[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 fourth lecture is titled, Modeling Populations and Species Interactions. And now, Dr. Corina Tarnita.

[Applause]

[TARNITA:] Thank you, I'll try to earn those. So ready for some more math? I do the cleaner part of the work. Once the samples are collected, I--

[Laughter]

[TARNITA:] So we'll look at populations of individuals, and we'll try to understand how modeling can help us get at some of the processes that underlie some of these patterns. So whereas before, we were looking at patterns that are kind of spatial, so you could see them, some geometric kind of patterns, here, we are going to look at temporal patterns or patterns of growth or not growth. So we're kind of trying to explain what can happen to very different species that are coexisting.

So for that, I am going to go to Africa, and I'm going to go to Mozambique to Gorongosa National Park. So Gorongosa National Park was this beautiful, beautiful park in the heart of Mozambique. It was thriving, with lots and lots of different species. Unfortunately, in the seventies and eighties, war came to Mozambique. And as a consequence of the armies being basically based in the park, a lot of the animals were killed either for food or to sell for money to support the army. So in the end, starting with a lot of species that were all represented or all thriving in this space, everything basically collapsed. They didn't go extinct, but basically by 1994, we only had a handful of each of those species.

Now, this offers a really interesting kind of--it's a very, very sad story. But at the same time, now that the park is being--there are huge efforts to restore the park, it's also a very, very large-scale experiment. So we can basically see how populations recover once they've all been brought to these very, very, very small sizes.

So here's what was happening before the war. We had some aerial counts of these animals that covered a huge chunk of the park. And so we'll focus on three species that will help us tell most of the story of what's happening there now.

So elephant, waterbuck, and zebra--they're all herbivores. They have roughly similar numbers before the war. After the war, there are only a handful of them. Now, I should say that that only counted about 4%, so it was a very--it was kind of a sparser survey across the park. But still, these numbers are extremely small. And we go back in 2000, and that's the nice thing about this park that people who are involved in its restoration care about its fate a lot. So they're really censusing these populations very, very regularly, which is giving us this gold mine of data basically at looking at what processes are underlying their recovery.

So in the year 2000, you see that they've all grown, but basically zebra and elephant, not really significantly. I mean, they're kind of still very tiny; whereas waterbuck seems to be doing a little bit better. We at least have these 490 individuals. In the year 2007, we notice that the zebra are definitely not doing well. Clearly, they're just having some small fluctuations, but they're still in the single digits. The elephant are growing, it looks like. And certainly the waterbuck are growing. They're almost at the levels that they were before the war.

Now, we look in 2014, and this is really quite striking. So the zebra are really still struggling. After 20 years, they're still struggling. The elephant are clearly growing, so that's a pretty robust trend of growth, although growing pretty slowly. And check out the waterbuck. It really started being kind of like the other species. And now, all of a sudden, it's really taken over the park. We have 34,000, 35,000 waterbuck in the park at the moment.

So the striking thing here-- there are basically two questions to be asked. First is, why is the waterbuck growing so fast compared to everyone else. Why is it recovering in this crazy manner? And why is it recovering to a level that's really way, way bigger than what it was before the war? I mean, we thought that things were pretty great before the war and pretty stable, so what's happening now? How can the waterbuck reach such high levels? So I'm going to try to make models that help us get at this question. And the question is, why did the waterbuck win the Gorongosa lottery? So this floodplain used to have all sorts of different animals kind of coexisting together. Now, everywhere you look, it's mostly waterbuck.

The first model we're going to look at is the simplest model of population growth. So the simplest thing you can imagine about individuals is that they give birth and they die. Definitely all things do that. So let's start with that. First, we have births. So if we have Nt individuals at time t, we know that in between time t and t+1, there's going to be birth at a certain rate. There's going to be death at a certain rate. And that'll give us the Nt+1 individuals, so the number of individuals at t+1. You can also write this in terms of a growth rate. So instead of carrying around birth and death every time, you can think about it as a growth rate being the difference between birth and death.

