PROFESSOR: Why don't we go ahead and get going. Today what we want to do is talk about predator/prey interactions. In particular, how a predator and its associated prey can in principal oscillate over time.

Now in this area there's this very important model block, a Volterra model, that has been used as kind of the standard model. It's given us some intuition for how this might happen. But mathematical biologists really don't like this model very much, because the oscillations that it give are neutral, or neutrally stable cycles or orbits.

What I mean is that it's not a limit cycle. It doesn't have a characteristic amplitude, nor a period. And associated with that-- and it's not a concidence-- and associated with it, what it means is that if you make sort of very small modifications to the model, then you can get qualitatively different outcomes. In particular, you can either abolish the cycles-- i.e., you can turn these neutrally stable orbits into stable limits-- or I'm sorry. Into a stable spiral. So it may have damped the oscillations.

So it could be that the oscillations kind of go away over time. Or it could be that you turn them into true limit cycle oscillations. And this could just be from very small changes in the model. That's associated with this fact that the logical Volterra model was neutrally stable.

Then we'll kind of switch gears a little bit and talk about these experiments-- that Yoshida paper that you guys read-- where they looked at this question of what happens in kind of a laboratory experiment where you have a predator and its prey. And in particular what they found is that if there is evolution in the prey population, that you can get qualitatively different oscillations in particular. Instead of having a 90 degree phase shift between predator and prey, you can end up with 180 degrees phase shift, so kind of anti-correlated oscillations. But also that the oscillations could be much longer than what you'd. Expect

And finally we'll say something about these noise-induced oscillations, which I believe that you guys have been playing with a bit in the context of your homework. Is it the next one? Oh, I get it. Well, you will get a chance to play with a great deal. So pay attention then. All right.

Any questions before we get going? Problem set's due tomorrow so that you can enjoy Thanksgiving with your family or friends. And then we'll have one more problem set.

So this Lotka-Volterra model. There's kind of a fun history of this, which I'll tell you about. But I just want to highlight that there are two important things that you should be remembering. And I'm getting these two points from Mark Kot in his book *Elements of Theoretical Ecology*, where he says there are two things you need to know about this model.

One is that it's a bad model. And of course you can argue what you mean by bad. I think it's maybe overstating it. But we'll try to be explicit about why he might say that.

But then it's sort of profoundly important. He kind of says from a historical perspective. But I would say that maybe both of these statements are sort of true. It's a bad model mathematically in some ways, because it's somehow structurally unstable, but also profoundly important.

The mark of intelligence is being able to keep two incompatible ideas in your mind at the same time. Somebody said something like that. More than two? OK. Well, we'll try to figure out what we mean by this. All right. So Kot, it's a nice book on mathematical ecology, if you're curious.

The history of this is that it was in the mid-1920s. And there was a marine biologist named Humberto D'Ancona. Does anybody speak Italian? Well, he was a marine biologist. And he had been studying the prevalence of different fish species in fish markets, and kind of throughout Italy.

So he went to fish markets. Over the course of about R-K. For about 10 years. Right? So kind of roughly from 1912 to 1923. Something like that.

And he basically asked, well, what is the kind of the composition of fish being sold in all these fish markets across Italy. And he noticed something that was very interesting, which is that there was a marked change in the composition between more predatory fish as compared to more prey-like fish. And this was associated with something that was happening in Europe around that time.

World War I. OK. So World War I in the middle. And what he found was that in the middle of this period there was an increase, and then later a decrease of what he called selachians, which is apparently a word for sharks and shark-like fish.

But for our purposes, we'll just say they are typically kind of predators. So what he saw is that this number of selachians, a function of time, kind of went like this, right. Where this was kind of roughly World War I.

And he wanted to try to understand why did this happen. Why is it that war favors predators? Probably not just having to do with the general zeitgeist at the time.So it's probably a more mechanistic explanation. And luckily, Humberto was engaged to the beautiful Luisa Volterra. OK. Oops. Engaged to Luisa Volterra.

So one day mid-1920s, our hero Humberto was visiting his girlfriend. And he started chatting with his future father-in-law, who was Vito Volterra, and asked him this question. And luckily, Vito Volterra was a famous mathematician. So he could write down a fancy model and try to get some insight into this question.

So this is a case of random personal interaction leading to something interesting. That's the Volterra-- Lotka had actually studied these equations almost 15 years earlier. First in the context of auto catalytic kind of chemical reactions and so forth. But then later indeed, in the context of population dynamics.

So Lotka wrote a book in the mid-1920s. Volterra wrote an article analyzing D'Ancona's data. And then now it's called the Lotka-Volterra model. And we'll come back to this thing about why is it that war favors predators after we get a sense of the model.

So what Volterra wrote down was the following. First of all, we should all make sure we can figure out which one is the predator and which one is the prey. So let's think about this for 15 seconds. And then we're going to yell it out verbally.

Is y the predator or the prey? Ready, three, two, one.

AUDIENCE: Predator.

PROFESSOR: Predator. All right. So we have a predator here and prey. Is the total size of the population constant? i.e, is x plus y equal to a constant? Ready, yes or no. Verbally. Three, two, one. No.

It would be a constant perhaps if these two terms-- if b were equal to d or so. No. That's not even true. Never mind. Yeah. OK. I guess really what I'm thinking about is this tells us about how many predators can be created from a prey. But then there's also the growth in death rate. All right.

But even this act of converting prey into a predator, even on that level it's not conserved, right? And of course, vegetarians like to point out that you can create many corn burgers for the price of making a hamburger. Something like that. OK.

Except in the case of salmon. This is not true. Well, all right. We can analyze the ratio of d over b for a variety of different newt sandwiches after class, perhaps.

