PROFESSOR: OK, more about sociobiology. See what kind of subjects they study. I can tell you about later this week we will have a quiz on Wednesday. It'll be a short quiz just based on the mating behavior chapter in Scott that I talked about last week on Wednesday. And then on Friday we started sociobiology, so it'll be on the first two chapters of the sociobiology book, things we said in class including today.

I know you have a homework due, but it's not due till Friday, and you've had quite a bit of time for it. All right. These are just some major issues in sociobiology and major different definitions.

When sociobiologists use the term fitness, they're generally when they talk about fitness costs, fitness benefits, what do they mean? It's not like survival of the fittest, but it's related to that. It always means, it's always talking about survival of your genes. So it's defined as the number of surviving offspring or more precisely, the number of an individual's own genes passed on the surviving offspring. So fitness costs are anything that reduces the probability of gene survival and benefits things that increase the probability of gene survival.

So a little bit about how sociobiologists think about it. Think of possible fitness benefits and costs to a female bird if she engages an extra pair of copulations. She's got to mate, but she flies off and mates with another male too, not necessarily deserting the first male.

So what are the fitness benefits, and what are the costs to her? And are they the same for the male? So I want you to think about how you could get information to test those kinds of things. What would you have to look for?

We can make up reasons for why it could help her pass on more genes, having another nest, laying eggs there, having more offspring, but that only works if the first ones survive. Like if the male is taking care of those eggs and wouldn't want to desert them because then his fitness would go down, it would cost him his fitness. But there are certainly costs too.

The male can change his behavior towards a female to make it more difficult for her to pass on genes. So what kind of data would you have to collect? You'd have to follow these birds over a period of time, and it's difficult to do it precisely unless you can collect DNA data on the younger birds and find out how many offspring does she really have. And you then would compare birds that engage in this kind of extra pair copulation and the ones that don't. That's the kind of thing that sociobiologists do.

So let's deal with some of the misunderstandings, and there's been a lot of them that have appeared. Alcock quotes these three people. These are the quotes that I selected from Alcock. Derek Bickerton says that when a bird practices what zoologists call extra-pair copulation, can we really call this adultery? The intent of the two activities is completely different.

Michael Rose said there's the fundamental problem that if most people calculate Darwinian plans of action, they certainly aren't aware of it introspectively. Net Darwinian fitness doesn't figure in the great lyric poems. And then William Kimler, he criticizes the sociobiological claim that adulterous women have sometimes raised their genetic fitness by cuckolding a social partner on the grounds that she might be seeking more emotional satisfaction rather than simple genetic benefit

So you can understand their statements, and there's a lot of truth in them. But is it really a criticism of sociobiology. First of all these first two guys are confusing conscious intent with the outcome. sociobiologists don't care about the conscious intent of the animal or the person, He only cares about the result, the outcome, in passing on genes. So fitness is not about conscious intent.

And Kimler is a more common kind of mistake in these criticisms that you see of sociobiology. They fail to separate proximate cause from ultimate causes. They don't separate proximate motivational states are very distinct from the ultimate results, meaning passing on the genes. So Alcock summarizes it by saying understanding the difference between proximate and ultimate hypotheses which are different but complementary to one another can help us avoid the kind of confusion evident in Kimler's complaint about sociobiology.

OK, so make sure you understand that. You might be asked, I might make up something and say what's wrong with this criticism. You should be able to separate these two kinds of hypotheses, the two kinds of causation I should say.

So let's take one specific behavior and contrast approximate mechanisms and causes and ultimate outcomes. We did this before. Let's do it for the human tendency to eat high fat, sweet foods. So for proximate mechanisms, we want to consider psychological and physiological, anatomical mechanisms, the proximate causes, and then separately, the reasons that they evolved.

Those are the ultimate causes in terms of Darwinian theory and sociobiology, which uses Darwinian theory as it's main tool. So for example, this human desire to eat high fat, sweet foods, ultimate causes would evolve to increase genetic fitness. And that sort of goes without saying. Genetic fitness doesn't involve long term survival. It involves survival long enough to pass on the genes successfully.