And then we could then write-- so how do we write how many individuals? If we know how many we have at time t, how do we write how many we have at time t+1? Well, it's however many we had at time t plus however much this population can grow in one time step. So r is the growth rate times how many individuals were before. We can also write that as a difference because usually, what we're mostly interested in keeping track of is not all of these huge numbers, but basically the change. We care about how these populations change from one time step to another, whether it's per year or per month or per whatever kind of time unit you care about.

And so we could write that as a difference equation or a differential equation and say that the change in the population N as a function of t-- happens at a rate that's constant-- so constant growth rate r, and the change is proportional to how many individuals are in that population.

Now, we can try to solve this system. So again, we have birth. We have death. And that gives us the growth. And we have basically an exponential solution. So this tells us that if we know we started with N0 individuals-- so that's year 1994. By year 2014, we should have the exponential of rt, so t is 20 years from 1994 to 2014. So we can use this expression now and try to understand, did the waterbuck grow exponentially in this time.

Now, we have to go to the literature to try to estimate some of those parameters. We have an equation, but we don't know what the birth rates and the death rates are of waterbuck. So when we do that, we find that waterbuck give birth every nine months. And they always give birth to one young. So that makes it pretty easy. We can turn that into a birth rate by basically dividing the 12 months of the year by nine, and we get a birth rate per female of about 1.33.

Now, because I want to have a model that's really very simple-- I don't even want to look at the two different males and females-- but we know that males and females are about half-half in the population. We can just model all individuals, assuming that they all reproduce, but basically by dividing the rate of the female by two so that everyone in the population can reproduce. So that's how I get 0.67 birth rate per year per individual.

We also find out the lifespan. They tend to live about 18 years. We turned that into our death rate. So we divide 1 by 18, and that gives us 0.055 per year. And this is basically all we need, except that we need to understand how many individuals we had to begin with. And you saw that the initial-- the raw count was something like 6, but that was only surveying 4.3% of what we know is the waterbuck habitat. So we need to process that, and we need to adjust it and get an estimate for how many we expect to have seen in the whole park. And to do that and get this at N0, we divide 6 by the percentage, and we get 140.

So there were about 140 individuals to begin with. That's our estimate based on how many they counted. We take that to our equation. Again remember, it was ^Ie^I to the rt before, but the growth rate r was just the difference between birth and death. We plug in the parameters, and we get this expression. And so now, let's try to plot that and see how the growth curve would look.

So when we do that, here's one waterbuck. It stands in for 140 waterbuck. So I'll do this quickly because the point of this is to show that basically, pretty soon, they will cover everything and get out of my chart. So exponential growth means that they're really exploding. They're growing extremely fast. And within 14 years or 15 years, you see that you would get past 1 million waterbuck. So that means that within 100 years, the amount of waterbuck will actually weigh more than planet Earth-- which should tell us that there's something slightly wrong with our model, slightly.

So something else must be happening to temper this kind of exponential growth. So what tempers exponential growth? Well, you have things that you need to account for. Individuals have to actually fit in their habitat, so space is an important one. If they're very crowded, one next to each other, surely they won't be doing so well. Resources--they need water. They need food. So that's an important one. And so they compete for these kinds of resources. So that's going to--these available resources and space are going to set what's called the carrying capacity on this population. There's only this much that they can grow on the available resources and the available space.

Okay, so how do we modify our exponential growth from before to account for this carrying capacity? Well, in the beginning, when the population size is small, we still want it to grow exponentially. But when it gets high, we want that growth to slow down to the point that where it gets to the carrying capacity, the population shouldn't grow any more. So the initial part of the curve should still be exponential, but it should actually plateau as it reaches the carrying capacity.

