PROFESSOR: I want to talk about the last topic in the Scott book. And then, on Friday, we start talking about sociobiology. So you'll need to be reading the book by Alcock.

Mating and reproduction is very important for sociobiology. And of course it's important in ethology and other approaches to study of animal behavior. And so Scott is using mainly data, experimental ethology, as well as various observations by ethologists. But then you'll see it's closely related to some of the studies of sociobiology that we'll be talking about.

So when we talk about evolution, we talk about both natural selection and sexual selection. They were both discussed by Charles Darwin. And you should have a clear understanding of the difference in the meaning. We've talked about both of them in the class. You should be able to give examples of each of them.

And for every time you discuss a trait, besides understanding whether it arose from natural selection or sexual selection or some combination, you have to consider the likely costs and benefits. And what do we mean by costs and benefits? We always take the sociobiological view that we're talking about not benefits for individual survival necessarily, but for increasing the likelihood of passing on the genes. This is the way it's used in sociobiology.

And obviously, traits similar to evolve the benefits have to exceed the costs. It doesn't mean there aren't costs. And sometimes it's a puzzle, because cost is so drastic. Like if the female eats the male after mating, it seems to be a rather high cost to the male. So we bring it up later in class, because that's a typical Darwinian puzzle when you first look at the data.

So when we're talking, it's easiest when trying to contrast natural and sexual selection to first consider, is it sexual selection? We've given examples of that already-- like the tail feathers of the female peacocks, or pheasant. The bright red color of the male cardinal-- it makes him stand out particularly against the snow in winter. It makes him very conspicuous to predators-- as well as to the female. We've talked about the long tail-- the swordtail fish. The lion's mane of course is a common one. A stag's antlers.

Why do we say they evolved by sexual selection? Because they evolved because the female prefers males with those traits. So they benefit reproduction of the male because it makes him more attractive. If you can't attract females to mate with, then he won't pass on so many genes-- if any.

Now usually you're talking about the appearance of the male when you're talking about sexual selection. But it affects the characteristics of female, too, especially if males exercise choice. And so we'll talk about that, too.

Well, if it didn't evolve by sexual selection, then the traits evolved still by natural selection-- the factors that enable survival at least through the age of reproduction. And in many cases the age of reproduction includes brood-tending, care of young-- and maybe in our species care of the young of our young.

So we talked, remember, about the birds of paradise. This is one of the birds of paradise-- Goldie's bird of paradise. In the video clip we saw with the dancing bird of paradise-- it was paradise riflebird from Australia. These birds occur within Indonesia and also in eastern Australia. I believe the video we saw was all of Australian birds.

Why do you think the elaboration of these feathers has gone to such extremes? Doesn't it have costs? I mean a male that's having to carry around these feathers-- or look at this the peacock here. It seems to be somewhat of a burden to have feathers that long. And yet the females prefer it.

If you give a female peacock a choice between males with various-- I took this picture myself at the Boston Zoological Society park, and it shows the strutting male.

He's displaying his tail feathers. There's the peahen in front. With feathers like that, I mean, how does he get away from predators?

You see, now in the case of these birds, it's fairly easy to understand, because in the environments where these birds are found they don't have many predators. So are there still costs? Well, if it went too far, what would the costs be? It would start interfering with his ability to forage, just to locomote, get around.

So there's certainly limits to how far sexual selection can go. And see, Darwin of course had introduced this idea of sexual selection. And he was made fun of among other ways by cartoonists. And here it shows the Victorian cartoonists made fun of Darwin's ideas about sexual selection and the importance of visual displays. It shows him here inspecting the mimicking of steatopygia. What is that? The very large buttocks in females of certain groups of humans. And it became a Victorian style to wear bustles. So Darwin, of course, had a ready interpretation of that. They wouldn't do it if males didn't like it.

If you want to know more about steatopygia just go to Google. Don't go to Google Scholar, although you could go there, too, and you'll find the scholarly papers. But if you just go to regular Google you'll find all kinds of information, photographs, comments-- some of them with tongue in cheek, some of them claiming it's all racism, and others-- really most of it's just very interesting. It illustrates variety in human evolution. I think when we talk about sociobiology this will come up again-- this is a particular illustration. Not in cartoons, but in real people.