I should say it doesn't very much involve long term survival, just we pointed out, I think, before that even grandma and grandpa can still benefit their genetic fitness by taking care of offspring, providing funds to help their offspring, and help their grandchildren or children go to college. Things like that. So that's a role after they're no longer reproducing. Just how important that is in evolution of humans and certainly even more in other species where there may be more debate about that.

Now proximate causes are the kinds of things studied in this department, taste effects on hunger and eating, the innate releasing mechanisms, the same thing ecologists talk about. Brain mechanisms, hormonal mechanisms, various feeding reflexes and fixation patterns. Those are all the proximate mechanisms we could talk about, and we could map those out for human desire to eat high fats and sweet foods.

What about my question, what are the advantages of fat and sweet foods? Can you tell me? What's so good about fat? Why do you choose it if you're going on a long, cross country hike that's going to last for several days? You need a lot of energy to do that.

How much energy is there in fat compared with what there is a carbohydrate? Or protein for that matter. Aren't candy bars just as good as sausage? Well, candy bars with a lot of fat are the most beneficial for those long hikes. Think of the way humans evolved as hunter gatherers. You can get a lot more energy per gram, more than twice as much from fat. Nine calories per gram, actually kilocalories. We call them calories. Nine calories per gram in fat and only four for carbohydrate and protein.

Very good reason why we evolved, that desire to eat high fat and sweet foods. Why sweet? Quick energy. Fat is slow to digest. You might need the energy much sooner. For that, the sweet carbohydrates digest the fastest. That's why I carry glucose pills here. OK.

OK, let's talk about this interesting controversy that occurred in the 1960s, Wynne-Edwards and George C. Williams. Williams is great to read. If you ever get a chance, he's written some really interesting things. Wynne-Edwards wrote this book. He was British. It was published by a press in Edinborough, 1962, *Animal Dispersion in Relation to Social Behavior*. It became very popular, and the views expressed there persisted and they persist even today in public perceptions of evolution.
Pollution

I summarize it here. You interpreted almost every aspect of social behavior to be altruistic self sacrifice that advances the welfare of the species. That is, what evolves? Well, things that are benefiting to the species. Konrad Lorenz mentions species benefit in his book that summarizes many years of work in ethology.

Can someone tell me why that didn't hurt Konrad Lorenz if he was wrong? Well, let's first show that he was wrong. That's what George C. Williams did in 1966. Just four years later, he published a book at Princeton University Press, *Adaptation and Natural Selection*. He presented the counter thesis that evolved adaptations including behavioral ones were extremely unlikely to promote the long term survival of entire populations or species at the expense of individual reproduction. And you can read there on page 30 in Alcock his thought experiment.

You imagine a group of individuals. And most of them limited their reproduction. This sounds a lot like current problems we have with population control, doesn't it? They limited their reproduction for the benefit of the group as a whole. Let's say they're a small group, there's difficulty obtaining enough food, so they limit their reproduction to make it easier for the whole group.

But say you had a few individuals there, said heck with that. I want more kids. And they don't follow that practice. They're not feeling so altruistic. Where did my slide go here? OK. What would happen?

Well, the ones having more offspring, those genes are going to increase. The ones limiting their reproduction will not increase at the rate those people that violate that rule. And eventually the genes of those people that are think about their own reproduction, those are going to become dominant. And Williams argued that pretty forcefully in this book, and from that point on, any scientist read it, it totally changed the way people were looking at evolution by natural selection as applied to animals in general, not just humans.

So what about effects like this? I mentioned overcrowding results in population declines. We know that it does. And these declines are caused by physiological and behavioral effects of stress. Example, you can find in animals that live in overcrowded conditions overactive adrenal gland secretions, decreased immune system function, increased social conflict. Those kinds of effects reduce fertility, and that makes them what we call a Darwinian puzzle of great interest to sociobiologists.