OK. So this is pretty much the simplest model you can kind of possibly write down that captures this basic idea that when these two species interact, we're assuming that there's this mass action kind of rate. That it's just proportional to the number of the density of x and y.

Now I think that in the context of chemical reactions, this is going to be true over a huge range of densities, and perhaps almost even rigorously true if they are just single. There's just some x and y that bounce into each other. And at some rate they do something.

Whereas I think in the context of predator and prey, this is on much less firm footing. That's OK. So it's at least the simplest thing we can write down. And of course, then we'll have to ask, how is it that the conclusions of the model might vary depending on the assumptions that go in here.

One thing that we've spent a lot of time in this class doing is trying to look at a set of equations, and in words, be able to extract what the assumptions were that went into writing the equation. And associated with that, you can think about all these things about the nondimensionalized versions of these equations. You'll often see the predator/prey models written in some nondimensionalized version, where for example, you get rid of maybe the a and maybe the c.

I think that in many cases I prefer to just leave these terms in here, because that way we can immediately see what happens if we go hunting, or if we do this or that. OK. Can we try to figure out what-- there are four assumptions, at least, that have gone into this that are relevant and are worth saying.

Can you guys help me out? Yeah.

AUDIENCE: It's well-mixed. The interaction in terms of [INAUDIBLE].

PROFESSOR: OK. Right. So it's well-mixed. And there's two aspects that we might-- So one thing, it is certainly worth saying that it's well-mixed. But associated with that, you're going to say that it's because of x times y. Right?

Yeah. I guess that's what I feel you were about to say.

AUDIENCE: I mean, I guess.

PROFESSOR: Yeah. Right I guess. But I think we have to keep these things a little bit separate in the context of chemistry, those are maybe the same statements, right? Of course, we're writing these things. These are just quantities that are just functions of time. We have not included space explicitly. So in that sense, it's definitely a well-mixed model.

But just because we're assuming that it's well-mixed, we're not keeping track of the state of density as a function of position does not mean that they have to interact with this term. And for two molecules that are bouncing against each other, then I think that is the case. But we have to keep these assumptions separate.

AUDIENCE: You could imagine a colony of bacteria, for example, where they're all-- you can only prey on the outside.

PROFESSOR: Yeah. Necessary. I guess what I would say is that if it were not well-mixed, it could still be that they interact like this. And you just keep track of the predator/prey density as a function of position. And they could still interact in this way, possibly.

And in particular, in the context of Turing patterns, what we did is we allowed these things to vary as a function of position. But then we would have still typically written the interaction term as x times y. So it is true we're modeling this as a well-mixed population. But I think that's independent of this statement.

Do you agree or disagree? Or?

AUDIENCE: But if it's well-mixed, the encounter frequency will be proportional to [INAUDIBLE].

AUDIENCE: That's sort of the secret, right?

PROFESSOR: Yeah.

AUDIENCE: The assumption is the encounter frequency is proportionate, right?

PROFESSOR: Yeah. OK. So what I would say is-- well, certainly in the context of predators and prey, it could be that if the prey is full, then it's not going to be so simple. In a sense, is that I guess it could be more complicated than that is all.

But my statement--

AUDIENCE: So you're saying-- I'm sorry-- the interaction term would not necessarily be just a function of x times y.

PROFESSOR: That's right. It could be more complicated than that. And the other thing is that even if it were not well-mixed, in the context of these reaction diffusion models, we would typically say that the rate that these two things hit each other is x times y. But they're each a function of position. Right.

So it's not that there's-- it can either be well-mixed or not. And it can either be this or not. I guess.

AUDIENCE: But it's not quite the same variable, because in that case it would be the density, whereas--

PROFESSOR: I agree. Although here, it's not obvious whether we're talking about number or density, frankly. Right.

And we often talk about this as if it's the number of predator, number of prey. But then that's a little bit inconsistent with this in that if you were-- this should really be, if you're thinking about these terms being the product. And it should really be the density.

And if you're looking at the population size in some fixed area or volume, then it doesn't matter. But even in the context of predator or prey, I'd say that the way in which this would make senses is via densities. Does this discussion make sense? Maybe?

We are assuming it's well-mixed, because we're not thinking about these things as a function of position. But I would say that we cannot get that from just the interaction term. We are assuming it's well-mixed, though.

Other things that we've assumed here?

AUDIENCE: Something along the lines of the prey doesn't need the predator, for instance.

PROFESSOR: Right. The prey does not need the predator. And in particular, what happens to the prey in the absence of predator?

AUDIENCE: It grows.

PROFESSOR: So the prey grows exponentially.

AUDIENCE: Because it's not diet [INAUDIBLE].

PROFESSOR: Without predator. And the other thing that is perhaps worth mentioning in all this though is that this is a deterministic description of the world. So a here is telling us about-- the normal way that we would interpret a is it's the rate of division of the cells, or the rate of new deer being born, or whatnot.

But of course, a could actually be the difference between this growth rate and a death rate. So just because we don't have an explicit death rate doesn't mean that there's no death. So I think you can't actually say that the prey does not die in the absence of predator. What you can say is that the prey population-- we're assuming that a is greater than 0.

So what you can say is that the prey population grows exponentially without the predator at rate a. But this is really in principle the difference between the growth rate and the death rate of the prey in the absence of the predator. And in the context of a differential equation, this doesn't make any difference.

But if we were to go and do a master equation type formalism, would this make a difference? Yeah. Right. So this is the whole thing about the Fokker-Planck approach. And you can get different variances at equilibrium, depending on whether the rate of forward back reactions and so forth. Does that sound familiar to you guys? No.

What else have we assumed in this model?

AUDIENCE: The predator dies exponentially.

PROFESSOR: Right. So the predator dies exponentially when? So the predator dies exponentially without the prey. So it's a nice simple assumption.