Now this is the next concept that Scott brings up-- the variations in reproductive investment by the male and the female of the species, because often they differ considerably. We saw when we talked about sticklebacks early in the class that the male does all the nesting and care of the eggs. So the male is making a big reproductive investment. The female doesn't make so much reproductive investment.

In other species of fish, the male just leaves after fertilizing eggs. And in those species it's the male that's not making any reproductive investment. So of course then their strategies are going to differ. And you can predict very great differences in behavior choices of those of the male and female.

In lions, the female has to invest more than two years. That includes gestation and nearly two years of care of the young. The males do comparatively little, because even when the female is rearing young, she often is still doing much of the hunting, although the male will hunt as well.

The spotted sandpiper's an example where the males do most of the brood tending, and the female, she will help sometimes for a while, and then she just leaves. She goes off and lays another clutch of eggs-- she lays four eggs at a time in each nest. She goes off to lay another clutch of four eggs with a different male.

So again, it's the male making that reproductive investment. And I mean what would happen? So he leaves. What about the male? Well, if he leaves, then his reproductive investment goes to zero for that span of time. He's already put time into it. If he wants his genes to be passed on, he's got to stay and take care of those chicks.

Whereas the female, she gets it for free. Or not for free-- she still had to lay the eggs, and that takes a lot of energy and a lot of foraging. But she can increase her reproductive output simply by laying eggs, getting another male to bring the food and help her rear the eggs. We'll come back to the sandpipers.

So let's talk a little more about how the male and female can use very different ways to maximize their reproductive output. In many cases-- certainly we just saw examples where that's not true-- but the male can increase his number of offspring just by mating indiscriminately. Mate with as many females as possible. If the female is doing the brood-tending, and he doesn't have to do it, that would be his best strategy if he wants to maximize reproductive output. And you see that.

The female has limited egg production, so she is more interested in the male than in just maximizing the quality of the offspring-- that is, given the best chance of surviving and reproducing themselves. So she's going to have a great interest in finding good genes in her mating, or good resources from the male.

So because of these different interests of the male and female that often are considerably different, though it various just how in different species. But you always have this male/female difference in their production of the gametes. So the result is various-- you can call them compromises between the interests of the male and interests of the female.

And when we say this-- I'm talking about compromises-- I don't mean these animals are aware of it. But looked at as an evolutionary biologist or sociobiologist you interpret it in terms of evolution, not in terms of what they're aware of.

And of course we know the reproductive investment varies. We've already talked about that. And so now we have to talk about mate choice, which varies a lot, and there's a lot of studies by sociobiologists and others. Mate choice by females appears in most cases-- in almost all cases-- to be based on one of two properties of the males. So we want to know what those are. We want examples of each type of choice.

First of all-- material benefits. What kind of resources is that male capable of providing? Why should I choose him? So for example, in the common tern, if he wants to mate, he'd better bring her something good to eat. And he brings freshly caught fish to the female. The bigger the fish the better. If he's not such a good forager and doesn't bring her enough, she may not mate with him.

The black-tipped hanging fly. We're going to talk about that next. But he always brings food to the female also. The difference there is that he mates with her while she's eating the food.

There's other material benefits that a female can look for. Let me just jump to the goldfinch. We can talk about that now. But when he's got more brightly colored plumage, it means he's got more carotenoids in his body. And there have been studies of that that Scott does review in the reading that show that carotenoids at high levels are correlated with strong immune systems. So it indicates better health.

And that has to be because he's getting the carotenoids from his diet. So he's a good forager. And also studies indicate he's less likely to have parasites. All important if he's going to be helping the female. Let's just show that picture here. There's the goldfinch. And there's the female on the right, and a pretty brightly colored goldfinch on the left. So he's been taking in carotenoids. He's a good forager.

Well, what things other than material benefits? Well, how handsome the male is. How attractive he is just by himself.