Darwinian puzzles are things that don't seem to fit our view of genetic fitness. But we're neglecting one thing here, and it seems to have been neglected by Williams.

And that is, Wilson discusses the issue of group selection quite extensively. And he cites George C. Williams. He was very aware of Williams' book. He admired Williams. So he was careful to evaluate the conditions that could favor interdemic selection for genes. What's a deme. It's the population, the smallest population of people interbreed fairly randomly, at least in the modeling of their behavior.

So in other words, issues that favor some kind of group selection which involves altruism in most cases, but it's a very complex issue. And the arguments about it continue to this day. In fact, sociobiologists discounted group selection so completely after about 1975 when sociobiology appeared. It was actually in the 1980s when it really took hold and studies of animal behavior were dominated by sociobiological studies. And they weren't talking about group selection at all. It's only more recently where there's more people that are focusing on factors in group selection.

The exception was, of course, the social insects which in their colonies they function almost as a single organism, where of course things that benefit the group were paramount for reproduction of the social insect ants, bees, and other social insects. It's a special topic of Wilson's empirical studies.

I mentioned what a Darwinian puzzle is. And this is the way it's defined. Anything that appears to reduce an individual's chance of reproducing successfully even by a small degree becomes by definition a Darwinian puzzle. Because it seems to go against the very thing we're saying is the driver in evolution. I just took a couple of examples here.

The first one, very simple, we talked about it before. Why do whirligig beetles congregate so much when large groups of them are attacked more often than smaller groups? They congregate in order to forage. And when they're in these large groups, it does have a cost in reproduction of any individual if we look at it statistically, OK? But if you measure the attacks per individual as group size increases, you find out that it goes down. In other words, you benefit by being in the group because yes, the group might get attacked more if you're in a larger group than a smaller group, but the chance of an individual being attacked actually goes down. And this outweighs the costs.

Second one is why do humans love pet dogs so much? Even though dogs can spread disease and cause lethal bites. And yet it's a long history of humans' attachment to dogs. It could be a maladaptive side effect of proximate mechanisms that evolved for other reasons, like for example, caregiving responses, need for companionship. We're also very social animals. Desire for protection, human responses to loyal friendliness. Just interpreted in terms of modern conditions, for most people it's difficult to imagine that the costs are really less than the benefits.

But in earlier times, my belief is that dogs which have been associated-- and if you look at paleontological records you find bones of dogs in the remains of human settlements a very long time ago, at least 30,000 years, probably more. Some claims it goes back much further into ancestors of humans. But at least humans have kept dogs for a very long time.

What would be the big advantage to those early groups of humans of having a dog? Think of the dog senses, what the dog can sense that we can't. You have pet dogs at home. You must know some of this. Think about their hearing. They know if there's an intruder on your property or just a stranger or even grandma come to visit. They know long before you do. And they make a noise, and they let you know something's out there.

And we know their incredibly good olfactory sense. So they make incredibly good companions for hunting and for protection of the whole group. And I think those effects would explain, even though people were getting occasionally bit by dogs and suffering lethal bites, it probably didn't happen very often when the dog was socialized properly from infancy. Why? Because remember, this phenomenon of imprinting we talked about, there's something like that in dogs, and they socialize to humans, and they're not dominated.

Their allegiance is not dominated by other dogs, by humans. And that makes the chances of getting one of those bites a lot less. You'd get problems when the dog, especially some species of dog, gets very attached to guarding humans. And it's usually a stranger or a child that does something with the neighbor's dog or something, sometimes even their own. Dogs make mistakes, and sometimes the dog is so attached just to the master that the children aren't fully incorporated in the master's group. This can happen. So anyway, yes, they do cause legal bites, but I don't think it would have been, we wouldn't have kept dogs for so very long if there weren't benefits, fitness benefits, that outweigh the cost. So that's the way I would solve that Darwinian puzzle.

