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[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 sixth lecture is titled, Conserving and Restoring Ecosystems. And now, Dr. Robert Pringle.

[Applause]

[PRINGLE:] All right, so it's the last lecture before lunch, and you guys are all still with us and asking the most amazing questions, so we love you for that.

And this lecture is, in many ways, to me the most important. But unfortunately, I only have really 15 minutes to give it. And it's important because it's about taking-- you know, I hope we've been able to convince you, Corina and I, over the past-- over the course of the morning, that by coupling kind of creative problem-solving approaches, new technologies, mathematical models, and experimental tests, we can understand a lot about how ecosystems actually work. And that's a new thing in ecology, which is a relatively young science. But this lecture is about how can we take that kind of knowledge and apply it to the restoration of a severely degraded ecosystem that we've been talking about all morning, Gorongosa National Park.

So the collapse of large wildlife is not unique to Gorongosa or to any other system. So here's a heat map showing where there are the most species of large mammals. Not surprisingly, that map concentrated in Africa, eastern and southern Africa. And here are species that are threatened. This is a map of a number of threatened species--the point being, there are really quite a few. And actually, Africa is doing reasonably well-- three or four severely threatened species like our Grevy's zebra, for example, black rhino, white rhino, too, elephants.

So threatened mammal species-- large mammals are just vulnerable because people like to eat them. They often have parts like ivory tusks and horn that people, for whatever reason, like to harvest and sell for extraordinary amounts of money. And I've already showed you that these largest mammals are really important players in the ecosystem. They are setting limits on the abundance of other species, and they're influencing the diversity of other species and a variety of ecosystem functions that we're not showing on this graph, like how do nutrients cycle and how much carbon gets stored. That's a big one-- large mammals are influencing how much carbon gets stored in the ecosystem versus goes up into the atmosphere.

So it's a big deal that these herbivore populations are declining. That map that Corina showed in the previous lecture with the range map shrinkage of those three species is a reason for serious concern, not just because we love those species, but also because we love the ecosystems that they come from.

So here's Gorongosa National Park in southeastern Africa. Mozambique is shaped like a Y. Gorongosa is pretty much at the center of that. And I would say the real heart ecologically of Gorongosa National Park is this Lake Urema. That's a floodplain--call it a lake. In the wet season, it's a lake. It gets huge, and

it inundates most of the park. In the dry season, it shrinks, and what it leaves behind is this really nutrient-rich silt and mud that can grow very nutritious plant communities.

And so Gorongosa was established in 1960, and it was immediately heralded as one of Africa's greatest game parks. And you can see that in this headline. This is from a defunct newspaper called The Daily News from South Africa. And they're saying this new national park, Gorongosa, could be Africa's greatest, which is quite a big statement, especially from a country where you have Kruger National Park, and of course the Serengeti, so quite a strong statement here about Gorongosa.

And the reason why it inspired so much excitement is shown in this photo. It may look like a bunch of black blobs and white speckles, but what it really is, is a herd of probably 1,000 buffalo on the Urema floodplain. So this is that floodplain that I told you about, so the flood waters recede, and it leaves behind grasses, and that becomes-- the herbivores move in. So here's just a ton of buffalos. And these are actually cattle egrets that are following them.

Here's what it looks like today, same place. And those are not buffalo. Those are waterbuck. So what happened? Well, you already know what happened, the tragic history of this place. And it's an interesting history to read sometime; obviously not time to go into all of the social causes of it. But it's really heartrending, and not least for the effect that it had on wildlife-- not most for the effect that it had on wildlife either. But it really devastated this national park.

And you can see here this is actually postwar. This is 1994, two years after the cessation of hostilities. And in a place that has been economically and has just had the soul ripped out of it by 15 years of the most grotesque kind of war imaginable. And people are starving. Naturally, they go in, and they eat. And so this guy's got a bike full of duikers and is headed home to cook. This is a cart full of-- this is Lichtenstein's hartebeest and waterbuck. And here are some bones littering the park. Two years after the war, still hunting going on at very high levels.