Other things that you might like to point out about this?

AUDIENCE: A single predator is [INAUDIBLE].

PROFESSOR: OK. Right. So there is a sense that it's just x times y. So the most simple way to think about this is that it somehow is a single predator eating a single prey. There's maybe no group hunting type behavior.

So if we wanted to try to understand how a pack of wolves can bring down a buffalo, then you might not want to use this equation. So this is that the rate of predation is proportional-- we'll say goes as x times y. And that embodies many different kinds of assumptions. These are four findings.

OK. So since it's such a simple model, we can go ahead and we can just solve it. Right. How many fixed points are there going to be? Two. OK. It's always good to remember these things.

And so what we can think about, this as x. This is y. There's indeed going to be a fixed point somewhere in here. But then the other one is going to be at zero, zero. Because the top equation has x's everywhere. Bottom equation has y's everywhere. So indeed, there's going to be one fixed point at zero,zero. So-called the trivial fixed point.

Is this a stable, or is this an unstable fixed point? Let's think about this for a moment. And then we'll vote verbally. Stable or unstable? OK. Ready, three, two, one.

AUDIENCE: [INAUDIBLE]

PROFESSOR: So I think there were some disagreements there probably. It was a little hard to tell from the verbal. And one way that we can think about this as that we can ask, well, the predator in the absence of the prey, what happens to it? So it kind of comes down here. So along this axis it's stable.

However, in the absence of predator, if you think about the prey, that'll grow. So this is actually an unstable fixed point. Stable along one axis and unstable on the other. Incidentally, what does this tell us about the eigenvectors around this fixed point?

AUDIENCE: [INAUDIBLE]

PROFESSOR: That's right. The eigenvectors are really just 0, 1, 1, 0. Because you can see that if you start along one of these, you come straight down. Start along the other one, you come straight down.

And the other one we can just see by-- well, we can solve it directly. Just we pull out an x. It's when a minus by is equal to zero. And also when minus c plus dx is equal to zero. So the other fixed point, this x star, y star, and this is maybe the important one. It's going to be just c over d and a over b.

Super simple model. Right? You can calculate where the fixed points are kind of immediately. But it's actually a model that has many weird properties. Some of which you might think of as features. Some of which you might think of as bugs. But in particular, the location of this fixed point, I think, is really sort of surprising in that its dependence on this abcd.

This is part of why I really think that when analyzing this model, I very much prefer to keep the a's, b's, c's, d's, rather than using the nondimensionalized version of it. Because when you do that, you lose track of what's going on. So this model for example, makes very clear predictions of what should happen if you hunt the predator.

There are various contexts in which wildlife managers have been interested in trying to help a prey population. So if a prey population is suffering in some way, then you can reasonably think what you should want to do is kill the predator. And this is all these debates where you have the wildlife managers, where they buy automatic rifles in order to shoot wolves from helicopters.

We have a Canadian in the room, right? I mean, wasn't this a Canadian proposal?

AUDIENCE: I'm very American.

PROFESSOR: All right. We'll have to do some more research to figure out exactly. OK. Right.

So the question is, well, what happens at least in this model? And people apparently have seen this sort of thing occurring in natural populations as well, right? If you hunt the predator by going out and shooting them, what does this do to the predator and the prey populations.

In particular, we think about x star, y star. Well maybe this-- am I confused? Maybe this is the example that I'm confused by. Well we have to complete it now that I started it. But now I might have gone backwards. We'll see what happens, and then discuss.

All right. Ready. Three-- Oh wait. I don't have enough options. OK. Sorry. We should do one, then the other. Because sometimes things don't change, right? So how do I do this? OK. Sorry. OK. We should just do one, then the other, right?

No change. This is down. OK. There's gonna be a problem [INAUDIBLE]. Let's first do y star. Cause that's the most direct one. Sorry. I think that my story I got backwards. But we'll figure this out. OK. Ready?

OK. So the question is, there's a population that you want to-- all right. Now I'm going to redo my story to make it-- but there's a population you want to keep in check somehow. So you might reasonably go out and shoot it. Right? So the question is, if you go out and you do this on the predator, at least in this model, what happens?

All right. Ready. Three, two, one. Right. So although we actually have a fair number of disagreements on this. So we're actually kind of 50-50 at this stage.

What is it if you go out and from the helicopter, you start shooting this animal, what does that do from the standpoint of this model? Right. So we're shooting the predator. a, b, c, d, what you think? What should it change? c. And does c go up or go down? C goes up. OK.

Well, how does that affect y star?

AUDIENCE: [INAUDIBLE]

PROFESSOR: Yeah.

AUDIENCE: [INAUDIBLE]

PROFESSOR: Yeah. Right. You know, I mean, I'm thinking daily helicopter rides where you shoot wolves as you see them.

AUDIENCE: This is Canada.

PROFESSOR: This is Canada. This is Canada. Yeah, those Canadians.

AUDIENCE: So effectively, you're changing the death rate of-- that's what you're saying.

PROFESSOR: Well, OK. So that's my claim. Of course, all of these things can be more complicated. But it certainly is change in the death rate when you go and shoot them. So I guess I would say that in the context of this model, that's the simplest way to think about it.

So the statement is that if you hunt this predator, you're increasing the death rate for the predator. You're increasing c. Hunting predator. This causes c to go up.

And the striking thing is that y star does not change. OK.

AUDIENCE: I believe you. I think it's funny.

PROFESSOR: OK. [LAUGHS] You believe me. OK, I'm glad. One thing is believing me in the context of this model. Another thing is asking whether this is happening in real life. But I think people have seen such weird phenomenon in the context. But then of course, it's a matter of is this a dominant source? What's going on? Like many, many things. Right.

