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So, let's start with where we were. We were talking about exponential growth in populations. And, we said we could describe this as one over the  $dN/dt$  equals some growth rate,  $r$ .

And, in this case, we're talking about, let me ask that is a question. As a model for population growth, what's wrong with this? What does this project?

This is  $N$ . This is time. There's no stopping it. I mean, we'd be knee deep in everything if populations grew according to this model, OK, because it just goes off into infinity in terms of density.

So, we know that this is inadequate. In fact, some people describe the entire field of population ecology as a field that tries to determine why real populations can't grow according to this model.

In other words, the whole field is trying to understand what the mechanisms are in populations that limit their growth. So, they don't grow exponentially forever.

So, in this case, this is really a maximum growth rate.

We can call that  $r_{\text{Max}}$ . And in this case, it's a constant.

So, when we're talking about exponential growth, the growth rate per unit time is the maximum growth rate that that population is capable of under those conditions and it's a constant.

So, if we want to plot it this way, one over  $N$ ,  $dN/dt$ , as a function of  $N$ , is constant. It doesn't change as density changes.

So, now we're going to take a historical look at this.

Back in the 1920s, two fellows named Pearl and Reed wanted to model human population growth. And they looked at this exponential growth equation, and they said there's got to be something wrong with that. We can't just apply that to humans, although if they plotted as a function of time, and this is humans in the US from 1800 to 1900, and this is the human population size, if they plotted this on this curve, they got something that looked like this.

So, it kind of looked like exponential growth.

But, when they went in it actually looked at one over  $N$ ,  $dN/dt$ , which would be the slope along here, they found that it looks something like this. In other words, the actual growth rate of the population was decreasing as the number of humans increased. And this is called a density dependent response.

OK, so if we look at this, remember from last time that  $r$  is equal to the birth rate minus the death rate, right?

So, we can look at, this is just a simple cartoon drawing of what's going on here. Density dependent factors regulate population size. So, if we plot one over  $N$ ,  $dN/dt$  as either a birth rate or a death rate, as a function of population density, when you have density, really the one that's the most important here is looking at this one, that death rate increases as population increases, and birth rate decreases. And you have an intersection here where birth rate and death rate are equal, and your population's going to stabilize there where there will be no change in population growth.

And these density dependent birth rates and death rates introduce a stabilizing factor. As  $N$  increases,  $r$  decreases in the population. And that's what brings population back into some sort of equilibrium. OK, so all right, forget that.

So, let's go back over to Pearl and Reed. We're going to stay on the board for awhile. So the question is, how do we modify that equation, our simple exponential growth equation, so that it more realistically describes real populations that can't grow totally unconstrained?

So what Pearl and Reed did, how do we modify the exponential growth? So, here's what we want the characteristics to be of this equation. We want one over  $N$ ,  $dN/dt$ , to go to zero as  $N$  gets large.

And we want it to go to our max, the maximum growth rate, when  $N$  approaches zero. In other words, at really, really low population density is, you can effectively have exponential growth because nothing's limiting you.

When the density gets very, very large, you want this growth rate to go to zero. So, they came up, so let's plot this  $N$ . This is  $T$ , and here's our exponential growth equation. And they came up with a function that looks like this. So, this would be one over  $N$ , and to describe this, we have this equation.

And this is called the logistic equation for reasons that are historically obscure. This is a French term that has something to do with, anybody know, who speaks French?

It has to do with something military. Anyway, I've never been able to figure out why they call this the logistic equation. But it doesn't matter what it's called, this is what it is. And  $K$  here is the carrying capacity of the environment. It's the maximum number of organisms were the population levels off, OK?

All right, so let's look at this. Let's replot this, because it's easier to analyze the features. We're going to plot one over  $N$ ,  $dN/dt$  as a function of  $N$ . If we want to rewrite the equation, one over  $N$ ,  $dN/dt$  equals our max.

We're just rearranging that equation to make it easier to visualize.

OK? So that we have a line that we can put that on, such that  $K$  is the  $X$  intercept, and what's this?

