PROFESSOR: OK, I want to say a little more about these phenomena of cryptic female choice. And I just had mentioned one change on the male side that seemed to be an evolutionary response to cryptic female choice and what can the male do to close that. And we talked about several behavioral things they do.

We mentioned some research on primates. And we ended talking about this discovery of two different kinds of sperm. And this article gives you a pretty good idea. A sterile sperm caste protects brother fertile sperm from female-mediated death in *Drosophila*, one species of *Drosophila.* So that means that there can be some sperm that are the guards, and they can't fertilize the egg. But they can protect that sperm, the fertile ones, from being destroyed by female toxins or whatever that she may-- because females have evolved various ways to make their mate choice in their reproductive tract.

So that's what this-- and there's a lot of articles on this phenomenon just recently. This is all after this discovery about different kinds of sperm. It happened around 2000, 2001. And the articles have appeared on fish and insects. This is just that one article.

But Alcock points out that all of these things, especially the female reproductive tract, is adaptably designed to promote sperm choice. In other words, her choice-- which sperm she wants to use to fertilize her eggs. That kind of thing just never occurred to biologists before what he calls the sociobiological revolution that started with the publication, really, with EO Wilson's book who reviewed all that stuff. Of course, it had started earlier with the people we've mentioned that talked about the adaptive individual choice as being the major factor in evolution, the adaptationist approach.

But these are some reviews. I just wanted to mention a few of them that came out a few years ago. Look at the second one. This became a common term in the news media-- *Sperm Wars-- The Science of Sex.*

This was a book that had some extensive speculations about sperm competition in humans. Not based on firm experimental studies-- it was based on a few observations made by medical people. But it's still not all that certain how much cryptic choice-- most of it's quite overt in their behavior.

So all these articles are that. And you'll find many more. And just a few years ago when I searched the literature, I found reports on spiders, a cricket, a beetle, various flies, and fish. These are just examples of those articles. One on the beetle-- there's the red flower beetle.

So this is another topic. It's another concept of what can happen with this competition between the two sexes in reproduction. And it's our most blatant example of it. It's called genomic imprinting. It doesn't mean behavioral imprinting at all. It has a totally different meaning from the behavioral use of the term imprinting.

It's when one gene can have different effects on the offspring depending on whether the gene, the allele, comes from the mother or the father, because male and female interests are not identical unless they practice strict monogamy. And the early tests of that, they didn't confirm that. But I think that's just because they used to think monogamy meant just what it says. But in fact, many monogamous pairs are not completely monogamous.

So for example-- and I apply this to humans-- I'm asking here, what about human fetus sizes where the fetus can be so big that it damages or even kills the mother? Why would females evolve so they could ever produce such a large fetus? And yet, that has happened. And some women, without modern obstetrics, wouldn't survive the birth of all the fetuses that they might nevertheless carry.

So it's not adaptive for the female to do that. But it may be for the male in many cases. When you think about earlier evolutionary times, if the male had many choices, he might have had a number of different wives. What matters to him, just from the standpoint of genetic fitness? I don't mean what matters consciously to him. He might be madly in love with a woman that he makes pregnant and then has a fetus that kills her.

The point is what matters from an evolutionary standpoint is just his genetic fitness, how many genes can he pass on. And what he can do for that, it's promoted by the large fetus-- a large, healthier fetus. Of course, the fetus has to survive the childbirth for that to work.

But look at this. Sorry I didn't find a better slide. This describes genomic imprinting. And this is about one particular receptor and the molecule itself that binds to that receptor, IGF2. And it's a growth factor. So it promotes somatic growth. This is in mice.

Now, the genes from the mother, the receptor is turned on. The growth factor is off. But look. If it comes from the father, the receptor is off, and that molecule is on, the one that promotes growth. So you can investigate those effects by looking at-- so for example, you delete the mother's IGF2 receptor gene.

The one that is normally on for her, you just delete it. And what happens? Fetuses that are huge. You delete the father's IGF2 gene, and you get little, tiny offspring. If you delete both of them, then you get normal size offspring.

So the particular growth factor, its main function seems to be involved in this genomically imprinted gene, where the male and female alleles have very different effects. And they're the same gene. And so they just say here, the imprints on the IGF2 and the IGF2 receptor genes normally cancel each other out. Changing the imprint of one copy of the gene has a dramatic effect on the size of the offspring. So this kind of results supports the genetic conflict hypothesis in a particularly dramatic way.

