OK, so the last lecture we were talking about competition, and the result of competition between organisms.

And I didn't quite finish, so I just want to finish up on that lecture, and then will move on to predation, an interaction between two species which results in increasing the fitness and one, and decreasing the fitness in the other. But let's just finish up with competition. We were talking about character displacement and beak depths. And we have shown that when you have two closely related birds with the same beak size, if they live on islands separate from one another, they compete for the same food. But if you live on an island together, what happens is that you have this character displacement where the beak of what will get bigger and the beak of the other will get smaller. So they can exploit different food resources. And this character displacement is the beginning of species formation. And this is very common on islands.

And these are the famous finches from the Galapagos Islands that Darwin first based his theory of evolution, or it was an important part of his theory of evolution, where he realized that there must have been an ancestor finch, that all of these other finches that had different representation on different islands evolved from through the slow change in traits that is selected as a result of different combination of species being together or alone in different islands. And this is what's called adaptive radiation.

And this is really a powerful mechanism for evolution.

This is the Galapagos finches, but you also see this in an extreme form in Hawaii among the honey creepers showing this incredible diversity of beak types that have evolved to exploit different kinds of food. OK, so before we go on to predation, I just want to walk you through an evolutionary scenario, so that you can see how this might work on an island, Archipelago. So this is the mainland, and we're going to start with an ancestor species, A, and our Archipelago is going to have three islands. OK, let me draw this.

Here's the same three islands.

So this is time passing. So as we move, these are the same three islands as a function of time passing, OK? So at the beginning, we're going to have our founder species flying and colonizing the island. OK, so A is on this island. And so, the first thing that happens is that A evolves and becomes B.

So each one of these is just the name of the species, OK? This is species A, species B, through what's known as the founder effect. And that is when you have a few members of the species colonizing on this island. You have a tiny gene pool, and the genetic composition of this drifts such that it actually becomes a different species from the one on the mainland.

So, A becomes B. So the full arrow means becomes B on the islands through the founder effect. And now, we're going to have B migrate to a new island. So, A is now B on this island, right?

And B is going to colonize this island. And through that same founder effect, B becomes C. So let me just write what's happening here. B becomes C. I think you can see what's happening on one island, and then it migrates back.

So, let's let C migrate back to where B is, and C also founds a new island. So, we're going to let C migrate here.

So we end up with C and B here now able to compete with each other, C here and C here. OK, so we've got a new combination of species, and we are going to let C become D here due to the founder effect, and D is going to migrate over to this island.

So, C becomes E when with B because of character displacement.

So, C becomes E here when it's with B. So you end up with E and B on this island. D is going to migrate to this island.

So, we have C and D here. And, C has evolved to be D here.

So, we also have C becomes D when alone.

OK, so this is just a scenario we are making up.

OK, you can make up any scenario. But it's to give you the idea of how this adaptive radiation comes about. So, starting with one single species on the mainland, if you have an island archipelago where species can be isolated enough from each other to restrict, but not completely eliminate, the gene flow you can have this rapid adaptive radiation. So, evolutionary biologists often study islands in order to study this phenomenon. OK, so just to summarize for competition, interspecific competition results in either competitive coexistence, which can be achieved either through niche differentiation. Do you remember, what was an example of that last time? The barnacles and the inner tidal. One took the high road, and one took the low road. That's called niche differentiation, or character displacement.

And this can happen very rapidly. I hesitate to tell you about really interesting things that you don't have to know, but I will anyway.

This is really interesting study by a couple at Princeton of the Galapagos finches. And they've shown that you can have character displacement of the islands over a period of one or two years, just depending on the amount of rainfall.

So, it can happen very rapidly by just selecting for different character traits, or competitive exclusion, which is the case where the niche overlap is so great that one of the species completely outcompete the other.

The example from last time was the zebra mussels and Gause's paramecia in the test tubes excluding the other. So, these are really important ecological and evolutionary forces.