Our max, exactly. So, you can see these features over here at this plot, right? So, as this goes to zero, or as  $N$  is very large,  $1/N$ ,  $dN/dt$  goes to zero. And, when  $N$  is very small,  $1/N$ ,  $dN/dt$  is near our max. You're basically growing. You're over here where the exponential growth curve and the logistical curve are essentially the same thing. Yeah? Do I have something wrong?

Oh, very good, very good, very good.

Thank you. Absolutely right. OK, so the slope here is going to be minus  $r$  max over  $K$ . . OK, so here we have a nice density dependent response. OK, let's analyze some more features of this. Just looking at the exponential and the logistic, just to summarize,  $1/N$ ,  $dN/dt$  as a function of  $N$ , and if we just look at the  $dN/dt$  as a function of  $N$ , for exponential we already said that this is a flat line, right?

It's a constant, but the actual change in numbers as a function of time is a straight line, whereas for the logistic,  $1/N$ ,  $dN/dt$  as a function of  $N$ , what does this look like?

We just did it, so we are summarizing here.

But here's one that I want you to think about. What does the  $dN/dt$  look like as a function of  $N$  if something's growing according to the logistic equation? Like this? Yes, there you go, like that. Right. Because there is an inflection point here, right? So, this is what's sometimes called the optimum yield, and believe it or not, this model is actually used in fisheries conservation for years.

Now we know that it's so much more complicated than that that you can't just set the model is. But one could argue that if you are managing a population that you want to harvest, that you try to keep them at the density at which the  $dN/dt$ , the production of organisms, is maximal. So, you try to maintain a population there at that point.

One of the features of the logistic equation is that it assumes instantaneous feedback of the density on growth rate.

In other words, it says in a population of a certain density, the results in terms of offspring will be instantaneous.

And we know that's not true. So, this is an oversimplification. Even in the simplest organisms, even microbes in a culture, say you suddenly starve them up some substrate that they're using.

It takes a while for their biochemistry to readjust before that.

They might have one generation that's still at the same growth rate as it was before, before the biochemistry readjusts and says, whoa, we can't keep going at this rate.

Slow down. And then for higher organisms, you might have a whole generation before that sets it in. Plants that make seeds, etc.

So we know that there's a problem here. So, people have tried to introduce time lags into the equation, and we don't have time.

I mean there's lots of really neat things that you can do with this.

If this was an advanced ecology course, you'd be modeling it on your computer, and putting time lags in, and see what happens and all that kind of stuff. So we don't have time to do any of that. I show you this more as a way, I want you to learn how population ethologists think, not that this is actually the most important model that ever existed.

So how do we introduce time lags into the logistic?

Well, the simplest way is to introduce time. So, we're going to say  $dN/dt$ . Let me just make sure that's not ambiguous.  $dN/dt$ , is equal to  $r \max$  times  $N$  at that time  $t$  times  $K$  minus  $N$  minus  $\tau$ .

In other words, the density at some time,  $\tau$  hours or days or whatever, earlier than  $t$ , divided by  $K$ . So, what this says is that the growth rate of the population is a function of the density up a little bit earlier, or some amount earlier than the time at which we're measuring the growth rate.

So  $\tau$  or  $\tau$  is the time lag between sensing environments, and change in growth rate. So let's look at what that means in terms of, this brings us to another level of complexity.

So let's look at the possibilities here. So, with no lag, we have our logistic equation, right? The population just reaches the carrying capacity and levels off.

With a very short lag, and of course you have to play with this to understand what I mean by short, long, and medium because you have to change all the different parameters. But if you have a short lag, what you get is an actual overshoot of the carrying capacity in the near term because the feedback hasn't kicked in.

But then, it will come back and it will level off at the carrying capacity. If you have a medium lag, you will often see something like this where you get a couple of oscillations in here.

But it levels off at the same carrying capacity.

And, a long lag, you can end up with behavior that ultimately ends up in the population crashing. And we don't have time to analyze this, but at the end of the lecture I'm going to come back to why this is so important in terms

of human population growth.

