[Music plays]

[NARRATOR:] Welcome to HHMI's 2015 Holiday Lectures on Science. This year's lectures, Patterns and Processes in Ecology, will be given by two leaders in ecological research, Dr. Robert Pringle and Dr. Corina Tarnita of Princeton University. The third lecture is titled, How Species Coexist. And now, Dr. Robert Pringle.

[Applause]

[PRINGLE:] Hi again. Now, I'm going to confront you guys with the classic problem of community ecology, and this is an enduring problem. We love it because it never gets fully answered, which means we can keep working on it. And generations of students and faculty and folks have been studying this problem for a long time. So the question is how can ecologically similar species share the same habitat? These are all large mammalian herbivore species, and they are all living in our representative savanna ecosystem, Gorongosa National Park.

So I'm going to leave that question there and tell you why is that a paradox; why should that be a problem. Why shouldn't there be all those species coexisting in the same place? Well, to understand that, you've really got to understand the competition-coexistence paradox. And so that's if you have two species that are competing for food. Here we have buffalo on the left and waterbuck on the right. And they're competing for a single food, which is buffalo grass, Panicum maximum. And buffalo grass is especially efficiently consumed and especially preferred by buffalo. And that makes them the dominant competitor in this situation. And over time, what that can lead to is competitive exclusion. This is the competitively subordinate species, waterbuck, in this case, will actually go extinct. Competitive exclusion is a classic phenomenon originally demonstrated with Paramecium in laboratory environments, but also potentially a risk in the real world.

Now, if you want biodiversity-- and I, for one, want biodiversity-- then you need coexistence mechanisms. You need mechanisms that enable ecologically similar species to coexist in the same habitat. And there are a couple classes of coexistence mechanisms, and we don't have time to talk about but one of them. But a big one that we're not going to talk about is--

[Laughter]

[PRINGLE:] --predation, and especially the phenomenon of keystone predation. You guys may have heard of keystone species. That term, keystone, derives from this idea that in this case, the starfish will disproportionately prey on the dominant competitors, which are constantly becoming more abundant because they're dominant competitors. And it'll therefore create room for subordinate mussel or barnacle species-- to coexist.

But what we're going to be more focused on-- exclusively focused on today is what we call bottom-up mechanisms, and that involves competition between ecologically similar species and how that leads to what we call niche partitioning, so differentiation in resource use.

Now, there's a couple of different ways you can think about niche partitioning. You can think about it in space. So here are six different antelope species that are coexisting in a sort of grassy, open woodland savanna with a little swamp in it. And they're occupying particular niches in this habitat, so the reedbuck in the reeds over there, the nyala in the deep woods. And this is a common form of niche partitioning. It's associated with the ecologist Joseph Grinnell. And another classic example you guys might have come across is Anolis lizards, which partition the vertical tree canopy. So ungulates, or large hooved mammals, can do that too.

Dietary niche partitioning is another key mechanism that we need to consider. And the way this has been thought about in the case of these big, large mammals here is largely in terms of something called the grazer-browser spectrum. So over here on the left, we have zebra. That's a grazer. It means it eats predominantly grass. And over there on the right, we have a dik-dik. And it eats almost exclusively nongrass, or browse. And for those of you guys who don't know what a dik-dik looks like, it's a 5-kilogram antelope. We happen to have a replica skull here. So that's the dik-dik, and it's got--if we were to look at the cranial morphology in the teeth of that replica, we'd be able to see adaptations to a browsing lifestyle, or rather, we'd be able to see the absence of adaptations to a grazing lifestyle. And then in the middle, we have what we call mixed feeders. So this impala might eat a 50-50 mix of both grasses and browse. So that's the grazer-browser spectrum.

Another form of dietary niche partitioning is that animals can separate out by height. So this one should make intuitive sense. If you've got three large browsers-- again, browsers being the ones that eat trees and don't eat grasses. So here we have giraffe, kudu, and steenbok feeding along a height axis on a tree. And the proportion of time that they spend feeding is there on the x-axis. And you see the giraffe spends most of its time feeding on the tall parts of the tree, the kudu at the intermediate parts, and the steenbok at the lowest parts.

Believe it or not, something similar is true for how grazers partition their grass. So if we have, again, our one grass species-- this is our Panicum maximum buffalo grass. This example is from the Serengeti, where they have a long dry season. And when the rains come, the grass grows tall. And the first herbivores to move in to start foraging on that tall grass are zebra, which--they're non-ruminant and large-body-sized animals, which means they have to eat a lot of food, and they don't digest it very thoroughly. So that's kind of their strategy. So they move in, and they eat this grass, which is relatively low-quality and has a lot of stems. They're followed by wildebeests, who prefer grass of a slightly intermediate height and slightly higher quality because as the grass gets shorter, then we're getting to the more nutritious parts of it. And lastly, the smallest and most selective herbivore species, Thompson's gazelle, is feeding at the smallest-- the shortest grass that you find, sort of six months after the rain, after the other herbivores have passed through. And this is a phenomenon known as grazing succession.