Now, since about 2004 unofficially, and officially since 2007, there's been an effort to restore Gorongosa National Park. And we call it the Gorongosa Restoration Project. And I'm a part of it. And it is spearheaded by this fellow, Greg Carr, up in the top left, reading a speech to a community meeting of community members. Here is a planning meeting that happened in 2010 about how the restoration should proceed. Here is the chief park warden, Mateus Mutemba, sharing a ceremonial beverage with local communities. And this is all part of the restoration process. This is the social and political embedding of the national park in the culture of the local place. And that's important.

And this is, of course-- this is the hippo house, which used to be-- I could show you a historical photo where people were sitting out on this balcony drinking cocktails, watching the hippos graze and the elephants trumpet and all that kind of stuff. Now, we have a single bushbuck. I don't know if you can see it; it's down there by the third pillar. And this is what it looks like today. It's a ruin.

And so if we're going to do this, we're going to spend probably \$80 million to \$100 million to restore this ecosystem over 20 years, we need to ask ourselves some questions. And we need to hold our own feet to the fire. So the philosophical question we need to ask is, should we-- what's the right baseline.

Do we try to restore how the ecosystem looked in 1977, right before the war? Do we try to make it look like it did before the scramble for Africa? Can we take it back to pre-European times? Well, those can be debated. And ultimately, it's a bit of a subjective question that science can't answer. But science does have a role here.

So the practical question I want to ask is how can science help achieve whatever goal is chosen. And then I'll just say that the goal that the restoration project has decided on is to try to restore the prewar state as the goal.

So you guys have seen a piece of this story already in Corina's lecture, that the floodplain grazer community-- so here, we're talking about hippo, buffalo, wildebeest, zebra, and waterbuck-- were disproportionately dominated in terms of biomass by hippo, buffalo, and to some extent, wildebeest and zebra. And then you had this kind of waterbuck, which was hanging around there, that following the near-extinction of all these other species, wildebeest--zero wildebeest were counted in 2002, just six zebra. The waterbuck have assumed outsize importance. And that has continued to the present day, even as some of the other species' numbers have started to increase a little bit. We have all these waterbuck. And we have a lot and a lot of individuals of species that were never counted before the war, so we don't know what their baseline is. But we just know that there's a lot.

And I've been in some African ecosystems. I have never been to a place with more warthog running around than Gorongosa. It's almost pestilential. They're in the camp; they're everywhere. And so it's a little bit pathological.

Now, we've also noticed-- these are people in my lab, my graduate students and postdocs, who have gone out, and we have systematically surveyed the vegetation of the floodplain and found that it has changed, too, not just the animals. So this very palatable grass, *Cynodon dactylon*, has decreased in relative abundance since 1972. And this rather unpalatable forb has increased in abundance since 1972. And this invasive South American non-native woody plant, which can choke many floodplain ecosystems, has increased pretty dramatically as well.

So this looks like a degradation of the plant community from the point of view of grazers. So we know-- these are our observations. We know that the bulk grazers have been replaced by smaller, selective herbivores. We know that the previous vegetation community, which was dominated by grasses like this *Cynodon dactylon* and had relatively few forbs, has now, in a situation where the grasses are few and the forbs are many. So what do we need to know from a restoration perspective? We need to know if this is going to naturally revert, this current situation today. Is it going to naturally revert to the prewar state that we had over there in 1972? Or alternatively, has it changed to a new stable state that will not change without heavy perturbation, heavy human intervention? How do we figure that out?

Well, first of all, we do have to understand exactly what processes are driving these changes. So I'm going to outline three hypotheses for you guys, and then I'll present you a little bit of evidence in support of each. But I should note that we're just starting this. This is very new science, and so these data are hot off the presses. I don't have nice tight conclusions for you. All I have is I'm opening up the

hood, and you guys are seeing science in action and data that I'm literally getting by email two days ago so I could put it in this talk.

So the first hypothesis is that these smaller selective grazers that are dominant today are suppressing grasses. Maybe they are too abundant. Maybe they feed selectively, and they avoid these nasty forbs, and they're going directly for the palatable plants. And because there's 35,000 of them out there on the floodplain, 35,000 and more, they're eating up all the grasses. Alternatively, maybe it was that these bulk grazers, which are not particularly selective-- they just eat--like a hippo has a wide mouth. It eats everything that's in the path of that mouth. And it can eat a lot of forbs, and it can eat a lot of grasses. And generally, they tend to crop it like a golf course. And what do you do when you don't mow the yard? It gets weeds. So maybe these animals are functioning like big biotic lawnmowers that are keeping the weeds out and maintaining the grass lawn. And then the third question is really whether these herbivores are competing with each other or not and whether that might impede the recovery of the prewar fauna.

