Lecture 8 Predator-prey interactions

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In this session we will be talking about species interactions and we will be looking at predation and herbivory.

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Learning Outcomes for the session, we will be looking at the interactions between predator and prey. Illustrated by the snowshoe hare and the lynx, we will be looking at their population fluctuations using simple Lotka Volterra predator prey models.

We will understand the choices in designing experiments looking at these population dynamics.

And then we will move on to the differences between generalist, specialist feeders herbivores.

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So today we are looking at predation when one animal eats another. We will also be looking at herbivory, where one animal eats a plant.

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So a predator is an animal that kills another animal for food. Prey is the animal that is killed and eaten by the predator. Predation is quite underdeveloped in terms of ecological theory and the models to describe and predict predator prey dynamics are quite underdeveloped. They are still based on Lotka Volterra models and have many assumptions.

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At a simple level, we can understand how predator and prey numbers are closely related. Here I have put the cycle of predator prey dynamics. In the first circle predators eat the prey. This means that prey numbers are reduced. Eventually they are reduced to such an extent that the predators go hungry. This means that the predator numbers reduce because they either die, their birth rate is reduced or they leave the area and search of other prey. When this pressure is reduced the prey begin to increase again. This means that after a short time called a lag time the predators will increase as well. Then we begin the cycle again.

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One of the clearest examples of predator prey population dynamics is the lynx and the snowshoe hare. This pattern was noticed by trappers who hunted the lynx for fur in northern Canada. The snowshoe hare is the main food supply for the lynx. While it may prey also on small rodents, the hare is the best prey for the lynx to meet its nutritional needs. Therefore, the two populations are very tightly linked. It could be that the relationships between predators and prey are stronger at high latitudes because food is very scarce for both the predator and prey. This is because the winter is very long and so vegetation becomes in very short supply.

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Here we can see the population dynamics of the lynx and the snowshoe hare over time. You see that while there are many more hares than lynx- if you look at the x axis for the hares on the left represented in thousands and lynx on the right, also represented in thousands- the patterns are remarkably similar. What is also apparent is that there is a lag time where the lynx population catches up to the hare. The hare populations cycle between eight and 11 years

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When hares are abundant lynx will prefer to eat them over other prey like voles. Hares increased in number and can reach a population density of up to 1500 per kilometer squared. This is far higher than carrying capacity. Then the food will start to run out and they will be easier for lynx to find. So the population will rapidly decline. The lynx will also start to go hungry and they will either begin to starve as well, or they will move away in search of prey. Eventually the vegetation will recover and the hares will begin to increase in number again.

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There are three types of response of the predator prey dynamics.

The first type is type one where as prey increase, the rate at which they are killed also increases. This is a linear response. It is a straight line. This response type is used in the Lotka Volterra predator prey model, which we will talk about shortly.

Type two is where the functional response is characterized by a slowing intake rate. It assumes that the predator is limited by its ability to catch prey. For example, at high densities of prey, the predators catch enough prey and are satisfied. There are too many prey for the number of predators. So the time the predator takes to find and catch prey is reduced and less energy is used.

Type three has a sigmoid, or S shaped curve. This response is similar to type two at high levels of prey density, where the curve flattens off because the predators don't need to catch any more prey. But at low levels it is more like type one. The point where I have marked prey switching is where a change happens in the hunting technique of the predator. It may mean that it changes its prey choice to different and more abundant prey. It may also mean that the predator is learning more effective ways to hunt for prey and so hunting time is reduced. The section of the graph is actually purely based in theory and has no mathematical equation to underpin it.

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Here we will talk about the other type of Lotka Volterra models from competition. This one considers predator and prey. It is based on the type one functional response. There are three main assumptions of the model.

Number one, if there are no predators prey will increase in number exponentially. This means that carrying capacity is not included in the model as a term.

Number two, the rate of predation, which is the number of kills by the predator over time is directly proportional to the product of the predator and prey abundances. This means that the more predators and prey in an area, the higher the chance of random encounters and kills.

Number three, the numbers of predators increase as numbers of prey increase.

Please bear in mind that for this model, we are considering one species of predator taken one species of prey.