The other thing I learned from your comments, which I was very heartened by, is that at least one person really liked the definition of the niche, of the N-dimensional hyper volume, which I have always loved and I think is fundamentally important because people throw around ecological niche in everyday language and think of it as a place in the environment. And I think that a more robust definition is so much more useful. So, let's move onto predation, which is a very strong evolutionary force. It can control population dynamics. It can shape community structure. We're going to talk about each of these. It actually influences competition, which in turn shapes community structure. And it's a powerful evolutionary agent. In other words, it's very important in influencing naturally selection.

So, let's start with the classic, here's a classic predator-prey interaction. There is two wolves and a moose being attacked.

The wolves are not evil. They're just getting their meal.

OK, this is a very famous classic study of the snowshoe hare, and lynx. Lynx is a cat: populations in northern Canada.

And these data were collected by the Hudson Bay Company trapping records. So, it's really from the amount of animals that were actually trapped that these abundances come from. And that's where these coupled oscillations, this is the hare, and this is the lynx showing these couples oscillations with a roughly 11 year cycle. And people spend a lot of time trying to understand what was driving that oscillation.

And mathematicians love these coupled oscillators.

And so, the first attempt to model this kind of thing was using a very simple model. Remember we said the dN/dt equals rN?

That's our exponential growth equation. And we also said before the dN/dt or that r is equal to the birthrate (b) minus the death rate (d). OK, so grossly oversimplifying the system, the first set of equations that were used to try to describe this, are if you use for the predator, you call the predator dN1/DT equals b1, 1 minus d1,N1. OK, so that's just this equation. And they said, well, how do we modify this equation so that the growth rate of the predator is somehow a function of the density of the prey?

Well, the easiest thing to do is just make it proportional, right? So what they do is put N2 in there. So, the prey population is going to be dN2/dt, and we're going to the same thing: b2,N2 minus d2,N2, and the question is how do we modify the prey growth rate equation so that it is somehow a function of the density of the predator? So what would you do? So here, this says the birthrate of the predator is influenced.

As prey density increases, the birthrate of the predator increases. How would you modify this equation so that the predator density has an effect on it? It's pretty obvious, but I'm trying to get you with me. Exactly. It would be the death term.

As the predator numbers increase, the death term would go up.

And it turns out that these are two coupled differential equations that make a beautiful oscillatory system, a couple oscillators, perfect oscillators like that. This is predator density.

So that would be N1, N2, and this is time if you chart their density with time. And how many of you have actually had this in the course? Yeah, see? [LAUGHTER] And what courses have you had in it? Differential equations, yeah.

Mathematicians love it. But real populations, predator and prey, don't really operate this way. I mean, you see these oscillations, but rarely can it be attributed solely to the interaction between the predator and the prey. There's usually many other factors.

So, and I'll just give you one example. So ecologists go ahead and say, OK, so what's really going on? And here's an example. It turns out that in many cases, the food supply of the prey is oscillating. OK, so the availability of food to the prey oscillates, making the prey population oscillate, which then can drive an oscillation in the predator population.

So, it's more than just the coupling between the two.

There are also an external oscillators driving both of them.

And again, I'd like to try to address the role of experimentation. Here is an experiment done with rabbits. And I don't know what the predator was. It might have been, I'm not sure the predator was, but anyway, rabbits, in which through experimentation they increased the food supply to the rabbits through fertilization. And they showed that, so this is the control. And this is the phase of the cycle in the hare population relative to the density in the controls.

So, showing that when the food supply was increased, the oscillation was still there. So, it wasn't only relieving the rabbits of food limitation, did not eliminate the oscillation, but if you'd excluded the predators, you still also had the oscillation there. And if you did both of them, it increased the amplitude of the oscillation, relative to the control.

So the conclusion from this is that both food supply and the predation affected the oscillation. Another very classic experiment is the experiment by Huffaker back when people began to be enamored of these coupled differential equations. People wanted to test the hypothesis of those equations in the laboratory. And they tried to set up predator-prey systems in the lab, and see if they can get them to go in these coupled oscillations for many cycles. And Huffaker set up a system of a predatory mite and a prey mite.