So how do we test this first one, that these smaller selective grazers are negatively impacting the grasses and benefiting the forbs? Well, to do that, we have-- this is an enclosure fence, so much like the one we described in the previous lecture. This one is keeping out waterbuck and reedbuck and the other sort of species that have increased in recent years. And we're going to be able to track how the vegetation changes. And if this hypothesis is true, that these--well, this hypothesis represented here-- if that's true, we should see a reversion. We should see grass increase in abundance inside the fences, and forb abundance and woody plant abundance decline.

Now, if my other hypothesis is true, that these are--basically the lawnmower hypothesis--how can we test that? We can test that by mowing the lawn at a very large scale. So this is actually not Gorongosa. This is the Welgevonden private reserve in South Africa, where they did a similar kind of rangeland experiment. They mowed, and they added fertilizer. So that's basically simulating the effect of a hippo or a buffalo. You're clipping the grass, and then you're adding fertilizer-- manure, fertilizer. And what they found is you can see those green patches, right? Now, you can. If you couldn't before. That's where they had mowed and fertilized. And they found--what's really cool is they found that if you do this, mow and fertilize, you can create a grazing lawn which is as nutritious like grass - - based patch that will expand and grow. And so this could be a way of seeding these environments.

And then the last hypothesis, how do we test herbivore-herbivore competition? We've already talked about one way, the DNA metabarcoding diet analysis. And I showed you that, in fact, we're finding this emerging generality that these large mammal species really partition the dietary niche. So they should not be competing strongly because they eat largely different foods. And this is from Kenya, not from Gorongosa. And we don't--I wish we had the hippo and the buffalo and waterbuck data to show you. Those samples are still being processed. But I do have samples for waterbuck and warthog, and I'll show you that they also are partitioning the niche in a very similar way, same exact story. So I expect this story to be generally true.

Now, we can use these critter-cam data. So here we are back in the mind of a waterbuck, seeing what it's seeing, and looking at what it's foraging. See, it's actually not going for necessarily-- it is foraging at

a very low and selective level. But it's not going for grasses. It's eating actually a lot of forbs. So to me, the notion that waterbuck are actually overgrazing the grasses, and that's why you're getting all these forbs, doesn't really hold up. And in fact, when you analyze the waterbuck feces with the metabarcoding, you find that they're eating more than 50% forbs and Mimosa. They love some of the forbs and the Mimosa plants and don't need grazers.

Now, if you contrast that-- here's a critter-cam around the neck of a buffalo, and look what it's eating. That's tall, thick grass. And that's very different from the previous clip. We've got a sample size of 1 here, but I would expect this to be fairly representative-- another indication that these things are not strongly competing; they're eating different kinds of food.

And so my assessment is as follows: that my hypothesis 1 is unlikely, that I do not think it is the overgrazing. Really, there's no more biomass of large herbivore in the floodplain at Gorongosa now than there was. It just happens to be a different species. And that probably has a big effect of some kind, or at least a temporary one. But I don't think it's causing the vegetation changes as we've observed.

My second hypothesis, I think, is quite likely, actually. I think that these big mammals act as biotic lawnmowers, and that when you pull them out of the system, the forbs get a competitive edge. And we've actually seen this in long-term data from some of those herbivore exclusion experiments in Kenya, that when you pull all the large mammals away, forbs start to replace grasses. And so we're looking forward to testing this using that mowing experiment, seeing if we can revert using mowing and fertilizing.

Finally, the data we have do not really suggest any strong role for competition between these two groups of organisms. So my overall prediction is that the system will revert. That is, Corina implied with her lecture, waterbuck are just going through this exponential phase and-- or this logistic growth, and sooner or later, they're going to hit that carrying capacity, start to decline as the other species, like buffalo and zebra, start to become more abundant. And then they will be competing, and the system will start to shift back into its-- so that is nice because it suggests that we don't have to do necessarily this.