We take the equation that was the exponential equation from before. And so instead of having now the constant growth rate r, the growth rate has to somehow be dependent on the population size. So it has to respond to the population size, so we'll multiply it by 1 minus N/K. So if you now look at that term, if your population size is small, N is small, then N/K is basically tiny compared to 1. And so this grows more or less exponentially. It'll be kind of like rN there. But if N is very large, it's close to K, then 1 minus N/K will be very close to 0, so that'll give us that it basically stabilizes, and it doesn't change anymore once it reaches K. So that's our logistic growth. You may see it like this more familiarly just because it's easier to write down like this. But the previous was just giving you the intuition.

Okay, so now, let's take this logistic growth, and let's try it for our waterbuck model, except that there's one other thing that was oversimplifying in the logistic growth. And that's the fact that populations--waterbuck don't immediately make other waterbuck that can immediately reproduce. First, when you have waterbuck, then you must also have an offspring, a juvenile waterbuck, that takes some time to grow. So during that time, the juvenile can't really make more offspring, so we have to take that into account. So we have a birth rate. It's the rate at which adults produce juveniles. We also have a maturation rate. Juveniles turn into adults at a certain rate. And both of these, juveniles and adults, are subject to mortality. So there's a death of juveniles, and there is a death of adults. That's all. And we have the carrying capacity that we really need to consider; otherwise, we would get this pathological kind of growth.

So now, let's try to write the equations for this flowchart. The nice thing is-- so models give you this way of putting the assumptions in there and having an equation that once you solve, you can tell well, clearly, I'm getting what I-- kind of a good fit with the data, or I'm not getting a good fit with the data. So we need to go back to the assumptions. So here all our assumptions are put in this flowchart. Once you have a flowchart, it's really nice because you can follow the arrows. Following the arrows tells you how to write the equations. So we'll do just that.

We'll write a population change for the juveniles. So our two variables in the system are the juvenile population and the adults. And we'll write how each of those change. So now, let's look at the arrows. How do we get more juveniles? Well, the arrows going in are pluses, so you always add whatever arrows go in. So you get more juveniles only by birth. Someone has to make them. And who makes them? The adults, at a rate that's constant rate bA, and proportional to however many adults there are. Now, how do you lose juveniles from that class? Well, they can die. So death is one arrow that goes out, so it's minus the death rate dJ times however many juveniles there are in the class. And then there's one other way in which you can lose juveniles. It's when they mature, and they turn into adults.

So we have one more arrow coming out of the juveniles. And so that's a maturation term. So that term-- so they mature at a certain rate, m, times however many there are.

But here's the tricky part where we're going to include this carrying capacity that we're talking about. So how do we expect that available resources are most affecting the population? It won't affect so much maybe the adults that are already big enough to find their own resources. But juveniles are going to be strongly affected by limited resources, so we expect that if resources are very limited, then they're not going to be able to all mature. The fewer resources there are available, the less likely it is for juveniles to survive and turn into adults. So we introduce the carrying capacity term that before was 1 minus N/K. But now, the total population size N is basically adults plus juveniles, where you're competing for resources with all other adults and all other juveniles. So we have the term... so that's the modified rate. And (A + J)/K reflects this dependence on the population size.

Now, how do I get more adults when I construct this? Well, there are only two arrows: one coming in, so you get more adults when juveniles mature, so the term from there just comes in here. And you get more adults--sorry, and you lose adults when they die, so there's a death term, as before.

So now, we have it. Now, we have our system of equations. It's an age-structured model, meaning that we have two ages. These are differential equations. We're keeping track of the change in population size for our two different classes of individuals. And it has overall a logistic kind of growth because growth is set by the carrying capacity. Now, we have the parameters from before. We saw that we have a birth rate. We have death rate. All we need now is the maturation rate and the carrying capacity. So we need to estimate those.

We find out that juveniles, as we read the literature-- that males and females mature at different rates. Males take about 18 months, which turns into a maturation rate of 0.67 per year. Females mature faster, about 14 months. So that's a rate of 0.86 per year approximately. And because we said that in this model, we treat them as being the same-- that's why we divided the birth rate by two-- we're going to use an average maturation rate here of 0.77.

Again, these are all assumptions. So it's very important when you make models to keep all these assumptions in mind and have them very clearly so you can go back and revisit the model if you don't-- when you have your answer in the end.