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Now this is a simple equation for the prey model. The prey model looks at the rate of change of the prey population over time, which is dR/dt. The prey model includes the growth rate of the prey multiplied by its population size, but there is predation, so the amount of prey eaten must be removed or subtracted from this total. We assume that population size of predators and the population size of the prey are related and that the probability that they will meet increases, if there are more of both in an area. The probability is proportional to the population sizes. This probability will dictate the reduction in prey population, but it won't catch the prey every time. So we need to include capture efficiency or c in this model.

Now the predator model. The rate of change of the predator model shows that this time we include the rate of change of the predator. So you see that cRP has been brought down from the prey model.

So this time, we've included the rate of change of the predator, it will grow in size depending on how much it meets the prey. The rate of increase of predators is proportional to the amount of prey that they meet. The effect on the prey is larger than the effect on the predator. To the predator, it is one meal. To the prey, it is its life. Therefore, the term on the left of the model is the reproduction rate of the predator, which is assumed to be based on rate of food consumption, and the efficiency of the predator at turning this food into offspring. So if there are no prey the predators will start to die which is why we have a mortality rate m. The reason we have different constants included here is because while one predator may eat one prey, one prey does not mean that the predator will produce one more predator. Therefore, the rates of change for prey predator are different. However, the two populations are very tightly linked and they increase and decrease together.

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If the population growth of the prey is zero, what is the predator population? To solve for the predator population size p, we see that to get zero R must be equal to cRP. Now in algebra, you must multiply or divide the same time on both sides of the equal sign. So to get the predator population size on its own, we divide cRP by both sides. This means it disappears from the left of the model, and appears on the right as the denominator, the bottom of the fraction. We can cancel R on the top and bottom and end with P equals R over c. We are left with the predator population size as the growth rate of prey divided by the capture efficiency of predators. This does not depend on the prey population size.

The isocline in this graph shows the P is constant. If the number of predators is below this line, then prey will increase. Prey can reproduce faster than the speed that the predators can eat them. If it is above, the prey will be reduced. This is a prey zero growth isocline.

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This is different from the competition model because the change in prey population occurs at any abundance of prey. The change in prey population is completely dependent on the number of predators. So it all depends on the number of predators.

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So what about the predator part of the equation? As for the competition model we keep the axes on the graph, the same. The isocline, as you can see, is now vertical. We are solving for R this time, which is the prey abundance, the algebra is very similar. Now the predator isocline is m/fc. If the prey abundance is below the predators Isocline, the predator population will decrease. There is not enough prey to replace the ones that are dying. If the prey abundance is below the predators isocline, the prey predator population will increase. There are lots of prey. The model indicates that the prototype populations birth rate as predicted by the amount of prey eaten is higher than the mortality or death rate.

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Now, as before, we need to consider both graphs in one. We know that the predator and prey cycles are very tightly linked and so we cannot look at the isoclines independently and hope to predict predator or prey abundances. If we have high predators and low prey as this dot shows we would find decreasing predators and decreasing prey. There is not enough available prey, but lots of predators. So both will begin to die out. If we have low predators and low prey, prey will begin to recover. The predators will take a little bit longer as there's a lag time for the increase in prey to affect birth rate and mortality of the predators. After some time, the increase in prey will result in an increase in predators with a higher birth rate than death rate. Now in this bottom right corner there is enough food. Finally, the predators will increase enough that they affect the prey numbers and the prey numbers will begin to decrease again. This is a cycle that results in the population oscillations or fluctuations seen with the lynx and snowshoe hare in this graph.

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In this figure we put together the cycle from the previous slide. There is one cycle of both predator and prey. So we see in the first part of this diagram that the prey population increases, then, so does the predator population. In the second part of the cycle, the increase in predation means that the prey population then declines. The third section shows that because the prey are becoming fewer the predators, then also decline. Finally, the prey can increase again with fewer predators.

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There are some more points to make about this model. The assumptions made mean that it is very oversimplified, the main assumption is that if this one prey species is gone, the predators will have fewer births and die more rapidly. So they cannot switch prey to a different one.

