to say yes-- if the female will remain receptive after mating and still could be impregnated. It's all related to genetic fitness. The male does it to increase his own fitness. What about the female? It actually might benefit her to mate with more than one male. Maybe more of her eggs would hatch, like those birds we talked about last time. But now we're talking about the genetic interests-- genetic fitness interests-- of the male-- why he engages in mate-guarding. And yes, you do find it. This is the damselfly. Type of dragonfly really, at least similar to dragonflies.

Let's go to another topic now-- in fruit flies. Why have male fruit flies evolved so they inject chemicals that harm their mate? They're toxic chemicals they inject along with their sperm. It's harmful to the female. How do you explain that in terms of evolutionary fitness, following the logic of George C Williams? What's the male interested in? He's interested in promoting his own genetic fitness-- not hers. But he needs the female to reproduce, right?

So from the perspective of the male, what counts is the number of eggs capable of hatching that he inseminates. It's in the interests of his genes to destroy sperm from other males. And that's what he's doing by injecting that chemical before he mates-- even if injecting the chemical entails reducing the genetic fitness of the female by shortening her life or by reducing the total number of her eggs-- as long as the reduction is not extreme. Because if he doesn't do it, a lot more of her eggs could be fathered by other males. So that's how we have to interpret that.

We met this phenomenon previously. The hanging fly-- do you remember? Randy Thornhill studied it, published back in '76. Why does the male present the receptive female with the gift of food, like a dead moth?

There you see the female with a dead moth. That's not the male. That's the female that she's about to consume. And why does the gift have to be above a certain size? Why? Do you remember? We had several slides on it. It was in your reading.

Yes.

AUDIENCE: [INAUDIBLE] copulate with the female while she's eating.

PROFESSOR: Yes. He copulates while she's eating. And the other thing you need to know is it takes quite a bit of time for him to inject all his sperm. And if the food's eaten before the male is finished-- and sometimes even before he's begun transferring sperm-- the female just uncouples, flies off to find a mate with a larger food offering. You see, it's not necessarily in her interest to mate with that particular male. It doesn't matter to her. She wants to produce her genes. The male wants to reproduce his.

So after the sperm transfer is complete-- it takes 25 minutes-- then the behavior changes. In fact, the male and female often fight for the remaining food. Before, we said the male has a doggie bag, but actually the female can struggle with him for the remaining food.

So the conclusion here of all this is that the interaction between male and female hanging flies is marked with genetic conflict as each individual jockeys for maximum personal reproductive gain, and thus maximum genetic success. Now this is the interpretation just based on individual genetic fitness, not on group selection at all. But that seems to be how you have to think to explain what's going on in these animals.

So in studies of mate choice by females, which has occupied a lot of the sociobiological literature and the animal behavior literature since 1970-- Thornhill's papers on the topic of female choice-- and there were a number of them-- and the conflict between the sexes-- it marks the start of an era which still continues even now-- not just up to the time of Alcock's book-- in which these issues have been actively explored.

A battalion of adaptationists who have adapted the gene-counting view of evolution are asking questions like how do female mating decisions promote the propagation of their genes? What exactly do females and their genes, of course, gain when females reject some males in favor of others? How do males manage to compete with rival males in a game whose rules were established by females? So we're talking about female mate choice, which is the most common type of mate choice. Sometimes the men in my class get quite deflated by all this, but I'm afraid, I'm sorry, the majority here is females.

All right. Let's talk about the phenomena of cryptic female choice, which came up once before just briefly. What do we mean by cryptic female choice? And when we talked about it before, I don't know if you remember. There were two ways. We talked about a bird, and we talked even about plants. And Alcock introduces it in his book with an example from botany, describing a female flower's response to pollen of various origins.

The gene-counting view led botanists-- not just animal behaviorists-- to start thinking differently about plant reproduction. They thought about things that before that time had just been overlooked. They discovered the equivalent of sperm competition by chemicals released from pollen that landed on nearby parts of the style. In other words, if pollen from one tree lands on a tree in the blossoms, how does that pollen prevent other pollen from other trees carrying different genes from succeeding in inseminating that particular flower? Well, how about deposit some toxic chemicals that affects the others? They actually do that.

And for the birds, this is the example we had before. Remember the female spotted sandpiper. She leaves her first mate with her first clutch of four eggs, and she flies off to establish a nest and a second clutch of another four eggs with another male.

However, she may inseminate with the stored sperm from the first male instead of the second male. So she's just using the second male to rear more chicks. She leaves the first one, and he stays and takes care of those. So she now reproduces up to eight individuals-- four chicks in each nest. Each male reproduces either eight or only four-- if she actually mates with the second male. So the female is exerting choice, in other words, but it's cryptic choice. It's nothing evident from just observing the behavior. It's happening inside her.

So related to that topic is a strategy that's evolved in females of many species. It's called last sperm precedence. It's based where the last sperm to enter has got the best chance of fertilizing the eggs. It's based on the ability of female birds to store sperm. In other words, the sperm doesn't get to the eggs right away. It takes quite a while.

And they can store sperm in tubules near the junction of the vagina and uterus. They fill up from the back, so the last sperm in are the first to be released at the time of fertilization. Fertilization may not take place right away after the mating. But when the sperm are released so they can inseminate the eggs, it'll be that last sperm in. And as long as she can do that and store them in this way, then she can mate with a number of males constantly looking for better and better genes. So that's another way she's exerting choice. Not mate choice, behaviorally, but father choice.