And finally, let's look at the carrying capacity. The carrying capacity is very hard to estimate, actually. It's one of the hardest because in the absence of truly knowing what everything eats, what all the waterbuck eat and exactly what sets their carrying capacity. Is it habitat? Is it food? We have to assume that they're limited by food. And what we're going to do is we're going to take the park and assume that the park is food that turns into herbivore biomass. We're going to simplify everything and say we kind of assume that they're all the same. They're all a bunch of herbivores. And that clearly is a huge simplification. But maybe for a first step, it's not an absurd one.

So we take however many we had before the war, when we assume that the park was being used efficiently, and so we take all their numbers, multiply by their weights, and we get an overall herbivore biomass that was supported by the park in those ideal conditions. And that was about 15 million kilograms. A lot. It seems like a pretty thriving park. Now, we divide that by the weight of a waterbuck, which is about 250 kilograms. And we restrict it to-- we also multiply by the range, so we actually know the waterbuck habitat and how much of the park is waterbuck habitat. And when we do that, we get our final parameter, K, which is about 30,000 waterbuck there should be in the park. So remember, we were at around 34,000, so we're actually very close to the carrying capacity, maybe even overshoot it a little bit if this is a correct understanding.

So we have this, and we plot it. And so here's our model prediction. Once we have our model, we can simulate it. Many of these models--some of them can still be solved analytically. Some of them get to be pretty complicated, so then you have to use something like any kind of programming language to write the simulation for it. And this is the prediction for how this population would grow. See that it plateaus, so it reaches a carrying capacity, but it does so by actually fluctuating a little bit back and forth. So that's because you have these offspring, so sometimes, they overshoot. Maybe more offspring are born, and then there's not enough resources for them. So close to the carrying capacity, there's a little bit of overshooting before that population can actually reach the plateau.

So now, let's see how this compares to the accounts that have been collected in all these 20 years. So when we put that there, it's actually a pretty close fit. So notice that there are some points that are clearly not on this line, like the point here in the year 2012, I guess. But we also can tell that some of these must be errors in counting or errors in how the counts have been done because a population that has been increasing so overwhelmingly throughout the time can't have big dips just out of the blue. So overall, if we account for these errors, this seems like a pretty close fit.

So the interesting point here is that we picked the simplest model. We made the simplest assumptions about what this population does. And we have a pretty good fit with what it's been doing. This tells us there's actually nothing really surprising about the waterbuck. What's surprising-- they behave just logistically. That's the simplest assumption you can make about a population. What's really surprising is that they behave as if they have the whole park to themselves. So basically, the thing that's most surprising is not so much how incredibly quickly-- how incredible the waterbuck growth has been, but more what happened with everything else. Why isn't everyone else doing the same?

So this is the waterbuck. And we see all the other ones kind of trailing behind. So we're going to look at the two of them that I started at the beginning with, elephant and zebra. And we're going to ask the same question. Are these growing logistically as well, and maybe we're not seeing that. Well, zebra clearly aren't. They're basically at zero. They're somewhere in the single digits, maybe double digits. So clearly, something is awfully wrong there. And this is a very important point here.

This kind of logistic model only works when your initial population size is not too small. If it's very small, if you have only 5, 10, 20 individuals to begin with, then very random effects can--a disease that comes into your zebra population can wipe out 90% of the population. So in very small populations, randomness can drive-- can overwhelmingly drive the process. And so there are models that can work for this as well. But they're not the kind of logistic models that we discussed.

Now, let's look at elephant, that seems to actually be growing. We'll use exactly the same model as before. But we have to estimate the elephant parameters. So we have a gestation period that now is significantly longer, 22 months, as opposed to 9 months from before. So that gives us a birth rate of only 0.56 per year per female, and then half of that per individual. They live for a very long time, which is great. They live up to 70 years, so we have a very low death rate. But they also take a really long time to mature and reach sexual maturity. So they take 20 years, as opposed to the 14 to 18 months of the waterbuck. So this is a very, very slow growth process. We can estimate the N0, which unlike for the zebra, where it was really very low here, it's about 172 individuals. So we can really try to apply logistic growth. And we estimate their carrying capacity as before, and we have 15,000 individuals.