And for those of you who are interested in complex systems and chaos theory, the logistic equation in its discrete form actually will go chaotic for certain parameter values. And for a long time, for those of you who don't know what I'm talking about, just ignore me. And for those who are interested ought to spend a minute on it. For a long time, this equation goes into a state of sort of chaotic oscillations, but that can be described mathematically.

And for a long time, ecologists kept looking at populations trying to see whether, indeed, they were growing according to this chaos theory and it hasn't really developed to anything, but it was interesting. Chaos theory first started coming to light; the sea collision was one of the first that people started looking into, coincidentally. But just because an equation has certain properties, it doesn't mean that thing it's trying to model has those properties. So that was a really interesting development. OK, so let's go back to Pearl and Reed.

Where did they go? Oh, they're up there. OK, so this was all a digression. So Pearl and Reed were looking at the human population data, and trying to model it. And they showed that they had this density dependent response.

They developed this equation in order to describe it.

And then, they looked at the data again using this graphical formulation. So, let's look at that.

We're just going to use the graphic method, because it's easier to illustrate. And now, we're looking at the human population in the US, and this is one over  $N$ ,  $dN/dt$ , and this is  $N$  in millions. And so, they have some data points that they put on here. This is 1800 to 1810. So, they have different data points for different intervals, and their last point here was 1900 to 1910, an average of the population size. And so, they projected down here there were 100 million people then. So, they said, so they asked the question: OK, we're modeling this population, we're saying it grows according to the logistic equation, we can predict what the carrying capacity in the United States for humans by simply doing a regression through this, and seeing where it intercepts.

So, that should be the carrying capacity. And they predicted that we'd have 197 million when we reach the carrying capacity.

And that was in the year 2030. So that was a prediction of their model back in the 1920s, that the carrying capacity of the US for humans was 197 million, and that that would be reached in 2030. Well, they missed it by a lot. So, let's look at the data, which is not surprising. Here's 1965. We reached 200 million way before 2030. 1990, 250 million, and actually today, at 10:45 this morning, because I looked it up on my trusty population clock on the Web, we had 295,979, 38 people. This is also done by modeling, we're not counting people one at a time.

But this website is keeping track based on various models.

And, based on the models that we have today, in 2030 we should have about 345 million. But these models are based on something entirely much more complex now than the simple logistic equation. OK, so the contribution of Pearl and Reed was to be yet to get people to start thinking about the feedback mechanisms, how to model population growth, and think about the feedback mechanisms in that model. You don't have that in your handout, but it's not important. It's not on the web, but if you care about it, there is the website that keeps track of human population in the US.

So, here's the total population number that I got this morning at 10:14 and 17 seconds off the web. And these are just some interesting statistics for the US, and I have them for the last three years: one birth every eight seconds, one death every 13 seconds, one migrant every 26 seconds, and a net gain of one person every 12 seconds. So they're keeping close track here.

OK, all right, so now are going to move on to global population growth, humans on the earth, the whole shoot and match. And, there's this wonderful book for anyone who's interested by Joel Cohen, called, How Many People Can the Earth Support? And, it's a great book for MIT students because it's a wonderfully nerdy account. I'm a nerd, so I can say that.

I'm a total nerd. But it's just a wonderful account, analysis, if you analyze human population growth, and at the same time looking at the phenomenon in a totally objective way. He's a theoretical ecologist. So, this is in your textbook. But, it's from this book. And, it's from 10,000 B.C. up to here we are today, the population on Earth in billions.

And, this is back in the hunter gatherer era. We had 4 million people. And this was a small revolution at the time, the introduction of the agriculture and domestication of animals allowed for higher birth rates, and so had a little blip, went up to 7 million here. And then for a long time, there was just no change in human population on Earth.

And so then, here you start to get, I'm not sure what started this up rise. Maybe when we see the next slide we'll see.

No, I'm not sure what started that. We'll have to look into that.

