

Slide 1: Evolutionary Biology (00:00:12)

I work at Cal State L.A., just down the 10 (freeway). My Ph.D. was in Marine Biology, but most of my research has always been in evolutionary ecology or the evolutionary biology of marine organisms. And so the organizers were kind enough to invite me to come over and talk today. This is kind of a pared-down version of the typical first lecture I would give in an introductory biology class or an upper division evolution class, so I teach both, and it just goes over the basics of how I would pitch evolution by natural and sexual selection to an audience of students. So I'm just going to go through it the way I normally would, and if you have questions, feel free to throw up a hand as I go – and we can talk them over at the end.

Slide 2: Lamarck - "Acquired Traits" (00:00:54)

I'm not sure if you'll be able to read all this from the back. I usually teach with a great big projection slide next to me, so a lot on this is sort of a text based outline and if you can't see it, just let me know.

I always start by talking about Lamarck because one of the things that all biology professors sort of kibitz about when we get together is that all students are Lamarckian – all the way through college they still think this way, and you know, we sort of feel like this is something that would have gotten covered in high school, but as we were just talking about, it's something in our brains. It's easier to grasp what Lamarck, who was a French biologist, first proposed for how species changed over time. And Lamarck gets short shrift in the literature because he was wrong about his mechanism, but he was a visionary, in that he was the first person to really say, "You know what? Species now, didn't always look like this". They have changed over time, and the modern species are related by this phrase, "common ancestry", which we'll talk more about.

What he didn't understand was how you got an adaptation, like the ridiculously long neck of a giraffe. And he thought that traits were acquired over the course of your life, and then passed on to your kids. So the giraffes would try to get a longer neck by stretching to reach the tree branches, and the ones that got really long necks would then have babies that were long-necked. Ok, so that was his mechanism for how species changed over time, but if you think about it, we know that this is not correct, right? If you get a tattoo, your children are not born with a tattoo in the same place. And if you dye your hair blond, you do not have blond children, ok? Because children look like their parents due to heredity due to their genes, the information stored in their DNA (deoxyribonucleic acid), not the stuff that happens to you over the course of your life. So Lamarck's model was wrong, but it's amazing how intuitive it is to think about organisms trying to adapt.

Slide 3: The Birth of Evolutionary Theory (00:02:47)

And the genius of Darwin and his fellow originators of evolutionary biology, was that they grasped how things really worked in nature. And I kind of always teach Intro Bio with kind of a story of the history of Darwin and Wallace because I think it's a fascinating narrative, and it's full of intrigue and gossip and danger and adventure, and that seems to get people to pay attention. And so, that's just what I'm going to do.

Darwin was one of a generation in the early 1800s of young guys who set out to explore the world, the way some people might go backpacking through Europe after college. He came from a wealthy family. He knew it was his destiny to sort of settle down and run a quiet little church somewhere in rural England and you know, dammit, he wanted to get out there and see the world first. He booked passage on a boat, because his family was pretty well off, and he just sailed around the world for five years, on this boat called the Beagle. And everywhere he went

he obsessively collected all the animals and plants he found wherever he went, and he had a phenomenal eye for seeing pattern in the natural world, pattern meaning trends or tendencies that were out there, and he was brilliant at deducing process. Process means how the pattern got there – what's going on in nature that produces the patterns we can observe today. And of course, this year is Darwin's 200th birthday so there's a lot of attention now being paid to his accomplishments and to some elements of his story.

Slide 4: Evolution and Islands (00:04:16)

So this is a figure taken from the textbook that I use, and it's just one illustration of, sort of, what started Darwin thinking about the process of evolution, of species coming into existence and adapting to their environments. So he spent a lot of time in the Galapagos Islands, which is this little chain of islands off the coast of South America. And he observed, for example, that there were four different islands or clumps of islands, that each had a different mockingbird on it. And we should be probably familiar with mockingbirds, or those birds that learn to do car alarm imitations, that are very common all over North America. And he reasoned that the reason there were four different species of mockingbirds on these four nearby islands was that they were all descended from one ancestral mockingbird that got blown off South America by a storm, that got blown on to the island, and maybe it was pregnant, had a family and its descendants populated this island chain.

The way we would express the relationships among these species now, in modern biology, is in one of these branching diagrams. And I knew nothing about State Standards of Education until about a week ago, when they were emailed to me in an Excel spreadsheet, but I know that there is actually an expectation that students will have some familiarity with these kinds of phylogenetic trees, or family trees if you will, of species and how to interpret them. And this is one of the hardest things to get students to actually understand, is this way that we represent relationships and descent per time. So in a tree like this, one of these nodes or places where different branches come together, represents some extinct ancestor of the modern species that lived a long time ago and that's not with us anymore. And the tips are the modern species, the things that are around today. So this thing [points to open circle at base of tree diagram], might be that first mockingbird that got blown onto the Galapagos, and then over time, its descendants adapted to the environment on each island and evolved into their own separate species.

Slide 5: Evolution and Islands (00:06:22)

And so that's how we come to have these four different, recognizably different species today. So if this was you and your cousin, this would be your last common ancestor, or, as we would term her, grandma. And if this were you and me, say this was me and this was you, then our last common ancestor would be great-great-great.... great-great-great-grandma – you might have to go back thousands of years until your family tree and my family tree flowed together, but at some point that would happen. And if you go back a billion years, all species of animals, their family trees, would flow together into one last common ancestor. And so Darwin grasped that whole concept of common ancestors and the flowing together backwards through time of species.