So when we do that, this is our logistic growth. It's a very slow logistic growth. Basically, when I plot it up to 2060, I don't even get to the plateau part. But it does get there at some point. And so now, if we place the data, it actually looks like the elephants have also been growing pretty logistically.

So these animals-- it seems like you can break them down into two classes. One class either has been reduced to population sizes that are so small that stochastic effects are keeping them fluctuating at those very small levels. Or populations that, for whatever reason, they got a little bit lucky, and they have larger population size to begin with, and they were able to grow logistically. But within those kind of different populations, there is a big difference in rates. So the conclusion of this is that the logistic curve accurately captures population growth in diverse species, so you can apply it to elephants just as well as you can apply it to waterbuck, as long as the initial population is not small. And in small populations, those random or stochastic effects can play the driving role in whatever happens to that population that can keep it low, or they can get a boost. And then once you have the logistic growth, though, the difference between species will be given by the difference in their parameters: birth, death, and maturation rates. So waterbuck and elephant are behaving very similarly, but at completely different rates.

And now, the really interesting point comes in. These have been behaving like the park is kind to themselves, especially the waterbuck. But now that the growth is picking up for all the others, within the next ten years, we're expecting to see the most exciting kind of start of species interactions, like true competition occurring. We have the waterbuck that are taking over the entire park. But surely they're also decimating their food, so they're kind of using up all their resources. That's transforming the environment for everyone else, so that's transforming how the park looks based on what these many, many waterbuck are eating. And so now, there's competition that's going to start playing out, and it'll be really exciting for the next 10, 20 years to keep counting these kinds of--these populations and trying to get at the processes that will underlie not just their growth, which we are kind of understanding, but now their interactions. And with that, I'll take questions.

[Applause]

[STUDENT:] Have you looked into the specific effects that could have kept the zebra population so low?

[TARNITA:] Yeah, that's a great question. People are actively looking at that, especially since it seems like the zebra is kind of a special species of zebra that you can only find in Gorongosa, so they are actively thinking about what to do to help it. I think we don't fully know. They're clearly reproducing fine. People see foals every once in a while. They see offspring. But predation is a key factor. If you have 18 zebra, and they make a couple of offspring every year, if a lion comes in just then or a lion herd, then you're left without offspring basically for the next year. So anything like predation, disease, hunting, poaching. All this kind of stuff can play an important role.

[STUDENT:] I was wondering, in some other ecosystems, there are these cycles of populations exploding and then cratering when resources are overrun. I know the tundra is one of them. So do you anticipate this kind of interaction in the Gorongosa?

[TARNITA:] Absolutely. I think that's what we're kind of anticipating based on one other example in Africa, where right after a disturbance, a similar kind of disturbance, waterbuck have taken over-- they have taken off-- and warthog and a couple of other species. And then they crashed. But this is where you can make models and try to see what the predictions are and then wait and test them because it can be that the waterbuck by now have modified their environment so much that other things won't really be able to recover at the same rates as they would have been able had the waterbuck not really taken this huge growth spurt. So I have an expectation. We can make that kind of prediction. But we're working with various alternative hypotheses. Okay? There's another question... .

[STUDENT:] Hi.

[TARNITA:] ...there.

[STUDENT:] I was wondering if the zebra population wasn't decimated so much as it was, would it have grown at a similar rate to the waterbucks?

[TARNITA:] That's what we would expect. So if there had been about 100, 200 zebras left, everything would have been probably okay for them to start growing at a nicer rate. They still--they would have been actually pretty comparable with waterbucks, so we would expect that they would have actually grown faster than elephants, which are kind of an extreme case. So yeah, definitely the big difference there is in the starting population. All right. We'll take that later.

[Applause]

[Music plays]