Let's just take humans. The female is wealthy, she's already got all the material benefits she needs. Maybe she has servants. Well then, just choose the best-looking, strongest male. Get good genes. Just focus on that. It might not work so well, because her offspring are going to inherit her genes and his. So if he's not good at resource provision, her offspring might not be as well-off as she is.

But both of these things that are involved. In some species it seems to be totally amount of material benefit. But in many species other factors of how attractive the male is will affect the female and her choice.

Let's go back to the hanging flies. I said he brings food to the female and he copulates with her while she's eating. And they found in studies that if he brings a larger gift of food-- that is, a larger insect-- that she copulates longer with him. Why? Because it takes her longer to eat it.

And the longer he copulates, the more sperm he transfers. Because it turns out-- and this is what the studies show-- I'll show you a few graphs here. This one is done in nature. This is done in the lab. And so they plotted there on the ordinate in this case the duration of copulation, which is correlated with the amount of sperm being transferred; and the body size of the prey that he brings for her to eat. And look at it. As the prey gets bigger and bigger, up to a certain point she mates with him longer and longer. But then it seems to level off. And it's even clearer in the laboratory studies.

So the payoff to the male if he brings larger insects is increased quantity of sperm transferred. I mean, ejaculation takes, it turns out, about 20 minutes in this animal. So if she finishes eating before 20 minutes because he didn't bring a large enough insect, she flies off, finds another male. So he may not end up being the father-- at least not of all the eggs. If there's food left after 20 minutes, well, the male gets a doggy bag.

So there's the goldfinches.

Now I brought this up in the introduction. We talk about evolution as survival of the fittest. The question is, what do we mean by that? If it's survival of the fittest, then why is it that certain species of spiders-- and also occurs in certain insects-- the male is eaten by the female in the act of copulation?

It happens in the Australian redback spider. And there are some reasons we can discern for how it's still benefiting him. But there are other species, too, that do that. The praying mantis is the best-known. The female tarantula-- it commonly eats-- that's the burrowing spider in the American Southwest, for example. They often eat males. But it's not always their mate, but it might be. So here's the Australian redback spider, just to see what they look like.

These are the reasons why it can still benefit the male in terms of his passing on his genes. First of all, he's not likely to survive long enough to find a second mate. They're short-lived animals. And again, if she eats him she's less likely to mate again if she's well fed. And more nutrition, it can benefit her. She's more likely then to have his offspring. So what the hell? Go ahead.

Here's the praying mantis. There you see in the center I put the center picture of the male and a female. The female's the bigger one. And in the lower right, there she's eating the male.

This is a study I found in the literature-- "Sexual Cannibalism in the Praying Mantis"-- this particular praying mantis. They found that if the females are well fed, they usually don't eat the male. Females that are fed more are heavier, and they produce heavier eggs, and so more likely to survive. If you feed the females less-- these are in experiments where they control that-- then the females are much more likely to eat the male.

So they did an experiment where some females were prevented from eating the male. Others were not prevented. Those that ate the male produced heavier eggs, indicating that the cannibalism was adaptive for the female. But the males-- unlike those spiders we talked about-- the males do try to avoid being eaten, indicating from that behavior that it's probably less adaptive to the males. That may mean that if he was not eaten, maybe he would have a chance to mate with another female. That's not certain, but that's what the study indicates.

So how adaptive the behavior is can be different for the female and for the male. It's clearly adaptive for the female. The males of some species, as we said for the spider, probably benefits him more than it hurts him, because he's not going to live long enough to mate again anyway. But maybe for some, like the praying mantis, it may not be the most adaptive for him.

So what are the conditions that make the female more likely to be the one that is making the choice of mates? The studies have tended to focus on species with sex-role reversal. That is, the male's doing all the brood-tending and so forth. But there are exceptions. So they look into the conditions that seem to facilitate the evolution of selective mate choice by the male instead of the female.

First of all, if the male defends the nest-- like in the sticklebacks-- there's a limited number of eggs he can defend. He certainly would have a lot of difficulty defending more than one nest. So he can't maximize reproduction just by indiscriminate mating.