Slide 6: Origin of Species (00:07:06)

He didn't know that when he set out, like, he wasn't going off to discover the mysteries of life, he was just sailing around the world. But by the time he got back from his trip he had the basic idea of his theory of evolution by natural selection intact. And he had a phenomenal amount of data; the way we record our observations and information in science, from all of the specimens that he collected and all of the things that he observed. But Darwin was no fool, and he knew damn

well that if he proposed a mechanism for how species could come into existence that did not mention God, this was going to set off a massive controversy in Victorian England. And, hello!, 200 years later the controversy is just as alive as it was in Darwin's time, and he knew it. So he knew what he put out there in the public eye had to be iron clad. It had to be able to withstand any criticism that people were going to throw at it. So he sat in his basement for 20 years, writing his book 'Origin of Species'. TWENTY YEARS the man sat and wrote this book in secrecy and he only told a few of his closest friends what he was working on because he knew when it finally went out there, it had to be perfect. Ok, can you imagine the dedication of doing something like this? Of doing experiments, he did breeding studies on all kinds of animals, he did anything and everything he could think of to bolster support for his basic argument of how species changed over time. Really, really phenomenal dedication.

Slide 7: Alfred Russell Wallace (00:08:48)

So jump to another thread in the storyline. While Darwin was sitting in his room writing this book for 20 years, he wasn't the only person thinking about these things. And so I'd like to talk a little bit about one of the more obscure characters in biology, Alfred Wallace, who also was a young man who was interested in exploring the natural world, but his circumstances were radically different from Darwin. His family was poor, they had had money and his dad squandered it all on all of these crazy get-rich-quick schemes, and so poor Alfred grew up poor. He worked his way through school, he worked as a surveyor, he did odd jobs, and he would just go to the Royal Society meetings and would just sit in the back and listen to scientists talk. He was a museum rat. He would just go and hang out in museums. And as soon as he was old enough he started booking passage on trips to sail around, but unlike Darwin, he wasn't kind of, you know, lollyng around collecting barnacles and mockingbirds. He was working. Everywhere he went he would collect lots of specimens and ship them back to England where he had dealers who would sell them to eccentric old rich guys who wanted to have a display of birds and barnacles in their curio cabinet. So he literally worked his way around the globe, but because he was collecting 500 big blue butterflies and 500 little green parrots, that process clued him into some stuff. So he noticed things like variation within a species – all big blue butterflies are not the same, all little green parrots are not exactly the same. That's really important. He also got a lot of interesting data on geographical distribution of species. Where do you find certain things? Up to this point in time, the presumption was that you found the species where God had put it, and beyond that we couldn't understand why species were in a particular place. There was no logic to it. There was no pattern there that we could understand or learn from. And Wallace was one of the first people to say, actually, you know what, there's a pretty striking pattern there that might be understandable, that might tell us something not just about where you find species, but where they came from in the first place.

Slide 8: Alfred Russell Wallace - Amazon map 1 (00:11:04)

So Wallace spent years traveling around the Amazon river basin in the mid-1800s – very dangerous, life-threatening conditions, and he collected everywhere that he went. He noticed, for example, that if you went to this region in the Amazon, between these tributaries of the river, you found one species of spider monkey, and this is its scientific name [*P. irrorata*].

Slide 9: Alfred Russell Wallace - Amazon map 2 (00:11:31)

And if you crossed the river and went into this region, you found a different species of spider monkey [*P. monachus*]. And Wallace also noticed that monkeys don't generally like to swim across enormous rivers. So he reasoned that these species were found on different sides of the river because they had been isolated by the river for a really long period of time, and that isolation plus time gave you different species. And in fact he predicted that...

Slide 10: Alfred Russell Wallace - Amazon map 3 (00:11:57)

... if you went to a part of the Amazon he couldn't get to, you'd find yet another species of spider monkey [*P. pithecia*]. And he was completely right, although he never knew it in his lifetime. There is a third species exactly where he predicted it would be. And that's one of the things that makes evolutionary biology a science – it makes testable predictions. You make predictions, and then you go out and see if they are correct - that's what we do in science. And Wallace was absolutely correct about this.

His story is amazing, you know he was literally chased by head hunters Gilligan's Island-style. He got every disease you could imagine. His feet were infected so badly he couldn't walk, sometimes for months on end. His brother sailed over to meet him and died while they were in the forest together. He had yellow fever. All these horrible things happened to him, but he totally persevered and after years and years of work he had all his specimens together on a boat to sail back to England and they were somewhere in the Caribbean and the boat caught fire and sank. And he was sitting there in a rowboat with the boat captain watching all of his specimens sink beneath the sea after having endured all of that to collect everything.

And they survived and he got back to England, and unbelievably enough, six months later, was booking his way onto a boat to Indonesia to the opposite side of the planet to just keep going and going and going. So there's really unbelievable adventure and spirit behind these guys.

Slide 11: Darwin and Wallace (00:13:30)

So Wallace, right, he had sort of figured out that species evolve over time. He had the idea, the theory, really, of evolution. But what he didn't grasp for a long time and is what I would call the mechanism, or the "how" of evolution. How did species change over time? Ok, he figured out that it happened, but how did it happen? And he knew of Darwin's work, because while Darwin was secretly writing the big book, he was also publishing small papers about his ideas all along.