So then that raises this big question-- how have males evolved to counter these cryptic abilities of females? Because males aren't concerned with her genetic fitness. They're concerned with their own genetic fitness.

We talked about dunnocks before when we were reading Scott's book. The male dunnock can increase the chances of successful fertilization by his sperm by two behaviors. One is simply frequent copulation. And he does it. It's enhanced when he notices his mate in the vicinity of another male. But because of last sperm precedence, he just has to mate with her more so he doesn't lose out in this sperm competition.

And he also pecks at the cloaca region of the female before copulation, and the film studies have shown that there are contractions resulting in excretion of fluid. And they've looked at that fluid and it does contain sperm. So basically the pecking causes her to get rid of some of the previous semen that was put in there.

The female actually can choose whether to allow that behavior. She doesn't always. But it is a ritual that they go through. And if she wants to mate with that next male, then she will engage in that ritual, and she will permit that pecking that will result in expulsion of previous sperm.

So what other male strategies are there? Sperm removal we mentioned before. It's common among especially male invertebrates. Dragonflies and damselflies have penises covered with bristles and thorns that the male uses to scrub out the female before copulation.

The male bean weevil has a different strategy. He's got a similar penis, but he uses it to lacerate the reproductive tract of the female during copulation. It's like the toxic insemination by the fruit flies, but this time they're injuring the female. Why would they do that?

Well, it makes it much less likely that she'll copulate with another male. It's too painful. It does shorten the life of the female. They normally live about a month. It can shorten it to 10 days-- as much as 10 days, depending on how bad her injuries are. And the result is-- and this is what the behaviorists have observed-- they fight off male suitors, generally unwanted. But even if she had one of them before, she won't want them now because of these injuries. So it's kind of traumatic insemination. This is one of the animals that does that-- the bean weevil. It shows a female on a bean there. Often we use examples from beetles, because there's more beetles than any group in all of the whole animal kingdom.

And you find examples of traumatic insemination like that in a number of other animals. The fruit flies we mentioned before. The bed bugs. These are bed bugs. I thought you might enjoy seeing some bed bugs here. In case you ever look for them, here they are the edge of a bed. If you have them, you need to do something to get rid of them.

And then plant bugs and spiders. They've been found in all these groups of animals. And the bed bugs I first read about in this book by Wolfgang Wickler. Wickler in

1973 published a fascinating book that became quite popular. You might still find it in paperback. It's called *The Sexual Code-- The Social Behavior of Animals and Men.* It's translated into English, published by Doubleday. Early in the book, page 37, he has this description of the bed bugs' traumatic insemination. He has huge numbers of examples. You won't believe the variety in mating behavior in the nature of reproduction in different animals.

When I first went up to the Museum of Comparative Zoology at the time when I was working on my thesis, and I was looking for articles I couldn't find at MIT, because Harvard has everything. At least it seems so. And a lot of them were in this area over at the museum. And I went through some of these articles in biological literature on animals' reproductive behavior.

And it was amazing. The detailed studies of penis anatomy for example. Incredible variety you just wouldn't believe. And it raises this question right away-- why? Well. You begin to look at these insects and you begin to understand. It's so important in reproducing.

So bed bugs are an example of a different kind of traumatic insemination, because they insert sperm into the body cavity of females without using the genital tract. They go right through the body wall. And that's led some females to evolve specialized body parts-- the parts which the males usually are attacking-- usually on their back-- to make it harder for the male to do that. Protect them from injury. She's trying to reduce the trauma.

So you get this different kind of evolution of male and female. Now we're not talking about sexual selection in the usual way. We talked about sexual selection in terms of choice. Now we're talking about a different kind of sexual selection altogether. Different strategies of the two sexes.

And this was an example I found a few years back about research with primates-- evidence for some kind of cryptic female choice. The paper was entitled "Selective Polyandry-- Female Choice and Intersexual Conflict in a Small Nocturnal Solitary Primate." And this is the summary.

They were looking at this little primate, the gray mouse lemur. They were interested in the possible importance of female mating strategies realizing that her interests and the male interests could be different. And even though the males do try to dominate a female, they found that by gene-counting methods, they first of all-- behaviorally they found that the females mated with up to seven males up to 11 times with one male during the one night they become receptive. They have a very short period of receptivity.

And so they often have more than one baby, and mixed paternity was common. But the heavier males sired more offspring. Even though you could observe this behaviorally, somehow the females were exerting some kind of choice. And so they might be mating. It looks behaviorally like they're mating all the time with one male. But even if they mate much less with some heavy male, he's more likely to be the father. So how does the female do it? It means they have to have mechanisms that have evolved to allow cryptic choice-- just like in those birds.

Another discovery related to these sperm wars is the discovery of two kinds of sperm. They've been called eusperm and parasperm. They have different functions. This is one of the articles that was published online in 2006-- one of the early articles in this area. And this is a summary of that.

They described sperm heteromorphism. They examine two female-centered hypotheses for the evolution and maintenance of this unconventional sperm production strategy. They used models to examine it, and then they were looking at it from the female point of view. So they're trying to figure out how this could be used by the female in her cryptic choice.

But if you look into that-- how widespread is that phenomenon of sperm heteromorphism-- you find after 2001 it's been discovered in a host of animals. And we'll take a look at some of that next time.

So we'll start with this topic. And then I will finish going through these. We'll finish reviewing the Alcock book. And then I'm going to go back to Wilson just to finish up the topics from Wilson, because I would like you to go over that. I'll put all the slides in one file, all the slides on Wilson.