So it's in his best interest to choose the best female-- either with the most eggs for that one nest-- and that seems to be true for the sticklebacks-- or other signs that it's a female that's producing perhaps heavier eggs and so forth that have a better chance of survival. And if there's many more females than males-- and that's true of some species-- then mate choice-- males making the choice-- is more likely, especially if the male's also in charge of the nest.

Now you also have variations in mating strategies even within a species. So that's what I want to talk about here-- the different male mating strategies. I asked, for example, of how in some species different individual males adopt very different mating strategies, even though these males may all have the same genes. And these are the examples we'll talk about-- the scarab beetles, some of which are very big and they have horns. Some of them are smaller and don't have horns. So it looks like those big ones are a lot more fit. So we want to know, what are the smaller ones doing?

We find the same problem in toads, because some of them are very big and can croak loudly and attract females. Some are not. They're much smaller. Same is true of iguanas. As we saw in the picture earlier, we were talking about foraging strategies. We found out the foraging strategies were quite different in the large iguanas and the smaller ones. They have a more unusual mating strategy.

So first of all, the scarab beetles. They evolved two distinct morphologies. As I mentioned, the smaller ones have horns, but they're more agile. They're quicker. They have underground nests, and the male will defend the nest. He will try to keep other males from getting at his eggs, or from getting at the female who's there in the tunnel.

But those small males are often able to get past the big male, avoid his horns, and get to the female. Now he's got to be quick, because why doesn't the male just turn around and get him? Well, he's so big with these big wide horns, he usually has to come clear out of the tunnel and turn around. Well, that gives that small male just time to sneak a quick one with the female before he can attack. And then he just has the problem of getting past him, because he will come in.

Now with a small marine iguana, it's even more interesting. The copulation normally requires several minutes for the male to ejaculate. But these small iguanas have the ability to ejaculate in advance and store the sperm in a groove in their penis. So he only needs a very brief copulation, deposits the sperm, and gets out of there. And of course the bigger males will be trying to prevent him from mating. So they've evolved a strategy. They don't need so much time. So both the large and the small males are able to mate.

Let's talk about the various mating systems and why there is so many different ones. And here we mean polygyny, polyandry, polygynandry. This was studied extensively in birds by Nick Davies. Most of the studies were done on the reproductive behavior of the dunnock. It's a small European songbird. The hedge sparrow is its common name. And they found all the different varieties of mating strategy in this one species of bird.

And this is the way he summarized that issue. He said, "We should view the mating game not as a cooperation between the sexes, but as a conflict resulting in a compromise in the interests of one or both of them." It doesn't sound like lyric love poetry, does it? No, we're talking about evolution. And yes, it has affected humans very strongly.

Here's the basic mating systems. Monogamy. We all know what monogamy is, but we have to distinguish between social monogamy and genetic monogamy. What's the difference? Social monogamy means the female lives with the same male-- all the time, the same male. She's monogamous.

Genetic monogamy is who fathers her children. And here in many cases they thought social monogamy always meant genetic monogamy. But now we have the ability to look at the DNA, and we find out that that's often not true. Not for humans, not for birds. Well, these are where most of the studies have been done. Especially birds.

Polygyny. That's when you have one male mating with more than one female. And you have the resource-base polygyny, where females choose by the value of the territory. That's done in the iguana, the pied flycatcher. And there you find interesting choices. The female faced with a choice between a single male and a male that already has one female will often choose the male that already has another female. Why? Better territory. She's looking at the whole picture. If that male is capable, because of the value of his territory, of mating with more than female, she's happy to join the family.

Female defense polygyny. Well you know what that is-- the harem. If a male can defend more females, as some sea mammals-- marine mammals-- do that. The sea lions, seals-- the large males will have a harem. But they have to be strong enough and quick enough to defend those females. And that will limit the size of their group. But that's female defense polygyny.

And then lek-based polygyny. We'll bring that up again at the end. There's about 200 species that have leks. That occurs in the snipe, it occurs in certain fruit flies and various birds. This is when the female chooses among males that are lined up in front of her. That's the lek. It's like nature's singles bar, where the female comes in, she can get everything done. The whole group of females can deal with it at once, because the males are all there. And there's various reasons why leks form, and we'll bring that up in the end. But that's another kind of polygyny, because often only one male's doing almost all the mating. The hotshot male.