And that's what we do in science, we gather data, we write up papers, we send them to academic journals, they get reviewed by other experts, and if they're deemed appropriate and correct, they get published, and five people in the world read them. That's what I do with my time.

And so Wallace had read Darwin's work and he would correspond with him, like from the middle of nowhere he would send letters back to England to Darwin that were like... "Hey, Mr. Darwin, I'm a huge fan, and uh, I've read all your books, and ya know I had all these ideas and I kind of wondered if you, uh, what you thought of them..." And Darwin would write back... and so they corresponded for years and years. Then in 1858, nineteen years after he got back from his boat trip, Darwin got this letter from Wallace that was like... "Hey, I think I figured out how evolution works, by this process of natural selection..." and Darwin is reading a description of his exact theory that he has been secretly working on for twenty years that no one knew was his idea all along, except his best friends, and was like, "Ooh, crap!" He immediately got in touch with his friend Charles Lyell, who is a prominent geologist and the president of the Royal Society of Science, a very impressive body. And Charles Lyell had been telling Darwin for years... "Look, dude, you need to publish this stuff because somebody else is going to come along...", and Darwin was all... "Oh my god, you were totally right, and this kid is going to publish this paper and everyone is going to think he discovered it, and I wasted twenty years of my life, and I'm a fool...", and Lyell was like... "Chuck, just chill. It's going to be ok, it's going to be ok. This is what we'll do: I'm the president of the Royal Society. Wallace is going to send his paper to be published by - guess what august body? - the Royal Society. So, *you* really quickly, write up a

two pager on your idea and send it to me, by coincidence, we never had this conversation. And I will read both Wallace's paper and your paper at our next meeting, and they'll get published back to back in the journal, so you tie. And then next year, get your damn book out, because that's what everyone's going to remember. Nobody's going to remember these obscure papers published in the Proceedings of the Royal Society in... like whatever! The book, it's the book that people will remember." And that's exactly what happened. They did exactly that, the papers were published together and the following year Darwin put out his book and that's all anyone ever remembers and Alfred Wallace is completely forgotten by history. Great story.

Slide 12: Darwin's history-changing book (00:16:38)

In fact, it's partly Wallace's fault because he kinda went a little bit off the deep end. I think all the malaria and yellow fever and everything else finally caught up to him, so he did become kind of a crack-pot later in life.

But, the fact that two people on opposite ends of the globe looking at different island systems figured out exactly the same thing was very persuasive to other scientists and made it much more convincing that these guys were really on to something. And this is the full title of Darwin's book (*On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*) that we just kind of bullet as 'The Origin of Species', but what it presented was this completely new paradigm for how life on earth had come to be and the lynch-pin of it is this phrase 'descent with modification'. And that sort of captures the whole idea.

Descent, meaning modern species are descendent from extinct species. Modification, meaning they're different from what those extinct ancestors looked like; that over time species get different. And that process of getting different is what we now call adaptation. They adapt to their environment, and that's why they seem so 'perfectly' suited to their environmental niche; is that they have adapted over time to that set of environmental conditions. So they no longer look exactly like their ancestors.

You with me so far?

Slide 13: Evolution by Natural Selection (00:18:13)

So that's kind of my rambling discourse on the history of these ideas. And now I generally talk a bit about the actual theory as Darwin set it forward because it's a beautiful argument of logic and every point is so clearly illustratable with data from the natural world. And you can find examples from the marine literature or from any literature you want to back up each and every one of these basic proposals, or postulates, that Darwin laid forth. And so this is how he proposed that species evolved over time and became adapted to their natural environment. He coined this term 'natural selection.' I think he later lived to regret having used the word 'selection' because it seemed to have an intent behind it, like some mysterious force was selecting or choosing individuals, and it's kind of more of an automatic process because of these points that he made. And point one, individuals within a species are variable...

Slide 14: Evolution by Natural Selection - Darwin's 1st proposal (00:19:24)

...it's almost so obvious we don't think about it. Except if you're a professional biologist, you spend much of your time trying to ignore the variation and describe the property of a species as if everybody's the same, when in fact, so this is a marching band from a university [points to slide], I forget which one, it's from the evolutionary biology text book I use. And so this is height, everyone is arranged by height. This is 6 foot 5, and 4 foot 10 is down at the other end. And so you can see this really nice bell curve. The guys are in black, the women are in white. And you

can see how much scatter, or variation, there is in human height. And almost any trait you pick, you will find there is tremendous variation in natural populations, and that's true for every animal, for every plant, for every bacteria. Individuals are different. Some are very short, some are freakishly tall – I use myself as an example in a lot of my lecturing [note: Pat Krug is VERY tall.] And then what we usually talk about in science are the average, the mean, right, the typical, the average height. Although if you look at this distribution, there's actually relatively few people who are average. Most of the individuals are on one side or the other of the average. And this is something that Darwin noticed from his collections, and that Wallace noticed from his collections. Penguins all look alike to us, but they're not all alike if you look really closely. They can certainly tell each other apart.