OK, now in the appendix of Alcock's chapter, he raises specific questions in his question two. I just selected two of them that seemed to me to be a little less obvious than B and D. Number B is, I can read it to you. 225. This questions in the appendix are quite interesting, and we'll look at them every once in a while. The first one is actually, the first question is also very interesting.

This is question two. Part B is, the readiness of some adult birds with offspring nearby to scream loudly when in the grasp of a predator. Why would that challenge a Darwinian adaptations? It probably wouldn't challenge him as much as C would. But some people could argue with that, because how often is that scream of the bird going to either startle a predator-- of course it's designed to startle the predator, so the bird can get away. And then if the predator pursues the adult instead of going after her nest, the nest might be spared.

And in fact, the young birds, and some of them anyway, will have a response to that scream from the adult. And they will huddle and be quiet, and they're pretty well camouflaged, they might not even be detected. But what about A? The arduous journey of an ocean-dwelling salmon to locate and swim up a stream it locates by olfactory sense, swims up the stream-- actually the stream where it came from-- in order to breed.

It entails very high costs, as most of you know. Salmon will swim very long distances up such streams, often having to leap because the streams of course are flowing down, and they have to go back up to get closer to the source where they want to breed. So the costs are very high, and they don't all make it. So what are the benefits? What are the fitness benefits? Did we talk about that before?

What's the obvious benefit it must have? Why do any animals that migrate in order to breed, why did they go such long distances? What are the advantages? It would be the same if we talked about some of these birds that go very long distances to get to breeding grounds, even over mountains. They'll go thousands of miles in some cases. Some turtles do this too.

What are the benefits? Because the young are particularly susceptible to predation, you need to go to an area which is usually not the area where your food is most plentiful. You need to go to an area where the chances of predation are the least. In fact, for many species they go to an area where various members of the species congregate so even if there is a presenter, the chance that any one baby animal will be attacked are reduced. So those are the fitness benefits.

And then we talked about this before. We talked about parasitic nesting. Birds accept eggs from non mates, even from another species and take care of them. They feed the hatchlings. There seem to be no fitness benefits, at least not immediate ones. At least in Alcock's reading of it. The behavior may be a maladaptive side effect of caregiving fixed action patterns.

So first of all, what does that phrase mean? What's the caregiving fixed action pattern that the parasitic bird who lays eggs in another bird's nest is taking advantage of? Do you remember? It should be obvious. Response to the gape, and often these parasitic birds like the cuckoo, his gape is even bigger than most songbirds, so the parent is a super normal stimulus for eliciting the feeding response. So it gets fed even more than the bird's own offspring.

Is it completely maladaptive? What did I say about-- and this changes a little bit what Alcock said here. He says there appeared to be no fitness benefits, but in fact there is a fitness benefit because in the case of the cuckoo anyway, the spotted cuckoo in Spain where it's been studied, the adult birds that lay their eggs in other nests hang around, and they enforce that caregiving. The birds that throw their eggs out, that would be the adaptive response, the way Alcock's thinking. But in fact the birds that do that get their nests totally disrupted, their offspring killed. So basically, yeah, fewer of their offspring will survive, but at least some of them will survive.

But this is how you go about dealing with these Darwinian puzzles. So this is another. I want to know how an evolutionary biologist would respond to this argument of Marvin Harris about the origins of human welfare. He's a cultural anthropologist. And this is what he argued. He argued that human warfare stems from the inability of pre-industrial peoples to develop a less costly or more benign means of achieving low population densities and low rates of population growth needed to prevent over exploitation of essential central resources.

So what's wrong with the argument? Very simply, he's talking about species benefits. He's making them more important than benefits to the individual, benefits meeting fitness benefits, OK? Remember, they're always using these terms about benefits and costs very specifically to refer to probability of gene survival.

OK, more about sociobiology. And let's just review. These are from last class. This is where some of these beautiful statements of E.O. Wilson. Remember that the organism in a sense doesn't live for itself. Its primary function is to reproduce other organisms. It reproduces genes, and serves as their temporary carrier. You say, but wait a minute. You're totally opposed to religion here? No I'm not. I'm telling you what the mechanism is, how humans evolved. And we will talk specifically about that later, because I don't agree with Alcock in this point.