And then polyandry, where we mentioned the sandpiper, where the female will leave the first male and then have a second brood of eggs. So she's mating with at least two males. But this occurs in various other birds as well. And it occurs in some human groups.

And then polygynandry, where you have more than one male and more than one female. And you have all of these mating systems in the dunnock. And I've underlined here Figure 8.3, because I want you to study that. I didn't get a copy of it. I'm sorry. I actually have a disk, I think, that has these. But it's an interesting figure.

And in it, he shows the four kinds of mating. And then he shows what happens if the female leaves the monogamous situation, how can she benefit? And what happens if the male leaves? How can they benefit? And they've collected data on this. And then those groups, what are the selective factors that make them become polygynandrous in the last one?

And the data-- as I read it, I think there's a mistake in the figure, because it doesn't fully make sense. But most of it makes very good sense. And these studies by this guy Davies, I believe that was his group that collected that data.

But I want you to look at that, because it shows how the counts of genetic success can vary just depending on the mating system. And sometimes moving to another mating system affects one sex a bit more than another. And that's what's led-- because all of these occur in the dunnock, it was a good species to study for that. And he certainly did find different benefits to male and to female if they moved to another mating system.

So what makes monogamy happen? There must be some situations that favor monogamy. And these are specific examples of monogamous animals-- the Siberian hamster, the Djungarian hamster *Phodopus*. It lives in nature under very harsh conditions. It's very cold, food is limited, foraging is difficult. It makes it unlikely that pups could survive unless they have at least two caregivers. So that's a very good reason.

If neither of them can mate-- if there's only one of them, the female can't do it by herself. So it's not good for the male either, because he can mate with her, but if he doesn't stay to take care of the young, they won't survive. And they've collected data on this, and this appears to be the case with Siberian hamsters.

The deep sea anglerfish has a different problem. He's one of these sit-and-wait predators. He sits in one place until something he can eat comes along. And he hardly ever sees another anglerfish. So when he does, the male attaches himself to the female as a kind of parasite. Otherwise he's not likely to see another female. Too much time may go by. He may never have another chance. So it's good reason for a peculiar kind of monogamy.

But monogamy isn't as common as other mating strategies. In many species they have a kind of monogamy, but it's not that the female wouldn't go off and mate with another male. So the male simply practices mate-guarding. He watches her and drives away other males if they try to mate with her. He watches her. He guards her until she lays the eggs. He wants to make sure that it's his sperm-- the only sperm-- that inseminates those eggs. So that reduces the chances of extra pair copulations. And it occurs in many species, as we will see when we study sociobiology.

So what strategies do you have other than mate-guarding to enforce a kind of monogamy? So in other words, it may not always be the natural preference, especially if the female, she might readily mate with another male. So the males have evolved strategies other than mate-guarding.

For example, there are crabs in which the males' ejaculate forms a plug that makes it almost impossible for another male to get any sperm in there. It works. And of course, what would you expect in evolution? If that goes on too long, you'd expect other males perhaps will evolve a strategy to overcome that. Or the female will evolve a strategy, if it's to her benefit.

In dunnocks, you have the phenomena of last sperm precedence. That means the last male that mates with her, it is his sperm that are the most likely to be successful in fertilizing her eggs. So the males, before they mate with a female, will peck at her cloaca region. And they first weren't sure about why he does that. It seemed to be part of the mating ritual.

But then they observed that if he does that for a while she excretes a fluid. And if they look at that fluid under the microscope, they find out she's actually getting rid of sperm put there by an earlier male. In other words, that male wants to be not only the last one to mate, but he wants to reduce the chances that previous males' sperm will be able to fertilize any of her eggs.

The male invertebrates are even more interesting, because they've evolved special methods to get rid of the sperm of the female. Some of them have penises that looks like a bottle brush. They can put it in and scrub her out. Get rid of the sperm. And you can read about that on page 186 there.