Slide 15: Evolution by Natural Selection - Darwin's 2nd proposal (00:20:52)

So all individuals are different. Darwin's second proposal was, at least some of that variation is inherited, or passed down from parents to their offspring.

This is probably the worst figure I can imagine to show a 12 year old, but if I had time, I flew back from the east coast last night so I didn't have access to my scanner, but I have this picture of my college graduation, and it always trips my friends out because it's me, my younger brother, my mom, my dad, and then my little brother, who's down here, but he's 12 years old, and my mom is right here, and my dad is right here, and so if you realize that I'm 6 foot 9, you quickly catch on that my dad is 6'8", my mom is 6 feet tall, my brothers are 6'7" and 6'9" respectively. Ok, so you can easily find examples of inheritance.

Offspring resemble their parents, and that's because half of my genes came from my mom and half came from my dad, so naturally I'm going to tend to resemble them. I'm not going to look exactly like either one, but I'm going to generally resemble them. What this graph is just showing is the size of beaks of finches, little birds, from the Galapagos. A group of birds that Darwin studied a lot and were very influential on his thinking. And this is just a graph showing that the beak size of parents, as the beak size of parents gets bigger, the beak size of their baby birds also gets bigger. So there is a relationship there. Offspring look like their parents. One of Darwin's problems in presenting his arguments, was he didn't actually understand how inheritance worked. And this was a big problem for him because it's one of the lynch-pins of his whole theory.

But unfortunately for Darwin, Gregor Mendel, everyone's favorite monk with his pea plants, his short and tall pea plants... Mendel had chosen to publish his work in like the most obscure journal, I don't even know what it was, the journal of "Monastery Pea Husbandry"? or something. His work was lost. It was lost for about 50 years until it was rediscovered by a later generation of biologists. If Mendel's work had been out there and Darwin had read it, oh my god, it would have been like, boom, done. I totally get it now. But he didn't and so Darwin really struggled to explain this part, how inheritance worked. Because no one knew at the time how information was passed from parents to offspring, why offspring looked like their parents. He knew it was true, he just didn't know why. So he really struggled with this, and in fact, if you read 'Origin of Species' closely, he talks some straight-up Lamarck when he's trying to explain things. He fully says things like a beetle got blown onto an island and it stopped using its wings and then eventually the wings fell off and the beetles didn't have wings anymore. Like pure Lamarck, but Darwin talked in those terms sometimes because he didn't have a choice. He didn't know how to explain inheritance.

And so I took the slides out because I didn't think I'd have time, but this was all corrected long after Darwin, in the 40s and 50s, in what's called the Modern Synthesis, which was when a more recent generation of biologists took Darwin's ideas and merged them with our understanding of genetics. And so all the things that Darwin talked about in terms of traits, features he could observe like the size of a birds beak, we now talk of in terms of genes and alleles and allele combinations. We talk in genetic terms now. And so all of his ideas are perfectly explainable in the context of modern genetics, but at the time Darwin was limited in his knowledge so he couldn't explain it like that.

Slide 16: Evolution by Natural Selection - Darwin's 3rd proposal (00:24:33)

His third proposal very straightforward and very morbid. In every generation waaaaaay more offspring are produced by animals and plants and bacteria than could ever possibly survive. I have no idea where I got these numbers from, but I swear I got them from a reputable source somewhere along the line. Somewhere I read, aphids are those little bugs that eat your rose plants, right, and the ladybugs eat them... Aphids can reproduce asexually, they can clone themselves at a very fast rate. If the offspring of one aphid all survived, and their offspring all survived, and their great-grandkids all survived, in one year, from that one aphid, there'd be 524 billion aphids on the planet. And there's a lot more than one aphid to begin with on planet Earth, right? So what does that tell you? The overwhelming majority of those baby aphids never make it to adulthood. If all the offspring of one bacterial cell survived - bacteria divide every 20 minutes if the conditions are right - if they all survived the earth would be buried in a layer of bacteria 7 feet deep in 2 days. So obviously the vast majority of those cells don't survive.

This is the weirdest figure of all, I have no idea where I got this from, but starfish produce HUGE numbers of eggs. And if they all survived, in 16 years there would be more starfish than there are atoms in the known universe. So clearly, the mortality in nature is off the charts. You've got to be literally the one in a million lucky one that survives to adulthood to get to reproduce yourself. Darwin was very influenced by the writings of Malthus, who was very concerned about human population growth and about the exponential rise in populations, and [that] we would eventually face resource shortages. And his writings influenced Darwin to think about this point, that there were way too many babies being made, but very few of them survived into adulthood.

Slide 17: Evolution by Natural Selection - Darwin's 4th proposal (00:26:45)

So his fourth and final culminating proposal was that the offspring that actually survived to be adults and got to reproduce themselves, wasn't random. It wasn't like one lucky starfish out of a billion. It was the one that was best suited to the conditions it experienced growing up. Whatever those environmental conditions were, the temperature, the salinity, the predators, the diseases, whatever that whole generation faced, the ones that were best adapted to those conditions were the ones that survived. And their offspring, because offspring resembled their parents, had those same characteristics. And so over time that species became adapted to a particular environment.