But certainly in this model, there's this weird phenomenon where the death rate of the predator does not alter this y star. OK. We have to figure out what the y star means here in a moment.

What is the effect on this fixed point number concentration of the prey? It goes up.

So my original story, I think I was getting confused.

So at least in this model there's a sense that if you hunt the predator, it's true that you don't bring down the steady state, or the time average-- we'll see-- time averaged number of the predator population. But you do increase the prey population. Because in this case you can help the prey. But you don't bring down the predator.

Now I want to say something more about justifying this thing about why we might care about x star and y star so much. So this thing is x star/y star. Well, maybe all. Yes.

AUDIENCE: As soon as you stop shooting, this is a very temporary solution. When you stop shooting, c goes back to its original value.

PROFESSOR: That's right. When you stop shooting, c goes back to its original model, or original value. And then the prey population will come back down. So this is something you have to continue to do.

Yes. What do I wanna say? If you go ahead and you calculate the-- if we linearize around this fixed point x star/y star, that's our standard thing that we did early on the semester, what we find is that this Jacobian, this matrix A, the linearized matrix you get is-- all right. Well, we come here and we take the derivative with respect to x.

So we get a minus by. Derivative of this guy up top with respect to y. And we get minus bx. And derivative of this g function with respect to x. We get dy. Now aspect to y, we have a minus c plus dx.

Now we want to evaluate this around that fixed point at x star/y star, which is given here. We plug this in. So evaluate at y star. It's a over b 0. Evaluate at x star. This is just minus bc over d. Now y star, this is ab over b. And here we can get 0.

So this is telling us about the linearized dynamics around a fixed point x star/y star. Now for this sort of matrix, what are the eigenvalues? It's not that the eigenvalues are 0. It's a slightly different statement.

What are the eigenvalues for a matrix like this? What's that?

AUDIENCE: They're imaginary.

PROFESSOR: Right. They're purely imaginary. So the real part is equal to zero. So indeed, we can figure out this. Cause remember, to figure out what the eigenvalues are, you take the determinant of this vector a minus this lambda times the identity matrix. So we end up with, we want to take the determinant of-- we have a minus lambda, a minus lambda, and then minus bc over d. This is lambda squared. And then this is a plus, we have bc over d, ab over b.

So we end up that the eigenvalues are equal to plus minus square root of a times ci. So they're purely imaginary eigenvalues. And what does this mean again? What can you say when you do this sort of analysis and you have purely imaginary eigenvalues?

AUDIENCE: The orbits look like ellipses or something like that.

PROFESSOR: Right. So the statement is that-- OK. And then we have to be careful in all of this business. So what we've done is we've taken a set of non-linear, a pair of non-linear differential equations. We've done the linear stability analysis. And we get purely imaginary.

So one thing that you can say is that if you started with a linear system, and you got purely imaginary eigenvalues, that would tell you that indeed, you have these neutrally stable orbits, they go around. They can have a variety of different shapes.

But given that the order that we did things in is that we took a nonlinear system, and we linearized, and then got this. What does that allow you to say? Does that prove that you actually have these neutrally stable [INAUDIBLE]?

Yeah. Because this is one of those border cases, it unfortunately does not actually allow you to say that you have neutrally stable orbits. Because it turns out that the slight nonlinearities in the equations could cause problems, and cause it to go either to a stable limit cycle or to a stable spiral. The confusing thing is that in this case it is true that you have neutrally stable orbits. But that did not have to be true.

And guys will get the chance to do this proof and so forth. Because there some conserved quantities. Of course, people have analyzed this thing in more depth. And it is true that you have neutrally stable orbits. But what is very hard to remember is that it didn't have to be the case just based on what we've said so far. Yeah.

AUDIENCE: So you mentioned, it's not a coincidence. There is a deeper reason why?

PROFESSOR: Well, coincidence. I guess what I'm saying is that you can prove that this thing does have these neutrally stable orbits. But we have not proven that. And we're not going to.

Do these orbits go around clockwise or counterclockwise? Ready. Three, two, one.

AUDIENCE: Counterclockwise.

PROFESSOR: Counterclockwise. Right. And you can get that from thinking about what predator and prey should do. But also I've already drawn some arrows here. And that kind of helps provide some guidance.

So they kind of come around like this. Now is this the only orbit that I should be drawing here? No. Right. Because it turns out that in this case there are an infinitely large number of orbits that could possibly come around.

Yes.

AUDIENCE: [INAUDIBLE]

PROFESSOR: Yeah. Well, in the context of our simulation, the simplest thing that you guys would probably do is you would simulate and see what comes around. But yeah. I think even in the reading, did they prove it? Different authors in different books either prove it or don't. And there are a number of different-- you'll see in the problems, you can find that there is a quantity that is conserved along the equations of motion.

But the quantity's different for each of these orbits. Right. So it's really saying that as you go, there's some quantities conserved. And it still has the same value when you go around. And so that means you had to kind of come back to where you were. So there is a conserved quantity. You'll see it.

Now these neutrally stable orbits are kind of funny in several ways. Well, first of all, this eigenvalue tells you about the period of the orbits when you're close to the fixed point. And you can see that it doesn't depend on everything in the model. It depends on a and c. Does that kind of make sense, maybe?

Yeah. Sort of. Cause a is telling us about how rapidly we grow up here. c is talking about how rapidly we die over here. So you know, it has something that at least has units of 1 over time.

It makes sense that a and c should appear here. But I would submit that it's not totally obvious that b and d should not appear at all.

So neutrally stable orbits, there's no characteristic amplitude to the oscillations, nor period. And this is at least true far from the fixed point. This tells you about maybe these orbits. But then it doesn't tell you about what happens far away.