And this was just from the early discoveries. And just a few years ago, I found this website. The whole website's devoted to genetic imprinting-- because it was such a puzzle. It was only this sociobiological interpretation that made any sense, but it still seems so unusual. And there was this one study I found where they showed effects that went beyond the fetal and infancy periods-- in fact, effects later in life. And there were arguments-- what good is genomic imprinting, the function of parent-specific gene expression-- in *Nature Reviews* a few years ago.

And then, if you do look at that website, which I did today, I found-- and this is just 2013. Look at all these articles, all on this phenomenon, its variations, how long it lasts, and so forth. So that just gives you an idea of the impact of sociobiology also on human genetics. But of course, they're studying it mainly in mice. But the first question I was asking there, I'm applying it to possible explanation for very large human heads, human fetuses, born to women where it can damage.

So let's get back to bird behavior a little bit. We don't have too much to go. We'll talk a little bit more about EO Wilson. And I would like to have a little time at the end of the class to discuss your project because I think for next week, we're just going to have the homework. I know you've got a homework due today, right?

So next week, the readings are quite easy after these chapters that these classes are based on. So you can let me talk about those things, and you can work on your projects. And I will formulate the thing, put it online. I'd like you to come up with a couple of topics and several articles about each one. Give me your references. Some people know already what they want to talk-- they're pretty sure they want their project to be. But let's see if we have a little time for that at the end of the class.

Did we talk a little bit about helpers at the nest before? I think we did a little bit, and Scott. But some of the best studies have been done in this Seychelles warbler. So what are the advantages for a young bird if they help their parents rear siblings by becoming a helper at the nest?

It's a kind of altruism. It's very common in birds. And of course, it's very common in humans, where the mother and father get help from their own offspring in rearing further offspring. And Alcock does say a little more about it that Scott's book did.

This is a picture of this beautiful little bird in the sea shells.

These are the kinds of advantages it could have for the young bird. They gain experience in taking care of young. They're promoting the survival of close relatives, which means it does affect their own genetic fitness-- not directly, but indirectly-- by supporting the survival of their siblings. And that is critical if done, say, in poor-- where there's not that much food in the environment.

Sometimes if they don't have a helper at the nest, the chances of getting the offspring to even survive are very low because two birds just can't bring enough. But it works best on the richer territories. In such areas, if the territory is so deficient in food, then having the helper at the nest doesn't help, because you've got to feed him, too, or her.

So to gain experience, they promote the survival of close relatives. And they can also inherit that territory if they stay around. After all, the parents will get old, stop reproducing. Then they can take over the territory. The helpers are usually female. They're used by the adult pairs that have better territories.

And there were studies in the Seychelles of these warblers by this sociobiologist, Komdeur, published in 1997. He made this surprising discovery that the females can actually regulate the sex of their offspring. So why would that ability evolve?

Well, it's explained in terms of her fitness-- the fitness of the female-- and the behavioral differences between male and female offspring. If she biases her offspring towards the female, it's because she's on a good territory. She can make good use of the helper at the nest. And it's the females that are most likely to become helpers.

So this is the actual results. Before this study, no one ever checked to choose whether birds could actually choose which sex to reproduce in their offspring. And now it's been found to be more common. But it was first discovered in these warblers.

So on good territories, the helper at the nest is beneficial. The helper is usually a daughter. On poor territories, there's not enough food for the extra bird. So that led him to make this test.

And he found that on poor territories, 77% males were hatched. Better for her genetic fitness if she passes on more genes and more offspring, if she produces males. More of them will survive-- because only a certain percentage of them are going to survive anyway. And if only one survives, it's more likely to be a male if she has a lot of males. And on rich territories-- only 13% males. So the effects are dramatic in how much she can skew the sex of her offspring is.

AUDIENCE: How do you know it's choice and not a side effect of the environment?

PROFESSOR: And that has certainly been studied. And they've varied that. And of course, there are effects to the environment, but they're affecting that female. You'd like to know, well, if you control things like temperature, you could say nutrition could affect it. Yes, and they've had to control for those things.

And Komdeur tried to do that. And as best as he could tell, it was the female actually able to change that. But then it was discovered in other animals. In the tawny owl, for example, they had female-based clutches on territories with more abundant prey, which were the field voles. In June, although that's the month the chicks fledge, the eggs were laid in March. And yet the sex was biased.

It indicates that the parent owls produce more female chicks on territories with higher numbers of their major prey, the field vole, at the time the young are fledging. It's adaptive because the females, but not the males, appear to enjoy a subsequent reproductive advantage from being reared under good food conditions. So that's a direct effect on which animals will survive the best.

And then I'd point this thing out about the dates. The decision of the owls to bias the sex has to be made in March. So they're actually predicting what the prey density will be in June.