These are some data taken from professors that I had in college, who had spent forty years studying the population of these little birds on the Galapagos Islands that Darwin had studied before them. One of the nice features of these bird populations is that the islands are so small, there are so few birds, that they have tracked every single bird on the island and all of their babies for forty years. So they have the whole family tree of every single bird on the island. They know exactly what happens to every bird and they've measured every single bird on the island. [pointing a graph on the slide]

So this is a population on one island in 1976 and these are, this is a curve of measurements of all the beaks of all the birds on the island. And some birds have little tiny beaks and some birds have giant beaks, but there was an average, right, so the population had some average beak size. And in 1976 everything was hunky-dory and there were lots of seeds for the birds to eat. But in 1977, huge drought, withering drought, no rain whatsoever. And the only plants that survived and produced seeds were these great big trees with these huge, honking, massive seeds that you need a huge beak to crack open. So if you look after the drought...

Slide 18: Evolution by Natural Selection - Darwin's 4th proposal – after drought (00:28:46)

...which the Grants, these professors, did. In 1978, the average beak size had shifted pretty dramatically. And in fact, almost every bird left on the island had a beak that was bigger than the average two years before that. That shift in beak size was a response of the population to natural selection. It evolved. It got different over time. And that difference was genetically based, and we know that because we know that the beak size of a bird is genetically based. Birds have beaks that are sort of similar to the size their parents have.

So evolution is probably one of the most mystifying words in the English language. The actual scientific definition of evolution is just "a change in the genetic make-up of a population over time". Evolution is actually separate from natural selection because populations can get genetically different just by chance. If all the tall people go to a tall convention and are just hanging out in a field drinking lemonade and an asteroid hits them and kills them all just by chance, the population is going to evolve. It's going to change, and people are going to get shorter if all the tall guys get wiped out. But that's not natural selection. It's not necessarily better to be short, it's just that it was unlucky to be standing in that clearing at that particular moment in time. What's important about natural selection is that it increases adaptation to the environment. It is the force that makes organisms better suited over time to the environmental conditions that they face. It's reversible. The population evolved to have a bigger beak, but if the next year smaller beaks had an advantage, then it would evolve in that direction. So it's not directional. It's not going towards anything. It's just an inevitable response to the environment. Does that make sense?

Dr. Krug: Question?

From audience member 1: Are you saying that the fundamental event is the death of the small-beaked birds?

Dr. Krug: Yes.

Audience member 1: Pure and simple, they died off?

Dr. Krug: Yes, they died. These guys could not crack open the only seeds that were available in the year in between these two graphs, so these guys died.

Audience member 1: Did they, not to be overly fine, but they were able to collect their corpses, or how did they know they didn't just go someplace else?

Dr. Krug: Um, because they are isolated. So the nice thing about these Galapagos Islands is that they're so isolated there's no, or virtually no, movement of birds between the islands, and because they track every bird on the island they actually know that. Whereas

in most, in the continental U.S., you could never do a study like this because birds would be flying in and out all the time.

Audience member 2: I know that when we deal with, let's say, breeding German Shepherds, the gene pool is so small we have a problem with hip dysplasia, you know, and whatever, whatever. On the Galapagos Island, since there is very little outbreeding, how come there are not genetic diseases within a population?

Dr. Krug: Great question and brings up a bunch of really good points. One of the ways that Darwin was able to demonstrate a lot of the things that he argued was through artificial selection, or a human-directed breeding program, which showed the power of these forces. You can make a puppy to look like anything you want, if you pick the right parents that have the right characteristics. In these cases, the bird populations were big enough that they didn't become completely inbred. Whereas in dogs, what we do is, we keep picking the most poodle-looking poodle parents to make the most poodle-est looking puppy, but we're picking parents that have the exact same characteristics, so we're eliminating genetic diversity. And I know this very well because my mom only buys purebred dogs because "they're sooo adorable" as puppies, and then are sick for 12 years. It is a big issue.

One of the things the Grants have demonstrated very powerfully, though, is that there are rare hybridization events where the bird populations get so small that they will actually breed with a different related species. And that introduces genetic diversity that has been lost from a species, and can cause immediate and rapid evolution, when those new genes move into the population. So in that sense, sometimes these populations do actually kind of run out of genetic variation, which is the raw material that natural selection works on. And so rare events like hybridization or migration can actually be hugely important to allowing selection to continue to work.

Audience member 3: Even within the human race, like sickle cell anemia, within the African-American culture and the Jewish culture there's specific illnesses, and I think it's due to maybe people living in the ghetto areas or for centuries...[trails off]

Dr. Krug: You can understand a lot of the distribution of genetic variance that cause disease by understanding how those variations might have been adaptive where populations evolved. For example, the trait that causes sickle cell anemia, which we recognize as a disease, also confers resistance to malaria in sub-Saharan Africa if you have one copy [of the gene] but not two copies. So, an adaptation that helps you in one environment can be harmful if you get two copies of [the gene] in another environment. There are arguments that the allele that causes cystic fibrosis may have actually conferred some protection against black death, or bubonic plague, I think, in Europe in a certain period of time. So a lot of traits that sometimes help you in some conditions can sometimes hurt you in others. It's all dependent on the environment.

Audience member 4: When you talk about survival of the fittest, does that refer to this fourth idea of natural selection or more of the third idea?

Dr. Krug: Bingo. It's this [4th proposal]. It's the survival of the fittest, in this case the fittest are the ones on this end of the scale who had the biggest beaks, because they could handle what the environment served them up.