And these are not the kind of oscillations that from a mathematical standpoint we like the most, which are limit cycles. And remember, a limit cycle would look like this. If it were a limit cycle, it would be that there's some orbit that is stable in the sense that if you start inside of it, then you would approach it over time. If you start outside of it, then again, you would approach it over time.

And this orbit then would have a characteristic amplitude, and a characteristic period, because it's one orbit. Whereas here, this has kind of an infinite number of different orbits. What this means is that just any sort of noise-- demographic fluctuations and so forth-- would cause the system to drift over time in terms of this amplitude of period.

So it's true that if you got it started in the absence of any noise, it would keep on doing that oscillation forever with that amplitude. But any random noise will cause the thing to drift.

The other thing that is worth stressing in this is that if you do a time average of the predator concentration, or the prey concentration, so if you do the average or the mean, x as a function of time, or y is a function of time is indeed x star y star. That's also something that you'd have to show. Not at all obvious from this.

It's not a surprise for these orbits that are out here that the time average is indeed x star /y star. But for these big orbits, they probably already didn't have to be. So this is telling us that the analysis that we were talking about-- well, what happens if you do one thing or another thing-- that's actually kind of a reasonable quantity to be trying to calculate, because that is the average or the mean number of predator/prey in this model.

Yes.

AUDIENCE: So in a zombie apocalypse, how do we thin down the zombie [INAUDIBLE].

PROFESSOR: Yes. That's a very important question. In the event of a zombie apocalypse, what do we have to do in order to thin out the zombie population? All right. Well, the zombie movies typically are not yet at equilibrium.

But certainly at equilibrium, what do you want to do? This is not a formal recommendation, by the way. But in this model, if you want to decrease the number of the predator, what is it that we want to do?

Right. Well, OK. So in this model, if you want to decrease the number of the zombies at equilibrium, you want to decrease a, which corresponds to--

AUDIENCE: So it's a is equal to 0. So the birth rate is equal to the death rate, then there aren't new zombies.

PROFESSOR: Yeah. There are probably also no people.

AUDIENCE: But there are. The birth rate is equal to the-- so you have a stable population.

PROFESSOR: Right. So in the limit, as a goes to 0, it's true that the number of zombies goes to 0.

AUDIENCE: So you just have to beat [INAUDIBLE].

PROFESSOR: Yes. This is a good situation where it's important to ask about whether your assumptions in the model are good before making public policy based on them. OK? Indeed.

But can we go back just for a moment before we switch gears, to ask about this question of why it was that war might have favored these predator fish? And by favored, what he really measured, he measured the number of the frequency of these kind of predator fish at the markets. So it's somehow is maybe the ratio of those two, or so.

Yeah. That's right. Yes, it could that the fisherman just-- yeah. So they could have fished in a different region. And so the explanation could be something--

AUDIENCE: Because it's not very well controlled.

PROFESSOR: It's not a controlled experiment. That's why you need to have many different wars in order to average the importance of large data.

AUDIENCE: That's going to be a great [INAUDIBLE].

PROFESSOR: Right. And then of course, in all this business you have to ask, well, which thing are you varying more or less, et cetera, et cetera. But let's say that to first order, the fishermen are going out there and they're just catching all the fish in an unbiased fashion. But the war is making it more difficult to fish. So not as many fishermen go out.

And then what does that do to these parameters? Right. So it might increase a, because the prey are not getting caught as much. And it might do something also to the predator. What?

So the predator fish are also being caught, cause they're showing up at the market.

Right. So which other parameters does it change? So what's that?

AUDIENCE: [INAUDIBLE]

PROFESSOR: Right. So lets be clear. It's a war makes a go down. All right. And what other parameter might change?

AUDIENCE: Fewer fishermen.

PROFESSOR: Oh. I'm sorry. I'm sorry. You're right. You're right. I was starting to think about the next one.

OK. So a goes up. And what also happens? And c goes down. And this is just because a is a growth rate. c is a death rate. So it's not that the fishermen are preferentially changing what they're doing between the prey fish and the predator fish, but it's just that these are defined different ways. Right?

And in particular, what this means is that in times of war, Voltaire's argument to his future son-in-law was that what you expect is that the predator population should go up. And the prey population should go down. So the ratio of them should certainly shift in favor of the predator.

Or maybe it's just that the fishermen didn't go into the deep regions of water or something, where predator fish like to hang out. But it's striking at least that a simple model like this can actually provide some insight.

Any questions about where we are before we modify the model in some way?

Now, the problem with this model is that it's making lots of assumptions that we very much think are not true. So we have a few of the assumptions up there.

Which ones are you guys least happy about among those assumptions? Yeah. The second one, the prey grows exponentially, i.e., without bound. That's not physical. We should fix that.

So let's go ahead and do that. All right. So real prey populations-- and all populations-- populations saturate. Don't go to infinity, right. We can just make a quick little fix to our model to capture this, right? X dot. So now it's going to be this ax. But what we can do is we can add a logistic term here. And we can leave everything else constant.

So we just add this logistic row term. So now in the absence of a predator, what will happen is that the prey population saturates at some point, at some value k. Right? And k could be rather large, if you like.

And I think this is the kind of situation where you say, oh well, that could be just a really modest change. Because it's primarily telling us about what happens kind of in the absence of the predator. But really, the dynamics around here could be unchanged.

But what's striking is that because of this neutral stability of the model, any little change can lead to a qualitative change in the outcome at equilibrium. And in particular, adding a carrying capacity causes the sustained oscillations to disappear. Instead you get damped oscillations.

So in this case, xy, you still have this fixed point. But what happens is that you get-- it orbits the look. Kind of like this. Yes.

AUDIENCE: [INAUDIBLE].

PROFESSOR: Yeah OK. So that depends upon [INAUDIBLE]. And indeed, as k goes to infinity, the timescale of this decay goes to infinity as well.