Now there's still more to the story. In polyandry situations, in some species last sperm precedence doesn't predict paternity the way it does in the dunnock. And if it doesn't predict paternity, then it raises the possibility that somehow the female is able to control the situation. Maybe she can decide which male-- which sperm-- is going to fertilize her offspring. So that will certainly come up again.

And then you have really more straightforward things. Because the more sperm there is, the more likely it's going to contain the ones that fertilize the eggs. So in the dragon lizard, if they see their female with another male, they will mate longer with her to increase the quantity of the ejaculate. That increases the probability. It's similar to last sperm precedence. It may be a major reason why last sperm precedence works.

And there are many species that do that. The female is encountering other males a lot. They'll just mate for longer periods. They produce more sperm. And also, when they do that they occupy the female for a longer period of time-- and the more they can occupy her the less chance she's going to get to copulate with another male.

And of course they can also evolve production of more energetic sperm. They can beat the competition. It takes a while in the reproductive tract for the sperm to even find the egg. So that's another strategy. And sociobiologists have found evidence for these various things, as we will be discussing later.

I mentioned DNA analysis. It's been done on the sandpipers. Remember, they lay one clutch of eggs-- four eggs. They stay for a little while. Then they fly off and they lay another clutch of eggs. The first male has to stay with the first four, so she gets another male to take care of her second group.

So what have they found? The second clutch of eggs may have been fathered by the first mate and not the second. So in that case there's only one way this could happen. She stored sperm from the first mate and simply delayed its use. We call it a covert choice, because it's not overt behavior.

So she's simply enslaving the second male, getting him to raise her eggs. You see, she's made a choice in the quality of the genes by assessing the two males. And so when she meets the second male, he might be perfectly capable of nesting and brood-tending, but maybe not as attractive to her in other ways as that first male. So she stored up sperm from the first male. So she can make that choice.

It's comparable to what I know about kangaroos. Kangaroos will generally carry two fetuses, but only one of them will mature. The other one will be held in a kind of suspended animation. And then, if something happens to her first little joey-- he dies-- the second one will start growing in her. So she's got a spare. Similar to this in that it's the same father, but at a later time. She's got a backup fetus.

Last topic here-- the lek. How can a male in a lek who never seems to succeed in meeting with a female nevertheless benefit by participating in that lek? Why does he participate if he's obviously not the hotshot?

Well there's various models to deal with that whole issue of the lek-- the hotspot model. This is the advantage. Let's say the females are not going to mate for very long. Then you've gotta position yourself where all the females are coming. So they go to a place where all the females come. That's called the hotspot model. Hotshot model, well, you can benefit by being near a hotshot because he will attract the females, and maybe you'll get a chance. There's some evidence for that.

Another of the female preference model is simply that females, because they're facing predators-- and leks, groups of animals making mate choices-- are going to attract predators, too. So she wants this to be over with very quickly. So maybe leks have evolved in those species just to speed it up, get the whole thing done in a very brief period of time.

The model that is preferred by Scott-- and it doesn't mean these other things aren't factors in the evolution of the lek. And since it occurs in over 200 species, it's likely that more than one factor has influenced its evolution. But kin selection simply means that in many leks, most of those males are related to each other. So even if many of those males don't get a chance to mate at all, maybe they're still benefiting because they share genes with that hotshot.

Big brother can mate, but he carries a lot of the same genes I do. So you see, because when you look at genetic fitness, you have to consider how many copies of your genes are getting passed on. And you increase your fitness by helping your brother. So the females are more attracted to the lek. OK, only your brother gets to mate, but you're still passing on genes. That's the kin-selection model.

And I'm just pointing out they're not mutually exclusive, these models. And yet we know it seems like it's a set-up for reducing genetic variation. And yet the genetic studies indicate that somehow the females do manage to preserve a lot of variability, indicating that even though the behavioral studies by scientists haven't seen many of those other males mating, it's clear that a lot of them do.

So my guess is that the females are, in fact, in addition to mating with the hotshot male, they're probably mating additional times with other males before they leave. But this is unclear from the studies.

All right. Sorry I went over a little bit.