And it also relates to a concept known as facilitation because zebra are thought to be sort of preparing, if you will, the range or the pasture for wildebeests, and wildebeests further prepare it for Thompson's gazelle. So there's actually a positive as opposed to a competitive interaction among these species in this situation.

So that's the classical view. That's what we have from classic studies from the sixties up to today really. But my colleagues and I at Princeton, and particularly my colleague Tyler Kartzinel, got really interested in another form of niche partitioning that has received virtually no attention, and that is whether herbivores partition different plant species. So the interesting thing about the two different kinds of niche partitioning that I showed you guys up till now is that it really only requires two different kinds of plants if you think about it minimally. It requires grass, and it requires tree. And you can eat the tall part of the tree. You can eat the short part of the tree. You can eat the grass, or you can eat the tree. And it's pretty simple. And we actually know that savanna ecosystems are much more complex. The one that I work in in Kenya has more than 600 plant species. The one I work in in Gorongosa in Mozambique has more than 1,000--well more than 1,000. So there's a lot of plant species diversity that could be partitioned. And we don't know anything about how these animals do that, kind of surprisingly. You'd think we'd know everything about a zebra by now. So how might you try to go about finding out which species eat what? Well, this, again, until very recently, this is how you do it. You grab binoculars, and you go out, and you try to get looks at animals eating.

[Laughter]

[PRINGLE:] And you guys are immediately cueing in on the point, which is that is really, really hard to figure out, even in this--this was close. This thing was in my back yard, and I took a photo of it with a 400 millimeter lens. I'm right up in its face, and I still can't tell. It's not eating grass. It's in the middle of grass, but there's a little forb called Pollichia that makes red berries. And that's what's in there, and that's what the animal is actually eating. So what you see-- don't believe what you see.

[Laughter]

[PRINGLE:] And so this is really problematic. And of course, many herbivores are active in dusk, at night. And then this is what you'd see if you went on and tried to do the same thing. And that's even less informative about what plant species these herbivores are actually eating. So we need a different approach. I hope you agree. We need a different approach.

And this is where some new technology has come in and enabled us to do some really exciting things. So the strategy is called DNA metabarcoding. And I'll explain what that means. So a piece of animal dung has a lot of undigested plant cells in it. Those plant cells contain obviously DNA. And specifically, we sequence a short region of DNA that's called a DNA barcode. And we can then match that plant DNA barcode to a plant species from our reference library. Obviously, what we need to make this work is a good reference library. That thing that was scrolling along the right side of the screen is a library, and we need to have a good one for this to work. So how do we do that? Well, we start by collecting a live plant from the field. We press it into a voucher specimen. And we take that to the Smithsonian or the National Museums of Kenya or another museum that's willing to take it. And whether or not, incidentally, a museum is willing to take your specimen depends on how good a specimen it is. They're very picky.

And so once we've got this, we can sequence the DNA, the chloroplast DNA of that same plant. And then we take that sequence, and we add it to a growing online database. There's a community of people like us who are really interested in this stuff and have developed a repository, an online repository. And you can search it. So when you-- let's say I find my herbivore has been eating plant species X, well, fortunately, somebody in Zambia DNA barcoded that same plant species X. So I can use that to match my sample. So increasingly, this is a resource available to the whole community.

Now, how do we get samples? You can go pick a sample up off the ground. And we do that. We make sure to pick samples that aren't touching anything else that might contaminate it, and we use gloves, and we use bags, and we do some additional post-processing steps to make sure that the sample is clean.

But we can also do it a slightly more direct way. And so this is imagery taken this summer. And what we're doing here is getting ready to dart a kudu. There went the dart with a little pink tail on it. And we immobilized that female kudu and put a GPS collar on her that will give us an hourly fix. Over the course of the next year, we know exactly where that kudu's been. I could take you next break online and show you where this kudu was yesterday because the satellite collar uploads, and we can download it from here. So now, we know where this animal is going, and therefore, we have a sense for what plant species are available to it, what it could potentially be eating. And when we have the animal anesthetized anyway, we take the opportunity to collect the first of what we hope will ultimately be a series of fecal samples from this individual so that we can know what it was eating the day before--

[Laughter]

[PRINGLE:] --it had the misfortune of-- that's why we wear gloves.