It also assumes that predators can kill and eat unlimited numbers of prey and that they will never get full. As long as there is a prey individual the predator will attempt to capture it.

Finally, it's assumes that the environment has no complexity. So it seems that the model will be true all year round. There are no seasons and that there are no features of the habitat that could create advantages or disadvantages. It also assumes that the prey species has unlimited food.

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Now the lynx and the snowshoe hare cycles are a very well-known example of predator prey cycles and many people have worked on them. I'm going to explain now how a research team looked deeper into one of the assumptions of the model. The Lotka Volterra model made a number of assumptions.

So Krebs and his team in Canada, were interested to find out what the true reason for the hare population cycle was. What made it fluctuate like that. Was it that when they reached high densities, they run out of food? Or was it because the lynx would eat so many hares that it reduced the population?

This is a nice example of experimental design and I will share the paper because I think that the methods here are useful for you to consider in the future.

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The hypotheses for this study were based on assumptions of the Lotka Volterra model. You see that a hypothesis as a statement that it could be proved or disproved. You make a statement, based on your knowledge, and then you test whether it is in fact the case. So going forward, this is a good starting point for experimental design and ecology. If you look for the assumptions of a model or a concept, you can then test them.

The first hypothesis is that the hare will increase in population and eat all the food. Remember that this is in Canada. It has a long cold winter with thick snow. The plant growing season is very short. The hares eat all the vegetation when they are in higher densities and then they start to starve.

This is the first potential reason for hare decline.

One good way to find out how strong an effect on something is to remove the problem and then you test the size of the effect.

The second hypothesis is that the predators can kill almost all of the hares.

So this is a very elegant experiment because it is actually quite simple. It asks quite simple questions, and it gets a very clear result. Over eight years they added fertilizer and extra food to certain areas in the hares habitat, and other areas they put up fences. These fences allowed in hares but no lynx. This is to prevent the food, the lynx from killing the hares in these areas. And then in some areas they did both to see if there was a combined effect or interaction.

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This is a schematic diagram showing the design of the experiment. So if we think of this as a forest. We can see where the areas for each of these experimental treatments has been placed. There are some things to notice that I want you to take home about this design and I've just noticed that it should say one kilometer by one kilometer plots, not one meter by meter.

So the first thing to notice is that there is a control. Actually, there are three controls, you must have an unmanipulated control in any experiment where you have a manipulation treatment, it is vital that you have a comparison. That is the same in every way as your treatment, apart from the manipulation.

Then you can use statistics to be confident that you see an effect.

The second thing to note is that these treatments are randomly distributed through the forest. This is important because you need to make sure that there is no effect of features of the landscape like a slope or something that changes the animal's behaviour. The results of your study should hopefully represent the whole area you are testing if possible.

And that brings me on to the third important thing and that has replication. In this study, we have three controls and two each of all the other treatments. We have two food additions, two lynx removal and two where food is added and lynx are removed. This is actually not enough. We recommend that at least four of each type of treatment is used. There are a number of reasons for this. But the main reason is that if one of your samples has some odd numbers, some strange effect, for some reason, you will have enough other samples to be able to discard the strange one. Unfortunately, in the case of this experiment money, time and effort mean that you can't always design a perfect experiment. Here in this experiment, the maintenance of the fences to keep the lynx out was so much work that any more than the two of each treatment would have been impossible.

So this experiment took place in a spruce forest and Canada for eight years. These treatments were maintained every single day. They counted the hares using the mark we capture method we talked about in a previous lecture.

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So Krebs and his colleagues found some interesting results. I put the hypotheses here again as a reminder. Remember that we said that when hares are at peak density food becomes limiting and that prediction increases, but that we did not know which was stronger as an effect. After eight years of these experimental treatments the hares were counted in each area so Krebs could calculate the density. The lynx and snowshoe hare cycle was eight to 11 years long. So the experiment needed to be a minimum of eight years in order to capture the entire cycle.

In order to simply express the results, the density of hares were normalized against the control. So if the control was set to one, then all of the other treatments are adjusted accordingly.