OK. So he talks about the centers of this brain that is more a reproductive organ than anything else. The centers of the brain complex tax the conscious mind with ambivalences whenever the organisms encounter stressful situations. Love joint hate, aggression joins fear, expansiveness joins withdrawal, and so on. And blends designed not to promote the happiness and survival of the individual, but to favor the maximum transmission of the controlling genes. And that is the view of sociobiology. That's the theme of his entire book.

OK. The most important thing in this slide was what I've underlined here. You should know what, we will use the term deme occasionally. It's a special population, defines the smallest local set of organisms within which interbreeding occurs reasonably freely. But you should be able to separate population and society because they seem to be the same. But populations bounded by a zone of sharply reduced gene flow, whereas the society's founded by zone of sharply reduced communication. Now in many cases, those two things might coincide. But they certainly don't always coincide. They're defining a different aspect of the large group of a certain species.

The evolutionary pacemaker-- you're talking about that when both behavior and body structure change in evolution. And when that happens, when they are able to collect adequate data on it, it seems that the behavior of changes occur before changes in body structure. That means-- actually, it's a little overstated here, because you would have to say the part of the body that changes first is the brain. And then structure adapts to what's needed for the particular behavior that's evolving.

OK. You should know the term demography, because we will use it sometimes in the rest the class, and adaptive demography. Demography always means the way different ages of a species are distributed. How many really young, how many young adult, how many reproducing age, how many older ones, how many very old ones. This is demography, to talk about the demographics of the society. They're very different in different countries. And that will come up again. So we always talking about different ages or sizes. Sometimes size is the more important factor for some things.

We've already seen examples of behavioral scaling, and we'll see more. But you want to keep in mind this statement that evolution leads to compromises in social evolution. Because adaptations at one level may not be adaptations at another level. What's adapted for the individual may not be adaptive for the family. Family groups are small enough, though, that there might be conflicts, but they usually are resolved in such small groups, but certainly not at the higher levels.

And then of course ultimate versus proximate causation, he discusses. He made that a major point, and it's been ever since in the field of sociobiology. OK. So then he talks about the prime movers of social evolution, phylogenetic inertia. These are the factors that slow evolutionary changes in social behavior, reduce genetic variation, will slow evolutionary change. And that can happen in periods of very reduced population size, for example. With less genetic variation in a very small population, it will slow evolutionary change.

And the term genetic swamping means that if populations are usually divided into smaller groups, of course, and often one subgroup begins to change because of altered environmental conditions. But if they all aren't subject to the same environmental conditions, some live further north, some live further south, some live where there's a new predator, some do not. It only takes occasional interbreeding with another subgroup to prevent the less adaptive genes from disappearing. OK. That's genetic swamping.

When food sources change, a group may not change its habits because of genetic swamping for the same kind of reason. Food in some regions can change. So that's another one, that's all factors that can slow evolutionary changes. We talk a lot about the various ecological pressures, conditions that result in evolution-specific patterns of social behavior. He gives examples from anti predator behavior and other examples from foraging. I like his quote, when spider webs unite, they can halt a lion.

Colonies are a lot harder for predators to approach undetected. And attacks reduce the probability of harming any individual when they're in a large group. We've talked about that. He points out that even though organized colonies are the most effective, even an unorganized colony, an unorganized herd instinct will evolve in animal groups and still be effective. And some cattle groups, groups of fish or squid or flocks of birds are not that well organized, and yet they still have benefits of forming those groups. Locust swarms is another one.

Another example of this evolution of social behavior or because of ecological pressures related to predation, to synchronize breeding. We just mentioned that. Birds that reproduce in colonies, they may not live that way all the time, but for reproduction they might live that way. The social ungulates synchronize their breeding.