AUDIENCE: [INAUDIBLE] clean scaling.

PROFESSOR: A clean scaling.

AUDIENCE: But I mean just [INAUDIBLE].

PROFESSOR: I mean, I don't have nothing intelligent to say. But what I can say is that if you put in a k at values that are close to this fixed point, then the oscillations really disappear.

It's really only as k goes way, way out.

And I maybe won't do this calculation. But you can do it quickly. It's the kind of thing you can do in five minutes on an exam or so, right? But then the question you might ask me, well what can you do in order to get these oscillations that we really like? These sustained limit cycle oscillations?

And there are two ways you can think about this. One is by a kind of taking this sort of model and adding features and playing with it and so forth. Or you can ask a mathematician who kind of derives everything in kind of totality. And then you can see it. I'll say that one thing you can do on a concrete basis to change the outcome of this is you can add something that is kind of like some saturation effect at the level of the interaction between predator and prey.

So instead of scaling purely as x times y, if instead there some sort of Michaelis-Menten type behavior as a function of the prey, then this model is actually converted to one that has a stable limit cycle. And in this case, can you guys remember how you show that something has a stable limit cycle?

Yes.

AUDIENCE: [INAUDIBLE] use the Poincare--

PROFESSOR: That's right. There's this Poincare-Bendixson theorem, which tells us that if we can draw some box out here where the trajectories are all kind of coming in, indeed, here the trajectories are kind of coming in. Now in this case the trajectories have to come in everywhere. But this is typically true in any of these reasonable systems. Because they should, if there's just not that much food, they should be coming in.

Now in this case, there's a single fixed point. So then the question of whether there's a limit cycle is equivalent to the question of the stability of this interior fixed point. It's a stable fixed point, then all of these trajectories will spiral in. However, if it's an unstable fixed point, then you have to have a limit cycle oscillation somewhere in between.

Yes.

AUDIENCE: It could be that it's a stable midpoint. And then you have two limit cycles. Could that be?

PROFESSOR: Right. So the question is whether there can be a stable limit cycle and two limit cycles. I think that that requires more fixed points. Because let's say you had a limit cycle here. That this is saying that the trajectories come in. But it's also saying the trajectories are coming out.

I think that you have to have a fixed point inside here in order to have these trajectories going--

AUDIENCE: So what I'm saying [INAUDIBLE] two circles, and way outside, all the trajectory is [INAUDIBLE]. But between the two circles, the trajectories go from the outer circle to the inner circle. And then from the inner circle in [INAUDIBLE].

PROFESSOR: Are the circles encircling each other?

AUDIENCE: Yeah.

PROFESSOR: OK. So here's one circle. Here's another circle. And the trajectories are coming into this one and what are they doing?

AUDIENCE: So each of these limit cycles are only semi-stable. There are some--

PROFESSOR: Yeah. All right. All right. So you're talking about these limit cycles where the trajectories come to it from one side, but then leave from the other side. I'd have to think about this more. Everything that I'm talking about are the limit cycles that are stable from both sides. And I think that in the presence of any amount of noise, those are the only ones that we care about.

Because you can write these models where you have orbits that are stable from one side but not the other. But then they don't matter in any real system that is subject to noise. Because it's not a stable orbit in that case, right?

AUDIENCE: Then we can make the outer circle stable from both sides, and the inner circle [INAUDIBLE] from both sides, and we could get it [INAUDIBLE].

PROFESSOR: OK So it could go like this. So you're saying that this outer orbit is now stable from both sides. And then this one is unstable from here. And oh, OK. Now you're saying this thing is unstable from-- so now it's stable.

AUDIENCE: So we can have--

PROFESSOR: Yes. OK. So I can certainly draw the trajectories, as you pointed out. And it works. Yeah. I don't know if this is a loophole in the wording of the theorem, or if this is just not possible.

AUDIENCE: [INAUDIBLE] There's like one way in which it applies. And then the other way you kind of usually think that it applies, but then you're wrong because there are these counter examples.

PROFESSOR: I see. Well, how about this. I will look it up. And then I will tell you what I think the answer is. I'm certainly not going to be able to derive it on the spot.

But You're right, though. I can draw the orbits and they do it. I don't know what that means.

AUDIENCE: So I think the theorem is if on this large circle on the outside everything is coming in, then if your fixed point is unstable, then you must have at least one stable [INAUDIBLE] outside. Or you must have at least one that is [INAUDIBLE] or something like that.

PROFESSOR: OK. But you're saying that it--

AUDIENCE: But if you flip it so the fixed point is stable, then you could have--

PROFESSOR: I see. That may be right. I can't remember which direction. But I'll look it up.

But if you are curious about the situations in which these predator/prey functions will have limit cycles, you can look up Kolmogorov's conditions. So he basically has these four conditions in which you will get a stable limit cycle in the predator/prey populations. And maybe I will.

And they're surprisingly simple. They were in the reading. So you can look at them. But they're basically just these questions of the derivatives. And they're derivatives of the per capita growth rates.

So you take those functions, you divide by x. So it's x dot over x. And then it's some f, y dot over y, sub g. And the derivatives of those functions withe respect to x and y have to be something, at least in some limits. And then you get limit cycles.

But I want to talk about the experiments. Because I think that they were quite pretty. So this is a paper by Yoshida, et al.

This is *Nature* 2003. And the title was "Rapid Evolution Drives Ecological Dynamics in a Predator/ Prey System." Could somebody kind of say what they think is the big point of this paper?

Do you guys like the paper, dislike the paper? Too long? Was it three pages? Although it's really only-- I mean, one of the pages is figures. And one of the pages is essentially methods. So it's really basically a one-page paper, so it's not such heavy lifting, maybe.