Maybe just the accumulation of people that you can't see on this scale, here's the bubonic plague, a decrease.

Here's the beginning of the Industrial Revolution and the introduction of modern medicine, which greatly reduced mortality. So, you see this incredible, and here's fossil fuel, increase in the population of humans on Earth. So, if you look at this curve, you think, oh my God, we're in the middle of this incredible exponential increase. And, the reality is this doesn't fit at all in an exponential model at all. I mean, if you tried to fit that to our simple exponential,

it does not fit. We are going to explain what's happening here in a minute. So here we are at 6 billion people. And we hit 6 billion in 1999. And here we are with a steady increase. I've just got the last three years. This marks the lectures that I've given in this class.

Every year I check in and see where we are. It's kind of a living document. And, we're now projected to reach 9 billion and level off. When I first started teaching about human population growth, the projections were at 12 billion.

And I'm not that old. This number keeps changing, and luckily it's changing in the right direction.

We keep predicting fewer and fewer humans before it will level off.

But it's still 3 billion more humans than we have now, and many people think now were already beyond the carrying capacity of the Earth. So, I'm not saying not to worry, I'm just saying that at least it's going in the right direction.

So, in Cohen's book, he analyzes this, sort of the history of humans on Earth as having four major evolutionary changes where you have the dramatic change in population growth. You have local agriculture in 8000 B.C. And, the doubling time of the population before and after those evolutions went from what he estimates to be 40, 00 to 300,000 years for a population to double down to 1000 to 3000 years for the population to double.

In other words, this is an incredibly faster growth rate, because this is doubling times. And then, with global agriculture in the 1700s, again you have a shortening of the doubling time of the population. And then in the 50s with the introduction of real public health across the world, another reduction, and luckily in the 70s, with the introduction of fertility control, at least in the developed countries, is the first time you actually see a shift.

We've gone from growing faster, and faster, and faster to actually growing more slowly. The doubling time is extending.

So, the good news is we're not in some kind of runaway population growth that's going to continue forever. We've already peaked out as a globe, and we are going to level off in terms humans.

And the real big question is when we level off, will we be above the carrying capacity of the Earth? Have we overshoot K? And we don't know yet because these feedback mechanisms haven't come back.

So, let's now analyze this a little bit more before we look at it in that context, because this is an important thing.

First of all, before we do that, I want to remind you that all of these lectures are tied together because remember this from lecture 20 when we were talking about biogeochemical cycles?

And, here's the same population size and billions on Earth, the brown curve. It's smoothed over, and these are the greenhouse gases, concentration of greenhouse gases in the atmosphere. This is the human footprint. This is how we've changed the metabolism of the Earth, by this explosive growth of humans.

And one more slide just showing you that this is another way to look at it, showing that the growth of the global population has peaked.

So, over here, each of these is the population in billions, and it basically shows you the number of years necessary to add a billion. And you could see that it's taking longer and longer to add a billion. You can see that there is an inflection point here. So, using the tools that we've developed to analyze populations, let's look at why this growth is leveling off. What caused the growth to begin with, and why it's leveling off? And the really important feature here is what's called a demographic transition. This is what we are going through on the Earth right now in terms of human population growth.

And, the way we look at this, we are plotting birth rates here, which is the pink one, and death rate here, which is the green one.

And, when birth rates and death rates are both uniformly high, which is the way it was back in the early days when we didn't have fertility control, and we didn't have modern medicine.

So, you had a lot of babies and a lot of people dying.

And growth rate, and so this is the total population.

So, you don't have much population growth. Then, what happens, you get to a place where you have a very high birth rate. Birth rate continues to stay high, but with the introduction of public health, and modern medicine, we were able to keep people alive a lot longer. And, that came in advance of fertility control. So, what happens, when these two curves deviate from one another, you have explosive growth, and that's what this big exponential shoot is.

But then, if you then reduce the birth rates through fertility control to match the death rates, you then have low birth rates and low death rates. Then you have no population growth, OK? So, it's very simple and intuitive when you understand what's going on, but I don't think that most people really have come to the point of thinking about it like that.