[Laughter]

[PRINGLE:] --of being darted and having this funny necklace put onto it. And probably it goes back and tells its friends that something crazy just happened to it. You guys'll never believe what just happened to me. But this is a reversible anesthetic, and so we just put in the antagonist, and the animal jumps up and runs off. It's just fine-- a little bit wobbly at first, but totally no harm done.

So what we hope to do with that animal is then follow up, collect additional fecal samples over intervals so that-- just like if someone were following you guys around, writing down what you ate for breakfast, what you ate for lunch, what you ate for dinner, and what you ate for a snack-- doing that every day, we'd get a pretty good sense of what you like to eat. In a similar way, we're just trying to do the same thing for kudu. And that can help us answer the questions, for example, do individual kudus have dietary preferences. Like probably you guys-- some of you like Brussels sprouts; some of you hate Brussels sprouts. There's no reason really to necessarily expect that animals should be any less kind of individually variable. And that's something that we don't know about, and we're going to try to figure out.

But what we've done so far is use it to untangle this food web. I told you that this was impossible to do with binoculars alone, and therefore, we don't know anything about it. Well, we now know a little bit more about it. So each of these lines here in this array represents a single plant species. We know it's a species, and it's color-coded by the plant family that it belongs to. Now, there's only two that I really want you to pay attention to here, which is the Poaceae-- those are the grasses, which are obviously a hugely important plant in the food web--and the Fabaceae, and that's the pea and bean family, the legumes. And they include the acacia trees as well as a bunch of other plants that animals like to eat because they're very nitrogen-rich. They fix atmospheric nitrogen and therefore make very good food.

So you can see that, up on the left, there's a bunch of green bars corresponding to grasses, and down on the right, there are a bunch of red bars corresponding to those legumes. And now, we can look at a bunch of different species and ask exactly what they eat. So Grevy's zebra are a critically endangered species that lives in this part of Kenya, something like 2,000 of them left in the world. And you see they eat almost exclusively grasses. Plains zebra, similar set of grasses, but not entirely the same. And I should say also the width of the lines here connecting indicate the frequency of utilization of these different plants. There's cattle and buffalo-- these are all grazers.

Now, we switch on the other side to our mixed feeders and browsers. That would include elephant, impala-- and so you can see, especially with the impala, that it's eating a mixture of grasses and these red legumes, acacia trees and other things. So it's conforming to our mixed-feeder model. And our friend the dik-dik eating almost exclusively browse, very little grass. So what I just showed you is pretty, and it's cool. But it's very difficult to quantitatively interpret it. So we need another way of doing this.

And what we're going to use is something called a nonmetric multidimensional scaling plot. It's a statistical ordination technique. And the key thing to keep in mind-- for those of you guys who haven't encountered this before, is just that when I showed two points on this plot, ones that are closer together are more similar, and ones that are farther away are more different. So I can put plains zebra on this map, and you see that the points are kind of clustered, meaning that one plains zebra diet is pretty similar to another plains zebra diet, except there is one exception out there, an outlier. I can add Grevy's zebra. And you see something interesting, which is that, again, we have an outlier up there. And again, they're clustered with each other. But actually, they're overlapping but distinct from plains zebra.

I can do the same thing for buffalo and cattle. And again, you see the same pattern. Cattle eat what other cattle eat, and buffalo eat what other buffalo eat. But despite the fact that these are both two similar kinds of cow in the savanna, they have non-overlapping diets. And elephant and impala, a very similar thing is true.

And finally, for dik-dik, totally off on its own. So what this is saying to me is several things: first, that the grazer-browser spectrum, that classic mechanism for herbivore niche partitioning, is only part of the story. And you can see it very clearly, moving here from left to right. There's the grazers. The strictest grazers, zebras, eat, like, 90%--95% or more grasses. And the buffalos eat about-- buffalo and cattle eat 60% grasses and on down to dik-dik, which eat almost no grasses.

So this is the grazer-browser spectrum on the x-axis. The y-axis is a whole new dimension that we did not know about before of niche partitioning at the level of plant species. And what that means is that the Grevy's zebra and the plains zebra that eat the same total amount of grass, 95% in their diets, are eating different subsets of grass species. So specifically, there are 17 species that are not shared between the two, that either only plains zebra or only Grevy's zebra will eat. What the previous understanding was, as is often the case, was not wrong. But it was incomplete. And now, we are completing that with the aid of new techniques. So that's pretty much what I just said.