Some of these phenomenon of sex biasing were known, but they nobody had figured out quite what they meant. It was the benefits for genetic fitness that

Komdeur was investigating. And that's what affected his hypothesis. I'm sure he was familiar with some of these other sex biasing studies, but nobody had studied it in terms of why they might be doing it.

And so after his study and the tawny owl study, then it was-- this is from the introduction to that paper on tawny owls. He's citing the earlier findings, and he's citing findings on yellow-headed blackbirds where they-- you see it goes back to 1980. The kestrels-- 1992. The fitness gain to the parents of producing different sex offspring in conditions of different resource availability has seldom been investigated. And that's why he wanted to do it in the tawny owls. And he cites Komdeur-- actually published in both '96 and '97-- which shows that it appears to increase the fitness of the parents because females are the helping sex, more likely to be beneficial if the food is abundant.

Then there was this study on resource availability in goshawk offspring. Remember, we saw a goshawk attacking a rabbit in one of the videos? And it was related to spatial and temporal variation in the availability of the woodland grouse that they're feeding on. So the broods are large and male-biased when the grouse density is high. They're small and female-biased at times when the grouse density is low.

And they also found that, in fact, the effects carry over. If they have a lot more of one sex in one year, they're much more likely-- the other sex will be more dominant the next year. And they are suggesting that it maximizes go goshawk reproductive success. Although the details of exactly how they do it and so forth is not known. So there, in fact, have been-- I found this in a PhD thesis in 2007, where a specific mechanism is proposed. So now we're talking about proximate mechanisms for this sex biasing.

They found that in starlings-- the variation in plasma corticosterones related to maternal condition. And they tend abandon their nests if they had high levels of corticosterone, which would indicate they are under a lot higher stress of one sort or another. And if they experimentally elevate the yolk corticosterone in the eggs, it selectively decreases male offspring quality. It increases pre and postnatal male mortality.

So for the mother, the result is an allocation towards evolutionarily less expensive daughters and a sex-specific lowering of current reproductive investment. So ultimately, the way he's interpreting it is it increases maternal fitness, and it's the mother that's making this kind of decision. And he's relating it very specifically this steroid.

This is from just one more topic here from the discussion questions in Alcock. He asks, why would a male bird exercise the adoption [INAUDIBLE]? You can ask that about humans. Why do you adopt, like becoming a step-parent? Not your genes.

And so you have to consider benefits for the genetic fitness of those males. For one thing, a bird he rears that's not his own offspring could become a future helper when he does have offspring. It could result in-- let's say the mates are very hard to find. Well, he's got a potential mate there if he's rearing. And if it's a female, the bird gets older. Then he could have a mate.

These are possible benefits for genetic fitness. Or it may just be the result of proximate mechanisms operating in an abnormal situation. So it's not easy to decide in those things without pretty long-m term studies of the birds that do this.

I want to go through a little more from EO Wilson. And I will post the whole file of all these notes. These are the concepts we went over. This is where-- his general statements that we've gone over. And these are the definitions.

You should know the difference between population and society. You know what a deme is-- the smallest local set of organisms within which interbreeding occurs freely. And that's in use in theory. Of course, in reality, it's not always totally random and so forth. Then we talked about the multiplier effect. Small effect in proximate mechanisms, a detail about behavior can become multiplied in the social interactions of the animals and result in very different societies.

The evolutionary pacemaker, [? McLean ?] argued, was behavior. When behavior changes, if something is very adaptive, it could lead in evolution to structural changes. He talks about adaptive demography.

I'll talk about life tables later, where he brings that up again. It simply means that for some species, it's more adaptive that many of the animals are very young. Other species, it's not so adaptive. That depends on the way they reproduce. So we'll talk about that at the end here.

And of course, we've talked a lot about ultimate versus proximate causation. And we talked about behavioral scaling when we talked about, for example, density-dependent behavior, where animals in groups behave quite differently from solitary animals. They alter the way they're foraging and so forth. Or they behave differently if they're big than when they're small. And it has great effects on their mating behavior, for example.

We talked about phylogenetic inertia and both variation, genetic variation, and the effects of genetic swamping. You should know what that term means. And then we talked about various [INAUDIBLE]. This has come up in the class.

We talked a little bit about-- not much of inbreeding taboos, because there's not a whole lot known. But he did talk about how to compute genetic relatedness using path analysis. But this, we haven't talked about. This is the formula for rate of change in the size of a whole population, the dNdT-- the number, the rate of change in the number with time.