The removal of predators meant that the relative hare density was two. So removing lynx meant that hare populations doubled. This is a strong result, lynx are definitely reducing hares. Then we look at food addition. If you add food and fertilize the existing plants, you get three times as many hares. This means food is a bigger reason for hares to die, than the lynxes.

But what happens in the plots where food was added and lynxes were also removed? You may expect that the effect of food and lynx could be added together and you would get five times the number of hares- two plus three. But when Krebs looked at the numbers there were 11 times more hares in the plots with two treatments than with one. This is a synergistic effect. If the effect of two treatments combined is bigger than the effects individually, we must understand that they impact each other to increase the effect. A likely explanation is that food shortages make the hares slow and easy to catch, thus increasing the predation effect on the overall death rate. So when these problems are removed, you get 11 times more hares in an area. In statistics this is called an interaction effect.

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There are lots of examples of how top predators control numbers of food webs. Sea otters are a good example. They eat sea urchins, which you can see in this photo. The sea urchins eat kelp, which is a type of seaweed. They make vast forests underwater. If nothing eats the urchins, they can remove the kelp forest entirely. It is argued that in some ecosystems predation has a stronger effect on population numbers than competition can. It is also widely found that an introduced predator has disproportionate effects on a system because the native species are not expecting it and have no defence. It is particularly seen in freshwater ecosystems, such as rivers.

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We are now going to move on to talk about herbivory. We are moving from animals eating animals to animals eating plants. The broad definition is the consumption of the whole or part of a living plant. A subset of this are seed predators who only eat seeds, also known as granivores. There are also organisms that only eat fruit and they are known as frugivores. These herbivores have large effects on the reproductive successes of the plants. Organisms feeding choices can be divided into generalist and specialist. Generalist is where they will feed from a wide range of plant types and specialist is where they will tend to feed on one plant species.

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One key point is that plants co-evolve with herbivores. Plants evolve to survive or prevent being eaten, while herbivores evolve strategies to get enough nutrition from well defended plans.

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There are two types of mammal herbivore. Those that graze, which is to consume and plant parts near the substrate. In the case of this Impala on the left, the substrate is the soil. In freshwater snails are grazers on algae. Browsing is where the herbivore consumes plant parts that are high above the substrate usually trees and we can see very tall animals that have grown to be able to reach the high up parts of the plant.

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Here we can see the effects of browsing animals on the tree line. Therefore, the trees will put a lot of their growing energy into putting their leaves and their reproductive parts, very high. This is known as an arms race. So the animals will keep growing taller and so will trees.

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However, this does not always work.

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One of the main reasons that grasses are so successful globally is because their main growing point is just below the soil surface. The main growing point is called the meristem and this is where the cell division occurs, it produces new leaves and flowers above ground and roots below ground. New growth is often nutrient rich tasty and poorly defended against herbivores, so naturally they prefer it. Grasses have evolved so that their meristem is below the soil surface so it cannot be grazed so easily.

This means that the grass plant can always grow more leaves. This is one reason for the enormous global success of grasses.

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We have talked briefly about plant defences before. Unfortunately, it is beyond the scope of this of the course to go into too much detail, although I can recommend reading. If anyone is interested. Plant defences fall into four categories: mechanical such as thorns, chemical such as nicotine, which is a strong insecticide, developmental or phenological, so they can adjust the timing of their life cycle events.

It comes down to avoiding or tolerating herbivory which is similar to the stress response.

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In summary, predator and prey ecological interactions are often dramatic and very conspicuous, so very easy to see. Models can help identify factors that stabilize and destabilize these interactions, but they are still quite simple and cannot account for a number of complex variables.

The importance of predators in nature is being observed by many, and they have supported these assertions by experiments looking at a range of different aspects of predator and prey interactions.

Finally herbivory can result in an arms race between the herbivore, and the plant. Plants tend to employ either avoidance or tolerance strategies. And co evolution between plants and herbivores continues all the time.

Reading

Chapter 9 & 10 Begon

Krebs paper

Discussion topic for Thursday

1. How does competition and herbivory affect plant communities?

2. Is coexistence real? How do species interactions affect the ability of a species to exist with others?

3. How are ideas and knowledge about species interactions relevant to people?