Ecologists like to use insects as experimental systems because they're small and you can do it in the lab. And this one lived on oranges.

So it was an herbivorous mite. And the predator obviously lived on mites. And he set up a very simple system in the lab of oranges, and introduced the predator and prey, and inevitably he got this, where prey would increase, and then the predator would increase, and would overshoot, and the prey would die, and the predator would die. So he only got one cycle, with a simple system could not get this to persist, well, that doesn't even qualify as a cycle. So he realized, so this is a simple system. And he had a grid, which is shown up here in which he had oranges. And he had them interspersed with rubber balls to have a little bit of complexity in the system. But he found with that design, he could not get the system to persist. So he hypothesized that the reason it wouldn't persist is that it's much too simple, not close enough to nature.

So he introduced all kinds of complexity. He increased the size of his grid relative to the populations, which would give the prey mites more of a chance to get away from the predator.

He put barriers of dispersal, like Vaseline moats, and he actually put little launching pads for the prey. I don't know what they look like, diving boards, I don't know what they were, but little launching pads that just increased a lot of complexity so that it gave the prey an ability to move around relative to the predator. And he was actually able to, this shows his results over 200 days. He was actually able to get three full cycles of the predator-prey oscillation. And up here, it just shows you that they're sort of a cat and mouse game going on.

It shows you the location of the prey mites relative to the predator mites at these different points in time of this cycle, showing that they're moving around the system, and that the complexity allowed this coupled oscillator to persist. And of course, we present this because it was a classic experiment.

It was a pioneering experiment, but I mean, there have been a lot more since then. And of course, it has implications for stability of populations in the natural world.

As we make the natural world less and less complex, it reduces the ability of populations that are engaged in these coupled oscillatory systems to persist. It increases the likelihood of extinction. So this was like a tiny little localized extinction in his experimental system.

Another classic example that's often cited about the role of predation in regulating population dynamics has to do with rubber plantations over here in Malaysia. Did I spell that right?

That looks wrong. Oh well, is that OK? And I don't have any data for you. So this is just a story, but it's very compelling, and there is data somewhere but I don't have a slide.

But, in the first half of the century, in its rubber plantations in Malaysia they had a tremendous diversity of insects, but didn't have any real serious problems with insect pests in the rubber plantations. And, in 1950, they had a small outbreak of defoliated caterpillars. And that was right about the time that DDT was invented and synthesized, and became available.

And so, entomologists came down and sprayed the plantation with DDT hoping to get rid of this caterpillar.

In the next year, the outbreak got bigger.

They sprayed more. The next year the outbreak got bigger.

They sprayed more, and finally the whole thing was out of control.

And they said what's going on here? We are killing these things, and it's getting bigger. To make a long story short, what they were doing, this is a cocoon.

Oh boy. How do you spell cocoon? That's not right. Is that right?

Anyway, you know what I mean. Caterpillars live in cocoons, and there was a, that's a wasp with a big, long organ that it lays its eggs. It needs some legs, doesn't it? OK, I made some front legs too. There.

OK, so that's a wasp that lays its eggs in these caterpillar cocoons, and in doing so, kills caterpillars. And what they were doing with the DDT, is that they were killing the natural predator of the wasp.

And the caterpillars themselves, while they were in the cocoon, were actually protected from the DDT. So the more they put on, the more they killed the wasp, and the caterpillars were released from this controlling predation, and they had huge outbreaks. So, it's another example of in nature it's really hard, you can't see what's controlling what until you disrupt it.

You have to experiment either inadvertently or on purpose because everything is dynamic and turning over.

But it looks relatively stable. And that's why this is so hard.

And this is one of my favorite examples of this, because it brings together a lot of concepts that we've been talking about, is predation shapes community structure.