All right. Maybe I'll be concrete. What features of their predator/prey oscillations were different from a normal predator/prey oscillation? What were the features they were trying to explain?

AUDIENCE: There's a longer phase life between the maximum.

PROFESSOR: And this is an interesting history, actually, that these are authors-- they took what I think are basically like samples from the Great Lakes, or something like that. So they took a predator and prey. So it's a rotifer algal system. So the rotifer eats algae.

They had previously published a paper just a few years before, where it was called something like "Crossing the Hopf Bifurcation in a Predator/Prey System." And so what they did is they had a chemostat where there was some constant rate of dilution in their chemostat. And then they measured the dynamics between the predator and the prey.

And they showed that depending upon, for example, the nutrients or this dilution rate in their chemostat, they could go from a situation where you have a stable coexistence-- so a stable fixed point between the predator/prey-- but at increasing dilution rate, they started getting these oscillations.

So they went from stable to oscillations. And then at higher dilution rates, they got collapse of this predator/prey system. So this is crossing the so-called Hopf bifurcation, where you go from stable to unstable. So they could actually see that they could use a simple model to try to get some insight into why it is that a predator/prey system might oscillate or it might not oscillate.

And so that was great. But there were some features in their data that they didn't understand. So the features were that the oscillations had a really long period. Long period oscillations.

And in all this data, it's a little bit hard to get the exact phase lag, but in many of the cases they saw that the predator and prey were not at this 90 degrees out of phase like you would expect. And in particular, for the predator/prey, given that you have x and y, and it's going around some circle, the idea is that first the prey population peaks. And then kind of 90 degrees later phase, you get a peak of the predator.

And you can imagine that in any predator/prey model that you write down, not just Lotka-Volterra, but if you write down a differential equation with some x and some y, it's hard to get something where it looks much different. Of course, you can imagine maybe funny orbits or something like that. But generically you really expect this 90 degree phase lag of the predator relative to the prey.

Whereas in the experiments, they often saw 180 degree lag, lack of predator relative to the prey. Yes.

AUDIENCE: So when you say [INAUDIBLE] theory of oscillation, what does that mean? What's the time scale?

PROFESSOR: Yeah.

AUDIENCE: What would make this suprisingly [INAUDIBLE]?

PROFESSOR: Right. Yeah. OK. So this is really in the context of-- I mean, they wrote down a model where they did basically have something like this, where they said there's some--

AUDIENCE: [INAUDIBLE]

PROFESSOR: That's right. And in particular the predator, I think, was not really dying on it's own. Except for the dilution. So it's really the dilution rate from the chemostat gave them c. And they could see that indeed, the rotifer wasn't dying much.

And then a is telling you about what happens if you don't have the rotifer, you don't have the predator. And then at that dilution rate, you ask what the division rate is. And that's essentially the growth rate of that prey population minus the dilution rate of the chemostat. I'd say that they had these parameters pretty well.

Yes. And what they saw experimentally was that it took much longer. I mean, the period was 5 times, 10 times longer than what they would have expected based on the measured parameters for the predator and the prey. And of course, that was annoying for them, because they're actually doing the experiments. So they had to do these chemostat experiments that lasted six months or something like that, in order to see a couple oscillations.

And so this longer period wasn't just a mathematical-- I'm sure that they were disappointed to see these really long time-scale oscillations, because it was something that made it very difficult for them to do the measurements. But this is what they saw experimentally. And they didn't know what was causing it.

But they later then did more modeling where they asked, which of the assumptions in our original model might not be true. And the nature of these things is that there are an infinite number of things are true that are not incorporated in the model. And this makes it quite challenging to isolate what the effects might be.

But at the very least what they can do is they can go in. And they have some sense of their system. And they can make guesses of what might have been the primary things missing. And then they kind of went through the models and they asked, well, if we kind of change this assumption or that assumption, what does it do in terms of the oscillations.

And then what they found in a modeling paper-- so this is their previous experimental paper before this. What they found in their models was that prey evolution was kind of the one thing that if they allowed prey evolution, i.e. If they allowed different types of prey in their prey population that might be oscillating independently, then they could get both of these effects.

So from the models they concluded that prey evolution could give this, could maybe explain those two things. These are the two experimental features. Yeah.

AUDIENCE: It might be that you have [INAUDIBLE] symantic point. If you have two types of species, pre-species-- [INAUDIBLE] they have these characteristics and they're not evolving. They're just fixed.

PROFESSOR: Yes.

AUDIENCE: You would still be able to--

PROFESSOR: Exactly. Right. This is a major--

AUDIENCE: [INAUDIBLE]

PROFESSOR: Yes. You can argue about what you want to call evolution and not revolution. Over these time scales what they are not looking at is the de novo kind of emergence of new mutants spreading in the population. What they're looking at is variations in say, different types of prey.

AUDIENCE: So is that what we would call evolution?

PROFESSOR: Well, OK. This is a major question. I think different people call evolution different things. And in particular there's a distinction between the ecologists and the evolutionary biologists, or evolutionary microbiologists, or whatnot. And this is something that I certainly encounter.

For the experimental microbial evolution guys, I'd say that for them, if you use the word "evolution," what they really want to see, or what they're expecting to see is kind of new mutants arising in the population, spreading, fixing, and that changes the character of the population.

Whereas from that standpoint of ecologists-- and indeed, if you look up the definition of evolution, it's some change in allele frequency over time. And this could certainly be a change allele frequency over time in the sense that you could imagine this arising just from, for example, there could be a point mutation in some gene that leads it to do something or another.

And in this paper they didn't identify exactly what was going on. I'll tell you a little bit about a later paper where they get a better sense of it. But at least you could imagine it being the case that there's just a point mutation, some gene that has some fitness defect in the absence of the predator, but then allows the algae to avoid the predator in some way.