So what is r, and what is K? K you call the carrying capacity of the environment. If the population density goes above K, the as you can see from the formula, then the population won't keep increasing. That's why it's called carrying capacity. The environment only has enough resources to support a certain population level.

r has to do with the rate at which reproduction happens. So when you talk about r-selection, where you're talking about species with a very rapid growth in numbers by a very high birth rate, what are examples? Think of the frog. He lays hundreds of eggs. Those flies-- think of fly larvae. One fly, all these eggs can hatch in the cracks in your apartment, and all these maggots appear. Why do all these maggots appear if you leave food out?

There r-reproducers. They're opportunists. If they get the opportunity, then huge numbers will be reproduced. But of course, there's a huge mortality also in r-producers.

Think of mammals. Think of mice and rats. If they're able to, they'll reproduce. We say, they reproduce like rabbits. Well, they're r-producers. They are opportunists. If there's a lot more food available and not many predators, you get huge numbers.

If you kill off their predators-- you kill off the wolves. You kill off all the animals preying on deer. What happens? Like in New Jersey-- you get so many deer they're causing car accidents. They're eating up the corn in the fields and so on and so forth.

So what is K-selection? Here, we're talking about species with more stable numbers. It's often close to the carrying capacity of the environment. But there's much slower growth or even no growth of a population because of few births per female, more prolonged periods of development. And of course, humans and other large primates are K-producers. So I'd like you to know these. They're very basic in population biology, important for when you talk about conservation, important when you consider behavior of animals.

A little bit about life tables related to adaptive demography-- how many animals are different ages? And I took this just because of a mistake Wilson made. He talks about K-selection animals. This is the curve, sort of an ideal.

You have a little bit of fall off when they're very young. And then you're not getting much die off until you reach old age. And then the decline happens until they're all dead. So this is K-selection life table.

These are extreme r-selection animals-- huge numbers of young, but very high mortality when they're young. And then only a few of them grow to be very old. These are the animals with a lot of predators and perhaps other factors, too.

And then he does something interesting. Here he's got some animals in between, like song birds are there. So they're not all at these two extremes of r-selection and K-selection.

But then he just deals with humans, and if you ignore my dashed blue line there, he plots humans in Japan, which are fairly close to what he plots for humans up here. And here's this curve for India. He's claiming that in some countries, they're closer to r-selection. They have a lot of young.

Well, it's true. They have more young, and a lot of them don't survive-- but nothing like those mice, and certainly not like flies. And then I realized-- this seemed unlikely to me that it was so different, so I noticed that his ordinate wasn't put on the log scale. So here we're dealing with log-log plots. Here we're not dealing with log-log plots. This is all linear in his.

So I replotted using a logarithmic coordinate. And here's how India comes out-- not so different from Japan. So good science involves good quantitative work in many cases. And that just shows how even a great scientist like EO Wilson, who has been an incredibly good scientist in studying social insects, especially bees and wasps, can still make such a mistake when he's trying to review an enormous field like sociobiology.

Then he talks about group selection and altruism, and he introduces these concepts. He calls it the evolution of altruism, selfishness, and spite-- three very different types of social behaviors, all of which occur in humans. And he interprets it all in terms of inclusive fitness effects.

Then he goes on and talks about reciprocal altruism, the Good Samaritan behavior, which was analyzed by Trivers, and then giving various other examples of altruistic behavior-- [? thwarting; ?] cooperative breeding, like we saw in the cats; food sharing, which is common in many species, certainly in humans; ritualized combat. And he's dealing with humans at the end, and he has this arrogant chapter, The Field of Righteousness.

But let's look at this cute figure. There he just shows altruism, all interpreted in terms of genetic fitness. You see in black there the genes of one individual . So here, this individual is helping a sibling-- shares half his genes. What are the consequences if this guy helps this guy?

Well by helping, he's giving up resources or something. And it could result in reduction of his own fitness, but an increase in the fitness of the one he helped. So the end result can be still a good level of genetic fitness. That's altruism.

Now, what about selfishness? Here, the guy, he's going to protect his resources. So he fights with his sibling. He clubs him.

[LAUGHTER]

So the result is you're reducing the average fitness of his siblings if he behaves that way. But he's increasing his own because he ends up with more resources. So that's selfishness.

What about spite? Here, one of his siblings with an mate, perhaps, have resources that he had hoped to get, so he harms the unrelated individual. And he's much more likely to harm that one. That might help the related individual, but look what it does to him. It doesn't increase his genetic fitness at all, except very indirectly.

So he calls that spite. With spite, you hurt yourself. But presumably, that's adaptive. And then it will help your genetic fitness indirectly. So that's the concepts of altruism, selfishness, and spite that Wilson reviews in his book, *Sociobiology*.