And this is another example of introduced species. And this is St. John's Wort, which was introduced at California from Europe.

And, it, so I'm going to draw a couple of habitats here.

This is a forest, and this is a meadow. So this is grass, OK, this is trees. And these are St.

John's Wort. So, it could grow equally well in the meadow and in the forest. And it was getting out of control so they introduced a beetle from Europe that feeds on St. John's Wort to try to bring it in to under control. And what they found was that the beetle, because the beetle's preferred habitat was the meadow that St. John's Wort persisted in the forests but was eliminated from the meadow. Now, because the beetle prefers the sunny habitat of the meadow, so if you were an ecologist and you didn't know that this beetle had been introduced, you just walked into this state, you knew nothing about the history, you wanted to study the ecological niche of St. John's Wort, you would say, well, I only find it in the forest.

It must like cooler, wetter environments because you wouldn't really know that it was being controlled by the presence of this beetle. So, this is a perfect example.

If we draw the niche or two dimensions of the ecological niche of St. John's Wort, and we say that just on these two dimensions that this is the fundamental niche on the moisture light gradient, in the presence of this beetle, the realized niche is only this low light, high moisture environment that you find in the forest. OK, so in other words, to really understand what's regulating the ecology of a particular organism, you have to understand all of the other organisms that it's interacting with, and what their effect is on this.

And again, that's why it's so impossible to do this without some form of experiment, either manipulative experiments like I described, or experiments done in a lab, or inadvertent experiments by introducing species.

OK, now let's talk about a couple of other really classic experiments that have been done. And these are experiments that have illustrated the concept of keystone predator. There are some predators and ecosystems that are what are called keystones.

And that is if you remove them, the entire structure of the community changes. There are some that if you move them, it doesn't have a dramatic effect, but there are certain ones that are keystone predators that it does.

And these, of course, are species that conservation biologists want to first identify, and second conserve above others because there is a cascade of effects if something happens to them.

A classic example of this was a study by Robert Payne many years ago in the inner tidal community. I'm not going to go into the details of that, but the rocky inner tidal community is made up of the starfish, which is called pisaster, one of the top predators.

And there are also limpets, chitins, if you grew up in California you know probably what these are, mussels.

These are invertebrates-like barnacles that stick to the ground, or stick to the rocks, and also algae that stick to the rocks.

And Payne hypothesized that the predator was maintaining this diversity. And the way to test that hypothesis was to put a cage over everything and eliminate the predator from certain areas.

At what he showed was that that's what that ecosystem looks like if you eliminate the predator. You can see here, here's the algae.

Here are some articles. This is a new textbook, see if you get the full story there, but there's a lot of diversity of the small barnacle-like invertebrates.

Then you eliminate the predator, and the mussels just completely take over. And this is preemptive competition. They compete with everything else for space and nothing else can survive there.

Another example of a keystone predator is the sea otter, which keeps the sea urchins in check in the bottom of the substrate, and if the sea otter is not there the sea urchins takeover and they exclude the kelp, the entire kelp forests and all the fishes that lives in the kelp forests, and all of the diversity of the ecosystem relies on the sea otter's ability to keep the sea urchin population in check. OK, so some of the best evidence for predation as an evolutionary agent, or something that's driving the natural selection of organisms, are these defenses that have evolved to avoid predation. In other words, if you're constantly under attack, your fitness will be increased by features that reduce your susceptibility to predation.

So in this case, there are a lot of experiments. I'm going to show you a few, but a picture's worth a thousand words here.

I'll show you some examples. Cryptic coloration is when a prey organism has color features that make it blend in to the environment.

So here's a very famous example that was actually in another inadvertent experiment. This is a moth that comes in two forms. This is called the melanic form, which is dark black or gray, and this is the other form which is much lighter.

And here it is on a birch tree. You can see that this one blends it beautifully, whereas this one, if I were a predator looking for the moth, I would see this but I wouldn't see that.