Slide 19: Evolution by Natural Selection (00:34:58)

And so perfect segue. "Fittest" is sort of a term that we borrowed, and evolutionary biologist talk about this quality called fitness. The fitness is how much an individual contributes to the next generation. Basically, how many offspring do you make? Your fitness increases the longer you live and the more babies you produce. If you are immortal, but a total loser with the ladies and never reproduce, your fitness is zero. It doesn't matter how amazing you are and how long you live, if you have no offspring you have no fitness because you have not contributed to the next generation.

Natural selection produces adaptations to your environment and it increases the fitness of those organisms because the survivors are the ones who reproduce and their offspring have their same qualities, so they reproduce. So natural selection produces adaptation. Any genetic change in a population is what we call evolution. These are very observable in nature. So we observe natural populations adapting to their environment, to environmental change, all the time. So these are empirically verifiable, meaning you can go out and do studies in the natural world and document these things happening, just like the Grants have done on the Galapagos. I forget where I'm going next...

Slide 20: Sexual Selection and Female Choice (00:36:30)

Oh, Sex. How could I forget? This is something that bothers me, and I don't know how you would really do this with seventh graders, but um, or maybe it's perfect for seventh graders...

Darwin devoted his second book to addressing what he perceived as one of the huge gaping problems with his first book: The peacock's tail; the giant claw, useless claw, of the male fiddler crab; the vivid colors of so many male birds and fishes. Darwin observed that all across the animal kingdom, males often had these incredibly eye-catching display behaviors or characteristics, like a peacock tail, ornamentation. Whereas the females were drab and brown and nondescript, or had normal claws not giant freak claws. This is incredibly difficult, if not impossible, to explain as a product of natural selection because you would think natural selection should do exactly the opposite of this. If you are wasting your energy making a ginormous eight-foot-across tail that is basically nothing but five hundred bull's eyes saying "hello, tiger, please come and eat me!" and walking around with it, you're going to be the first to get eaten. So how did this ever evolve?

And so his whole second book was dedicated to explaining this process he called sexual selection, which is an equally powerful force influencing natural communities. And it is never talked about in the public realm, we only talk about natural selection. And in biology, sexual selection is a huge field of study and hugely important. (aside: I have the time right? I can keep going for a little while?) And so what it stems from is the fact that in almost any species of animal, males invest their energy and build structures and perform behaviors that are designed to attract females; to attract mating opportunities. Whereas females do not waste their energy looking crazy and eye-catching and colorful. They put all their energy into making their offspring as big and as healthy as they can. And that's because a female is intrinsically limited in how much she can reproduce. Think of a human female. You're going to, at most, be producing, like, one baby a year, right? You're intrinsically limited. A male can father a thousand kids in a year, right? If he's really good, if he works it. So a male's fitness is limited by mating opportunities. A female's fitness is basically limited by the quality of the father she secures for her offspring, the quality of the genes that she gets to use to mix with her own to produce her offspring. So the

females are all about choosing the best possible mate. The males are all about securing as many opportunities for sex as they possibly can.

Slide 21: Sexual Selection, Darwin's sequel (00:39:51)

And so Darwin wrestled with this to explain why selection didn't eliminate brightly colored males, and in fact, if we have time I'll talk about this, well, it does! If you're a vividly-colored male, you're absolutely at a greater risk of being seen by a predator and eaten. However, because of sexual selection, you have an advantage over males who maybe aren't so colorful.

Slide 22: Sexual Selection, female preferences (00:40:19)

It gives you the opportunity to secure mating chances. Males in all species are under some pressure to appeal to female preferences. We see this across the animal kingdom. Females basically just kind of sit back and decide which male they like the best. In some species, they base that decision on traits that indicate the male's quality, his genetic quality. There have been studies that show that frogs that can sing their song the loudest and the longest, "RIBBIT, RIBBIT, RIBBIT, RIBBIT", father larger, healthier, faster-growing offspring than frogs that make wimpy songs, "ribbit-ribbit, ribbit-ribbit", not a good father. The females judge the frogs accordingly. In other species there's pretty good evidence that the females are not making a choice based on quality, it's just based on what they like. Sometimes what color their eye sees better. If their eye pigment is more attuned to red, they like a redder guy. They see blue better? They like a bluer guy. If in my species, the females are arbitrarily attracted to dimples and highlights and six-pack abs, or what have you...

Slide 23: photo of Brad Pitt (00:41:34)

... well, great. My buddy Brad and I walk into a bar together, he's going to get all the attention and I'm just screwed. That's sexual selection at work. And it's played out all the time across the board in all different animals. Now, if while he's getting mobbed by ladies at the bar, let's say I were to walk up to him and beat him to death with a shovel, "take that pretty boy, and that's for Jen..." Well, he's dead, so now I'm going to get all the mating opportunities, right? That's also a form of sexual selection.

Slide 24: Sexual Selection – males compete (00:42:16)

In some cases, the appearance of males adapts to the female preference. But in a lot of species, the females just sit back and allow the males to viciously fight for dominance, and whatever male wins the contest is the one that the females will mate with. So you see, for example, the antlers of deer that they use in these ferocious clashes. Elephant seals, these monstrous two-ton males that beat each other to a bloody pulp on the beach, and last seal standing gets to mate with all the females in the harem lying there on the beach just waiting for the boys to get done doing their thing.