I will post a little outline. I don't know if I posted it yet. It's probably down below because I posted it in last year, of the later chapters. It just gives you a sense of that entire book and how he reviews individual behavior in different groups of animals. And that can be useful for some of you in looking for topics.

So what I'd like to do now is talk a little bit about your projects. So I'm going to-- read those instructions that I posted. They're posted right at the top there on the website. You'll see the assignment.

Make sure you understand the details of that. It's actually two pages. I really spell out what we're after.

And then you don't have a lot of time now. This is like a big homework. The smaller one is the preliminary to you turning in a PowerPoint presentation just before Thanksgiving. So there's not a lot of time. You've got to get busy on it now.

That's why I'm decided not to give any more assignments. I won't even give a quiz. I want you just to work on the projects now, because the reading is very easy now, the rest of Alcock.

Let's say you decided you wanted to study giraffes. Well, I don't want a paper just reviewing anything you can find on giraffes. I want you to come up with a question.

You could ask, for example, I want to know why giraffes have long necks. This is actually an example from reports-- one report, at least-- that I had in the past in this class. I don't want and ethogram of the giraffe, but it doesn't mean you can't cite some of that if it's relevant. But let's ask this. Why does a giraffe of a long neck?

Well, remember the why question now. It has different answers. Why could be proximate mechanisms. It could be some ethology. What does he do with his long neck in his social behavior? What does he do with it in his feeding behavior and so forth?

Or, why did it evolve? What makes it adaptive for the giraffe? How does it help him interact with his environment? Well of course, he could feed from tree branches. He's tall enough to do it.

Well, what evidence for that is it? And how does it hurt him? What are the costs? There are a lot of difficulties of having such a long neck. So you do have to deal with some proximate issues because you want to deal with costs and benefits for that species. That's just an example.

I want you to try to think in terms of both adaptive purpose when you ask why questions and with ethological details of the animal. If you have difficulty coming up with questions, please talk to us. You can always send me email, just propose some things. You can give me an example of the questions.

But I think most of you are following these things in the class quite well. You know how we're doing it and the way Alcock covers it, the way Scott covers it, the way Lorenz talked about behavior. Try to find actual experiments testing the ideas.

Now, there are journals of animal behavior, but these papers occur in other kinds of journals, too. So there's a journal called *Animal Behavior*. There's another one that's just called *Behavior*. They're two journals that deal only with this.

But then you will find ornithology journals if you deal with birds. You'll find menology journals, and they'll [? even ?] include a little. You'll have behavioral ecology, which has a lot of-- if you just search under behavioral ecology, you can find where people are publishing specific journals that deal with the effects of usually behavior and environment interactions. But there's a lot relevant to sociobiology in such journals.

If you just look at papers and the journals being cited by Alcock, for example, you'll get lots of examples of places to look. You can go to the library and look directly, or you can get on the library site, MIT library site, and pull up journals and scan them. That's one way to find them. Or you can just think of things you know about already, things you've heard in the class, things you've read about, especially in this class, and do your search.

I don't want a neurophysiology. I don't want a strictly neuroscience paper. It's got be on the topics of the class. Use the principles in the class.

And I spell that out in the instructions. I want you to be explicit about what you're talking about demonstrates. Interpret things in terms of these principles.

So in one week then, we want to see a couple of topics. I know most of you will spend a lot of time on more than one topic. But in the course of your doing this, you'll probably discover which one you're more likely to do.

Now if you do come up with two topics and you turn it in and then in the following time you have to prepare it, you decide to change your topic, please let us know because we might want to give you some feedback. And we will get busy and give you the feedback right away. We'll read all of these because we want to help you give good reports.

You'll be graded on the PowerPoint presentation, not the oral presentation. But we like you to have the experience of giving it. The class would like to hear other reports.

We'll divide into three classes. You'll be told which class to go to and where they're going to meet. I haven't figured that out yet. And when you make the PowerPoint, get familiar with PowerPoint if you've never used it, because we want pictures as well as words, pretty much the way I've done in the class. If you have videos, that's possible.

And you won't get a chance to say everything in the oral report. You might want to present some background. Just use the Notes section slides-- things that you could bring up in a talk if the talk were longer, but you won't have time in your report here because you're limited to 12 minutes. To allow a little time for questions, 12 would be the maximum. I tell people to aim 10 to 12 minutes so you can leave a little time for questions.

You don't have a lot of time. The problem here is coming up with a short enough report. So you can put extra information in those Notes section. But for the slides itself, come up with a talk that you can actually give, assuming there's four talks in a session.