Here's the same two moths on another tree with darker bark showing that in this case, this one would be more fit in that one would be less fit. And there's a very famous study that I don't have time to go into, but it's a textbook, that showed experimentally the relative fitness between these two forms, depending on the color of the tree trunks.

And this whole example is called industrial melanism because the reason this was noticed was that in areas of high industrialization the tree trunks are darker colored because of the air pollution.

This is back in England back in the days when there is a lot more air pollution. So, they were able to show a shift in the frequency of these two forms as a function of the amount of pollution and environment because their susceptibility to predation was reduced if this form dominated. That study is actually rather controversial now, so I won't teach you the details.

But you get the point. But these moths exist in these two forms. Here's another example that's really convoluted that's in your textbook. So I'm not going to write it on the board. You can read about it there. But it's an example of what's called the evolutionary arms race. And it has to do with Cottonwood trees. And Cottonwood trees produce a defense compound that the name of which is on the next slide: salicorten.

It doesn't matter what it's called, it's a toxic compound that makes the tree distasteful to predator. You don't think of predators of trees. The beaver is a tree predator.

It chops it down. So when a beaver chops it down, a Cottonwood tree, the Cottonwood tree sprouts new sprouts.

And the resprouts have much higher concentrations of this toxic compound than the parent tree had. In other words, the tree has a mechanism. And I'm sure we don't understand that yet, but someday we'll understand the genetic underpinnings of this, the molecular biology of beaver defenses.

But if it's been felled by a beaver, it increases the production of this toxin in the shoots that come out saying, OK, fool me once, but you're not getting to get me the next time. It means there's beavers around. But the interesting thing is that these shoots are much more susceptible to grazing by a leaf beetle.

In other words, this increased toxin, the shoots that have the increased toxin, are actually grazed more than the parent tree by this leaf beetle. So scientists went in and said, you know, what's going on here? This is weird. Why make a defense that makes you more vulnerable to a different predator?

And what they showed by experiment was that these leaf beetles were using that toxin as a defense against the ants that want to eat them. So, they were less susceptible to predation by ants because they had taken in the toxin from the shoots.

So, it's called the evolutionary arms race between predator and prey.

In these systems get very complex.

So here's the data that shows that, that the control trees, trees that haven't been felled by a beaver compared to trees that have been felled by a beaver, and resprouted trees have a much higher concentration of this toxin. And this is the larval survival time of these leaf beetles that these are from the control trees versus the browsed trees in the presence of the ants.

OK, I'm going to skip that one. That ones in your book, too, which has an experiment showing that anti-predation mechanisms are induced by the presence of a predator. So I would encourage you to look at this in a textbook, this example.

And then finally I'm just going to go through a series of pictures that show all of the types of defenses that have been evolved as anti-predation devices. They are the obvious ones like cacti with spikes, or porcupines with spikes, octopi with ink defense. This is a caterpillar that has evolved to look like a snake, at least that's the way it looks to us.

I mean that's a hypothesis, that the predation on this would be reduced because it looks like a predator itself.

These are two different ones looking like a snake.

And often, snakes have a bright colored thing on their tail to draw attention to the tail. If you're going to be attacked by a predator, you'd rather have your tail attacked than your head.

So, this is a common motif in nature. And this is an insect.

This is its head. And yet, if you're a predator you'd probably think this was its head. And again, whether that's been established by experiments, I don't know. So these are just examples. Moths often have features that look like eyes that what tends to ward off a predator. This is an interesting story that is in your readings that shows that there are just a few genes that control the phenotype of this particular butterfly.

I think it's a moth, between having these spots and not having the spots.

In the fall, when it's dry and it's more selective advantage to look like a leaf, they look like this. But at other times, they're visible anyway so their selective advantage is to have these eye spots that make them look like they have eyes.

OK, I think it's time to quit, so we'll pick this up next time, I promise you. Their wonderful pictures of the creatures in the deep sea that are very evil looking predators that fish with their luminescent light organs.