But these are both forms of sexual selection, and they're incredibly important in understanding why animals look the way they look. I also, personally, think it's incredibly important to talk about sexual selection because I don't think there is an 'intelligent design' explanation for these adaptations. And that's something that is just dropped completely out of the public discourse, but I think if we talk more about these kinds of things... it illustrates the importance of discussing things the way evolutionary biologists really talk about them because you can't talk about natural populations and not talk about sexual selection.

Slide 25: Sexual Selection – fitness (00:43:44)

Part of the reason I say there's no good 'intelligent design' explanation for it, is sexual selection can do terrible things to a species. It can drag a species' overall reproduction way down because the males are investing so much energy fighting with each other or because conflict between females and males drags the species, as a whole, down. There are many examples of that. The important difference is that sexual selection does not increase adaptation to the environment. It *only* makes you hot. It *only* increases your mating opportunities. And so in a lot of ways, sexual selection and natural selection can be pushing a species in two completely different directions. Sometimes one may win out, sometimes the other one may win out. It's not always predictable. Does that make sense?

Slide 26: A note about mutation (00:44:44)

A couple of things. I just finished teaching Introductory Biology, and every time I teach it, I remember more things that I always mean to get across because students in their thinking always make these same mistakes. Where does variation come from? So you asked this question, "Why don't populations become terminally inbred?" Part of the answer to that is mutation - that in natural populations mutation is constantly at work, this silent invisible force, mistakes in the DNA, changes in the genes, are always happening as we go about our lives. If those changes happen in reproductive cells and get passed on to the offspring, that mutation becomes heritable. We always think of mutation as a bad thing. You can't use the word mutation and have students, because of sci-fi or whatever, automatically think you turn into a gross green monster or whatever if you are a mutant. And it's true. It's very, very hard to improve an organism with a random mutation. Most mutations screw you up, they break something, they make a gene work worse, not better. But sometimes a random change to your DNA makes you better in a particular set of environmental conditions. Sometimes the mutation that causes sickle-cell anemia in two copies gives you resistance to a deadly disease that is very common in your area. Well in that case the mutation might be a good thing. So mutation creates the variation that you need for natural selection to work in the first place. And all mutations are not bad. If it wasn't for mutation there'd be no variation in nature. There just wouldn't. So mutation is ultimately critical. It supplies the variation that you need for natural selection to work, and although most mutations are bad, not all mutations are bad. So that's something that I kinda want to get across to students.

Slide 27: A critical phrase: variation precedes adaptation (00:46:46)

And then this is the other one, this is like the hardest one of all. And to me it comes down to this phrase "variation precedes adaptation". If you can understand this phrase, then I believe you understand how natural selection works. The point of this is that the genetic variation in the population has to be there first, and then natural selection acts on that population to produce adaptation. The genetic variation is not a response to natural selection. It's a precondition. It has to be there already.

When students try to explain how natural selection works, they say, "Well, and then the giraffes *tried* to mutate to get longer necks and they *tried* to change and then they were adapted." They are Lamarckian. That's how people talk about it because it's just intuitive, we just can't help it, that's just how we think about things, but it's not how it works. Once natural selection kicks in, it's too late to try. You can't ever try to mutate. I don't know how to mutate. You can't mutate if you wanted to, right? You can't try to change, you can't acquire characteristics during your life - they won't be passed on to your offspring. You have to have been lucky and just gotten some characteristic from your parents, that when a new predator shows up, lets you survive.

Maybe you're that freak who likes to hide under the table all the damn time and nobody knows why, but your whole life you've been hiding under a table. And then, suddenly, lions show up and eat everyone else except you because you were hiding under the table. If that behavior is genetically based and your kids are also weird table hiders, that's adaptation, right? But the trait had to be there first. You had to be hiding under that table long before the lions showed up, ok? It's never a response to the environment. It's something that was already there. Does that make sense? It's THE hardest thing to convey to students about natural selection, in my experience because this is not how we think about the process.

Slide 28: layer of pink bacterial cells (00:49:05)

I do it by tying in a little bit of biomedical relevance. So if you consider a layer of bacterial cells, maybe growing on your skin, on a table, on your lunch... Um, we like to eliminate bacteria, so I don't want bacteria on my counters, so I'm going to spray it with an anti-bacterial spray...

Slide 29: layer of pink bacterial cells with Penicillin (00:49:28)

... that, let's say, has penicillin in it. So I cover my counter in penicillin.

Slide 30: penicillin treatment with one blue cell (00:49:33)

Well, if one cell in a trillion happens to have a mutation that makes it immune to penicillin, it's the lone survivor on my kitchen counter. So I have succeeded in eliminating almost every single bacterial cell with my handy spray.

Slide 31: layer of blue cells (00:49:49)

Except, within a day, that one cell will have reproduced, 2 then 4 then 8 then 16, and eventually my whole counter will once again be covered with bacteria.

Slide 32: layer of blue cells with penicillin (00:50:11)

So I re-spray, but mutations are heritable. In an organism like a bacterium, every mutation gets passed on to its offspring because it's just a single cell. So my penicillin spray doesn't work anymore because every single bacterium is descended from that one cell, they all inherit their ancestor's mutation. They're all immune to my penicillin. So all I've done is rapidly caused evolution to render my own anti-bacterial counter cleanser useless. That's evolution.