And where we are on Earth today is the developed countries have gone through their demographic transition. And you have a sense of that just from looking at family size in these countries. So, if we look at, this is Sweden as an



example of a developed country.

And this was 1800. And this is 2000. You see something like this. This is just an approximation.

This is the birth rate and this is the death rate, and the population growth rate looks something like this.

The populations leveled off whereas if you look at a country like Egypt over the same time frame, and you can get these curves off the web easily, it looks something like this. You have a high birth rate. And death rate has gone down, but they're not matching each other at all. So, population look something like this. It hasn't even begun to level off.

So the real trick is, in terms of trying to level off at someplace lower than 9 billion, is to get the birthrates in the developing countries to drop as fast as we can.

And that will determine the level at which humans will level off on Earth.

So, let's just briefly, let me go back over here, and let's go back over this carrying capacity. And this is basically what Joel Cohen's book is about, where he says, how many people can the Earth support? He's asking, what's the carrying capacity of the earth for humans? And here are the possibilities.

And of course, I'm simplifying the most complex system that we know into a simple two-dimensional graph, but I think it's a good way to think about it. Here's the way we've been living on Earth.

We have been growing like this. Granted, we're starting to level off, but we've been growing like this. And what we've been assuming, is that the carrying capacity will grow with us, OK?

We can handle as many humans as we want to put because we, smart people, with technology can increase the carrying capacity.

If we don't have enough grain, we'll genetically engineer to make more grain. We can fix it; we can fix it, so let's just go with the flow. And indeed, technology has greatly increased the carrying capacity of the earth for humans. There's no doubt about it.

But there's got to be a limit. So, is this the model that we want to go by? So, some people argue, so, the climate, we'll fix that with technology. We can fix any of this with technology, and if things get really bad, we'll go to Mars; we'll terraform Mars. We'll colonize planets.

That's not that far-fetched, so why should we worry about all these humans on the Earth? We'll just figure out, we'll go out and find new places. So that's one model.

Another model is, if we're going to do this, here's what I call the optimistic model. Well, I guess this is the super optimistic model. This one assumes that it'll do something like this that we may overshoot. And then birth rates, and if you want to you can easily describe a scenario that says that we have overshoot, that this whole environmental movement, the measurement of toxins in our environment, the global change, all of that is really overshooting the carrying capacity. And we wouldn't be worrying about things that we're worrying about if we hadn't overshoot it, but that if we get our act together, we won't have eroded the Earth's natural system so much that we can come back to a stable level.

And then, of course, the pessimistic scenario is that, indeed, we've overshoot, and we've overshoot so much that we have eroded the carrying capacity, and that we will level off at some level that the Earth will no longer be able to support the level of humans that it can even support now, that we have lost so much topsoil, and modern agriculture won't be able to overcome that, that our water will be polluted, that the climate will change so dramatically, the fisheries will be eliminated, yada, yada, yada.

I shouldn't say yada, yada, yada. Those are catastrophic things. Erase that from the tape! Every once in a while, I remember I'm being taped. So, those are bad things, not to be yada, yada, yada'd. So, anyway, this is what some people are worried about, that we are, indeed right now, in your lifetime and in fact mostly in your lifetime, you are inheriting this, notice the time frames on this graph.

I mean, this is just this little snippet of time in the history of life on Earth where all these dramatic things are happening.

And we just happen to be living in it.

Just think if you're living back here, and thousands and thousands of years went by, and nothing changed.

OK, so we don't have any answers, but this is a way to think about it, and a lot of people are putting a lot of energy into modeling the systems, and try to figure out where we are the scariest trajectories.

So, the next two lectures Professor Martin Polz, who is a professor in civil and environmental engineering, and the microbiologist is going to come in and talk to you about, again, its population economy.

He'll talk to you about population genetics, and some really exciting work that's going on in the field now using genomics to decipher evolution and population biology. And then I'll be back with some really neat DVD clips. So, come back.