What this is, is these are some potential restoration actions, depending on the answer to the science. This is how you translate the science into management. And this is showing that you could introduce a bunch of buffalo if you wanted, but at a cost of hundreds of thousands of dollars and great stress to the animals and lots of time involved. So maybe you don't need to do that. This is why we need to understand this stuff because that's a lot of money to invest. If you're going to do it, you should only do it because you know it's going to work. Another thing we could do is go out and cull waterbuck-- go out and shoot a bunch and reduce their numbers.

And again, following from Corina's very nice lecture basically is a strong argument for why that's not necessary. They just haven't reached their carrying capacity, and they aren't in competition with other species, so don't go out and do the ethically dubious thing of culling wildlife inside a national park because you're freaking out that things aren't recovering the way they should.

Now, here's one that I actually think we should consider, which is to reintroduce some key predators. Right now in Gorongosa, we have lions, but we have no hyenas. We have no wild dogs. We have no jackals. And we have probably no leopards. Nobody's seen a leopard, anyway. If there are leopards around, there are certainly not many of them because we've been looking pretty hard. So bringing those animals back-- the hyena is an important predator of waterbuck in particular.

And then here's a management action that I find fairly--certainly as an experiment-- fairly appealing, is to go in with a fertilizer bag and a tractor and try to create some grazing lawns. And lastly, one that I find not so--if we cannot get a reversion of the system, if we think we're in a new stable state, we might try to apply herbicide that is specific to woody plants and won't hurt the grass as a way of bringing the system back into equilibrium. So hopefully, that won't be necessary because the biology in restoration often does a really good job of correcting itself if you understand enough about the biology to facilitate the biology in doing that.

That's all. I'll take a couple questions.

[Applause]

[STUDENT:] So how does the postulate of reversion to the mean affect the continuity of ecological succession?

[PRINGLE:] Yeah, that's really interesting. So ecological succession is the idea that a system will go through a kind of characteristic set of changes as it reaches a kind of climax or equilibrium community. And I guess what I would say is that this recovery process would be the equivalent of succession.

So what's happened is you've taken the Gorongosa ecosystem, and you've swung a wrecking ball at it and changed it all around. And the successional process is the process of re-equilibration that will happen if the animals are adequately protected from hunting, and the system is preserved, and natural successional processes should help restore kind of the balance. One more in the back, yeah.

[STUDENT:] What will reintroducing the predators--what effect will that have?

[PRINGLE:] Great question. I don't know exactly, but there are several things that we've noticed. One is that-- hyenas, for example, to take one species that is not really functionally present in Gorongosa-- are big predators on waterbuck. And they may help keep the waterbuck population a little bit more in check, which may help hasten the recovery of other species.

We also know-- remember my wolf trophic cascade? That was an effect not of the wolves eating so many elk, but of the fear that the wolves induced in the elk. So there is a sort of fear that's missing in the Gorongosa herbivores, and it feels amiss when you're there. You see--for example, we have a GPS collar on a bushbuck, which is a shy forest antelope. And this animal lives out on the edge of the floodplain and goes on these foraging journeys out in the middle of the floodplain where there's no

bushes. And it would not do that, I think, if there were predators around because it would be very vulnerable.

So in addition to whatever kind of population level effects that it has, restoring predators would have the benefit of sort of putting a healthy respect back into the herbivores to modify their behavior in ways that would basically bring it to a closer approximation of what it used to be.

And I'll add the last benefit, which is that-- I don't know if you guys know the sound of a hyena-- the spotted hyena calling at night. It's a very distinctive sound. It's kind of like [makes whooping sounds]. And if you spend any time in savannas or camping in savannas, then you know that sound, and it's kind of beautiful to be by the campfire and hear that sound all around you. Right now, Gorongosa does not have that sound. So it is sonically incomplete. And it sounds funny, but it actually matters, because the whole plan for restoring Gorongosa is based on revitalizing a tourism industry that can help pay the bills of the park, which are substantial.

And so if you don't have the elements that the safari-goer wants to experience or that would enrich their experience, then you're missing something that's economically hurting you as well.

[Applause]

[Music plays]