What's the name of the ungulate in Africa, the one that migrates long distances in the Serengeti? They all breed at the same time. So the big cats that chase them, are less likely to get-- they won't get all of them. The chances of an individual being caught are a lot less if they all are breeding at the same time.

And then we've already talked about group defense strategies. We didn't talk about the owl fly larvae. When confronted by insect predators, they gang together because individuals are less likely to be attacked. You have that in bee colonies. You have the meerkats that have their lookout or sort of a guard meerkat.

You have it in muskoxen that form this circle around their young. And muskoxen are pretty big, and they're a pretty good defense against wolves. So if they're organized, they do it as a group. They're much more effective at keeping the wolves from getting at their young. And the wolves are a lot less likely to be able to bring down an adult muskox. And then we've already talked about mobbing by birds. It occurs in primates as well.

And here's examples related to foraging where social behavior has adapted to conditions of foraging. Groups and cliques can increase competitive ability and feeding. They help each other in the smaller group to compete against other groups. That's certainly a social adaptation. Groups, coalitions, and cliques then increase feeding efficiency by social behavior.

He uses the term imitative foraging. We know the birds form territories when food is evenly distributed, but you'll still see imitative foraging in these birds. When one bird starts eating in a particular place, other birds just follow. And cooperative foraging, this is when you get birds flocking in order to more easily find food. And when it is find, you're more likely to see it because there's so many eyes looking for it. And then they;ll all get some, at least most of them well.

So it's a great benefit in foraging. The similar things for pack hunting animals and the cooperation of ants, honeybee communication which we talked about. And large prey, of course, is a factor that encourages group hunting in the large carnivores. But I point out there at the end that chronic foods shortages like faced by the moose here in the northern part of New England and the adjacent parts of Canada where there's a lot of moose, it makes solitary, anti-social behavior lot more likely.

OK, so I want to talk a little bit-- well, this'll be the last thing. I think there's a little bit more we'll talk about next time. Calculation of the inbreeding coefficient is also called the coefficient of kinship. We've talked about the importance of genetic relatedness in breeding and in behavior. Our own fitness can benefit by helping. I'm not talking about humans necessarily, but any animal will benefit if he helps animals that are closely related.

So let's just look at Wilson's discussion. He calculates here the genetic relatedness of the offspring of the mating of two half siblings. Here's the two siblings, male and the female. They have the same mother, OK? Different father.

This is the way you calculate that. Here's the individual. We know that here the probability that A and B are the same for anyone allele is one half. We know that the probability of A and A prime being the same is one half. We know that the probability of A prime and B prime being the same as one half. OK, so now we want to calculate the probability that B and B prime are identical. That's the coefficient of kinship. How related are you?

Basically, how many genes-- what's the proportion of genes you are likely to share with the individual? And see how that's important in calculating inbreeding. OK. So to get that, you simply multiply the one half by one half, and half, you get one eighth. So basically one eighth of the genes, the probability that any one of them one allele is identical is going to be one eighth. OK.

So now, here's what I want you to pay attention to. If we count steps backward from one parent to a common ancestor and back to the second parent, we get three here. OK? One, two, three. OK. So if we compute one half to the third power, we get that number, the inbreeding coefficient. This makes the assumption that A here is not inbred.

That's called path analysis. Every possible path leading to every common answer history is traced separately. It's the same as the probabilities obtained from every separate path. Let's just take one more example. The full sib mating. Here are the parents. Here's two of their offspring. They both have the same two parents, OK? They then mate and have this individual offspring. So you followed the paths.

This path C, A, D. Three steps gives you 1/8. And then C, B, D, the other path to the other common ancestor. You get an eighth. OK? You have to add those. So the probability in a full sib mating of getting the shared, the allele being the same at any one point is one fourth, which also means approximately 25% of their genes will have identical alleles.

OK. And then you can calculate for a first cousin or a more complex pedigree. It always works. And I will post this file online, OK? That's path analysis. Very important in the kind of gene calculations done by sociobiologists.