Slide 33: Which statement is correct? (00:50:36)

And so I always put up these two sentences and ask my students to close their eyes and raise their hand if they think A is correct or B is correct. And even immediately after this lecture, you wouldn't believe the number that sign on to "all the bacteria tried to mutate to survive, but only one succeeded in mutating, so he was the fittest who survived". This is the Lamarck explanation [A) All bacteria tried to mutate to survive the penicillin, but only one succeeded in mutating; that cell was the fittest]. But this is the correct Darwinian explanation [B) By chance, one cell carried a mutation that made it immune to penicillin treatment, so only it survived; its offspring inherited resistance to the drug].

And I also think it makes an important point. Why do we even care about evolution in the first place? Well you might care if you go to a hospital and get an infection that's resistant to antibiotics, because all of a sudden, you could die, right? You could die because most of the bacteria in hospitals have grown up in an environment where there are antibiotics around all the time. And most of them carry resistance mutations that let them survive in the presence of antibiotics that would ordinarily kill them. So we tend to put antibiotics in everything. It's in your soap, it's in your counter spray, you get it even when you have a virus; you get antibiotics from a

doctor because it makes you feel better even though it doesn't actually work on a virus. Livestock. We force-feed our cows and chickens antibiotics so that they grow faster and healthier. We cover the world in antibiotics. Then we wonder, why don't they work anymore? Why is it that when I get strep throat, none of the antibiotics make me better? Ok, that's why it's important to understand evolution, because it impacts our lives all the time in all kinds of ways. And if you don't understand how natural selection works, you can't make better decisions about things that are of biomedical relevance, agricultural relevance, etc.

How was that? Do we have time left? [clapping] So, questions?

Audience member 5: I have a few.

Dr. Krug: Hit me.

Audience member 5: First, is there a movie that you are familiar with that shows a nice kind of biography of both Darwin and Wallace?

Dr. Krug: As a video, no, not one that I've seen.

Audience member 5: Also, I recently read that, um, a couple different things, one regarding, I read that they found corpses, skeletal remains of farmers from about 8,000 years ago, and they studied the DNA of every one of them. I think it was like 8 skeletal remains, and every one of them was lactose intolerant. So does that kind of support this concept that now we're not, one in ten people say is lactose intolerant and the original farmers, apparently the extrapolation is that all the farmers 8,000 years ago were lactose intolerant. Does that support...

Dr. Krug: Sure, so if, say, over the course of a particular culture, that culture became very dependent on milk, dairy products, for their survival, you would expect that the most lactose tolerant individuals might be the fittest and that their offspring might be the healthiest. So if that gives you a survival advantage then the population evolves, the gene version that makes you intolerant becomes rarer and the gene version that makes you tolerant becomes more abundant. So absolutely.

Audience member 6: So if you have an animal that blends into the environment, like something that blends into the sand, is it just a coincidence that that animal looked that color and natural selection...

Dr. Krug: That there was some sandy-looking individual in the first place? Yes.

Audience member 6: Yeah, and just by chance this went on and on and on?

Dr. Krug: Yeah, so if you look at any population of animals, you will always find one, even if you look at these bright blue butterflies from the tropics, there's always one that's a little bit paler and one that's a little bit darker than the others. And so it's a gradual process, but you can, through artificial selection, you can probably start with a blue butterfly and, in 30 to 40 generations, get a pretty sandy-looking butterfly just by picking the right individuals to breed together. And natural selection does that sort of constantly by accident. So if the sandiest looking ones have the best advantage because they don't get eaten, then the population evolves to blend in with the sand. And it happens just by chance.

Dr. Krug: Other questions?

Audience member 7: This is how I bring up sexual selection with my 8th grade English class. I've read somewhere that the male *Homo sapien* generally breeds based on the visual stimulation of the female.

Dr. Krug: Girls, pretty.

Audience member 7: Yeah, and the females for whatever reasons are reluctant to marry down economically. And because we're educators, we get this literature that says the disparity between academic achievement between boys and girls is growing greater and greater. The girls are achieving more, there's more girls now and women in college, etc., etc. and getting more higher degrees. And so when I pass back those set of papers and all the best papers are written by the girls, and I say, guys, guess what, your chances, your breeding pool is getting smaller and smaller and smaller. And you know it's not much better news for the girls either because you're going to be now fighting over a few, a handful, of guys who are earning at the level you want them to earn or have been educated at the level that you're going to be comfortable marrying them. And they just scratch their head, and they go hmmm, ok...

Dr. Krug: That might very well be why for most animals there is no marriage because the females don't have to fight even if there's only one fittest male, in most populations, right? There *are* monogamous species though, and it's really cool to see the effects of monogamy because they essentially reverse a lot of what sexual selection does, because it takes a lot of conflict out of the equation and males and females evolve to be much more harmonious with each other because they share reproductive goals instead of being at odds with each other. But um, that's a great example. I generally try not to bring it too much into the human biology realm just to avoid trouble, but I did have a girl come up to me after one lecture and say, "Oh my god! I understand everything my boyfriend does now!" Oh, alrighty. I've touched someone today. Haha.

Dr. Krug: Ok, so we'll wrap this up, end it there. And I'll be around for a little bit if anybody has any other questions, but thank you very much for your time.