AUDIENCE: [INAUDIBLE]

PROFESSOR: That's right. That's right. As far as the model goes, it could be that the prey are really-- one species was just a point mutation. Then you'd say, oh yeah. That's kind of evolution. Or it could be two different prey populations and so forth. Right?

And depending upon what information you have access to, you would either be aware of these things or not. In this case, they just look under the microscope and say, oh yeah, this looks like an algae, or whatnot. And maybe they know that it's the same species. But they could be different in lots of different ways.

And I think this discussion is highlighting that a lot of the same effects that you see in ecology also you see in evolution and vice versa. And depending upon your focus, you might want to put it more in the bin of evolution or in terms of population dynamics. I think that's a matter of taste at some point, actually.

Yeah. Because they say rapid evolution. And I think--

AUDIENCE: [INAUDIBLE].

PROFESSOR: Yeah, right. So I think that different people will have different takes on this. I think, once again, this is really very much from the standpoint of an ecologist, this is rapid evolution. Because every cycle, the allele frequency is changing. And that's what's maybe leading to this.

But the thing is, it's very easy for you to read certainly the title, and come away thinking it's something different from what it was. I agree.

But one of the things I like about this whole line of research that took place over the course of say, 15 years, was that they did these nice measurements. They're guided by models. They saw some things that they were expecting, some things they couldn't explain.

And then they went and did more modeling. And then they could explain it. And that guided this experiment. Because before what they did is they just took kind of the sludge, or whatever, from the lake. So there were many different types of algae and of the rotifer, for that matter. And then they looked at the predator/prey oscillations between those.

And then in this paper what they did is they took individual prey populations that came from a single prey. So they were kind of isogenic. Of course eventually they would evolve, and blah, blah, blah. But in this case they took individual isolates from the prey. And then what they saw is that these two features went away.

The oscillation period was more what they were expecting. And they got the 90 degree phase lag. So it's was really a case of these models led to the experiments where they took kind of clonal prey. And then they recovered their classical predictions.

And indeed, they've recently done some other measurements that I think were quite nice. They had an ecology letters paper just a couple years ago where what they did is they took two different algae that had different types embodying these trade-offs that we were talking about. In particular, one of the algae can divide rapidly. But it kind of exists as singles.

Another algae is kind of clumpy. So this algal type was able to divide more rapidly than this algal type. But this type was harder to eat just because it was clumpy. OK?

It's one of things that once you hear it, you say, oh yeah. Sure. But then in the abstract, when you read this 2003 paper, you think, oh, I can't imagine what kind of behavior could possibly help the algae avoid these rotifers.

But then in this ecology letters paper, what they did is they actually tracked population densities of this type, this type, and of the rotifer over time. So then they could see all three sub-populations oscillating. So then you can really kind of see how this evolution, if you want, or you could just say it's ecology. Because it could be different species for all we care.

But in any case, it's certainly prey heterogeneity anyway you look at it. Whether it's evolution or ecology. It's heterogeneity in the prey population that leads to these very qualitatively different population oscillations. Any other questions on that before we--

And so just for the last few minutes I'll say something about this question of noise-induced oscillations. This is going to be something you're going to be playing with over the next week. So you'll be experts eventually.

And the discussion in the homework is really guided by this paper by McKane and Newman. All right. So McKane. Newman. McKane is a professor at Manchester.

And what they showed is that if you take this model here, did this model have limit cycle oscillations, sustained oscillations? No. So this model where we include the carrying capacity of the prey, this does not have sustained oscillations. So you take a model like this that just has a stable spiral. Now this is a model in the context of-- it's a differential equation model.

Now the question is, how do you incorporate noise? Just the fact that individuals give birth, they die at random times. The first order way that we often think to do this is we just add some noise on to the differential equations.

So what we do is, you might say, oh well, you could add some a to x, and some a to y. Maybe this noise should be proportional to x or something. So you could think about the strength of this might be some pre-factor. So you could just take kind of a [INAUDIBLE] approach where you add noise onto the differential equations. And then what you get is a noisy kind of path to that fixed point.

The perhaps surprising thing is that instead of adding noise to a differential equation, if instead you start with the individual based approach, and you take kind of a master equation approach where you say they're individuals and they're doing something. Individual predators are eating individual prey, et cetera.

So if instead you take a master equation, just like what we did for the chemical equations modeling the cells and so forth that we talked about at the beginning of the class, if you formulate this predator/prey system as an underlying set of kind of individual based interactions, then what you actually find is that you get surprisingly large sustained oscillations. So you really end up with a situation where this thing comes. And it's noisy, of course. But it kind of comes around here in some way that looks like this.

And you'll see this in your simulations next week where-- and I don't know if you can see this at all. But this is some plots of predator and prey at reasonably large numbers, where you can actually have 1,000 predator or prey. Somehow you can get some sort of resonant enhancement of these oscillations.

And kind of what's going on is that the demographic fluctuations of the demographic noise excites the system at all frequencies. But then there is a characteristic frequency given basically by this frequency of the inherent oscillation there that is somehow amplified. So you end up with a situation where you get these oscillations. And they're noisy and whatnot. But it's really because it's this particular frequency that was amplified. And just because it takes a long time for those oscillations to go away.

So you can imagine that the amplitude of the oscillation falls off as kind of a root end scaling, because it's kind of a demographic type noise. So it is true that the relative amplitude of these oscillations, it gets larger as you to smaller population sizes. But it still ends up being a surprisingly large effect.

And you'll see how this plays out in this model that's basically guided by this paper. And this was a PRL in 2005. Incidentally, other people have since studied how these sorts of ideas can result in noise-induced pattern formation, as well. All right, with that, I will let you guys go. Have a good Thanksgiving. I'll see you guys on Tuesday.