The conventional view--this is science. This is building on-- this was probably the most satisfying work I've ever been involved with in just the sense of being able to both confirm and build on previous work. We're standing on the shoulders of giants. The conventional view got us part of the way to understanding. The grazer-browser spectrum and the height partitioning, those all happen. But there's this additional phenomenon that people weren't aware about that we've uncovered. And that's super-exciting. And it's super-exciting to be able to use these cutting-edge approaches to derive really unprecedented insights into how ecosystems function and other ecosystem processes and patterns.

Oh, and finally, the future of where all this is heading-- believe it or not, DNA sequencing technology has improved incredibly, even in your guys' lifetimes. And the pace of improvement is ever-growing. And what we have now, and what's shown in this photo, is a DNA sequencer that's about the size of an iPhone. It plugs in via this port to your computer's USB drive. And we will be able to take this-- in fact, we're planning right now a field trial that involves taking this thing out to the field, using it in real time. And they'll get smaller, and it'll get cheaper, and soon, this is going to be the norm. And pastoralists in Africa who want to understand what their cow is eating, whether what the cows are eating is what's making them sick or whether the cows are competing with the wildlife in the area. Those are all things that will be answerable really starting now, basically. We're going to have smartphones with DNA sequencers attached. And it's not a joke. This is the proof. So on that note, I'd be happy to take any questions you might have.

[Applause]

[PRINGLE:] Hey.

[STUDENT:] Hi. When you see ecological changes like decreased rainfall for a couple of years, is there more overlap between similar herbivores in terms of their dietary preferences?

[PRINGLE:] Yeah, that's a great question. You guys should all come to Princeton.

[Laughter]

So the data I showed you guys were from a single wet season. And there-- in a wet season, you're expecting that the grasses are going to be growing green and high-quality, so more things should be eating grasses. And so what we expect to see in the dry season is that everyone will kind of shift away from grasses. And whether that leads to more or less overlap is actually not clear. We have the data from two additional seasons that I didn't show you because I don't have it yet. It was just sent off to the sequencer two days ago, and I haven't seen the data. I'm dying to see these data because I want to know exactly the answer to that question. How does this pattern of striking-- we couldn't believe these data. It was like winning the lottery, seeing this incredibly-- because I had never thought that it would be such a clear pattern. So I can't wait to do more and to see how it changes with seasonal context. It's a great question.

[STUDENT:] Regarding the DNA metabarcoding technique, besides the possible contamination of samples, are there any other disadvantages to using that technique?

[PRINGLE:] It's expensive.

[Laughter]

[PRINGLE:] Basically. I mean, but becoming ever-less so. Like any kind of analytical approach, you have to understand what you're doing and how to interpret the results. So it's not a magic--I mean, despite the impression I made given by whipping out the pocket sequencer, it's not a sort of a magic machine that you just take a blade of--a fecal sample and sort of shove it in, and it gives you out a list of plant names. There is all sorts of issues you have to think about with respect to do certain plant species get digested more completely than others, and therefore are they likely to be over-represented or under-represented in the fecal sample. Are we getting a quantitatively accurate picture of what the animal's really eaten? But I would say those fall in the realm of kind of methodological caveats and open questions, rather than drawbacks. To me, the main drawback is the expense. I think it's about to catch on. I think it's--actually, I think it's going to revolutionize how we study community ecology and food web ecology because we're going to find out, as we did for the large mammals, that what we thought were the food webs really weren't. And that's going to kick off a whole new additional round of theory, development, and experimentation to try to understand why food webs are the way they are.

[STUDENT:] So you had said your conclusion was that the conventional view of niche partitioning was incomplete. Do you believe that it's still incomplete? Is there still research going on showing other forms of niche partitioning?

[PRINGLE:] Absolutely. No, I would never dare to say that we've completed--it's not done. Right, I think this is a big advance. This helps us get a lot of the way. But no, this is just our first step. So our next step-- for example, we have many next steps. We have too many next steps. It's going to keep me busy for the rest of my life. And that's good. The next step is to understand those plant sequences. Like what are the traits of those plants? Why are they differentially selected? To a zebra, what's the difference between Themeda triandra and Cynodon dactylon, two grass species. What does the zebra perceive as the difference that causes the plains zebra to eat it but the Grevy's zebra not to eat it? And if we do that, if we understand how these plants are related to each other, we'll understand more mechanistically because this is really the pattern. I gave you the pattern, not the process. And the process--understanding the process is really to understand what is it about those plants that enables them to be selected. And I'm sure that there are as yet additionally unmeasured aspects of this problem that we haven't really thought of yet. But yeah, great question.

[Applause]

[Music plays]