Basic Course in Ornithology
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Nature Conservation Foundation

Lecture -10
Foraging Behaviour

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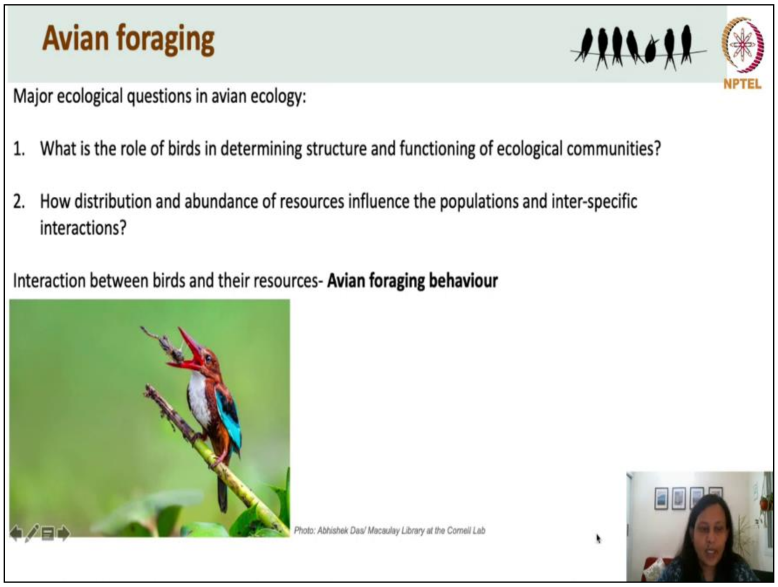

Hello, welcome to basic course in ornithology. In today's lecture, I shall be addressing various aspects related to avian foraging behaviour. A major goal of avian ecological research is to determine both the role of birds in determining structure and functioning of ecological communities and how the distribution and abundance of resources in those communities influence dynamics of populations and interactions among species. This interaction between the resources and the birds is mediated through their foraging behaviour.

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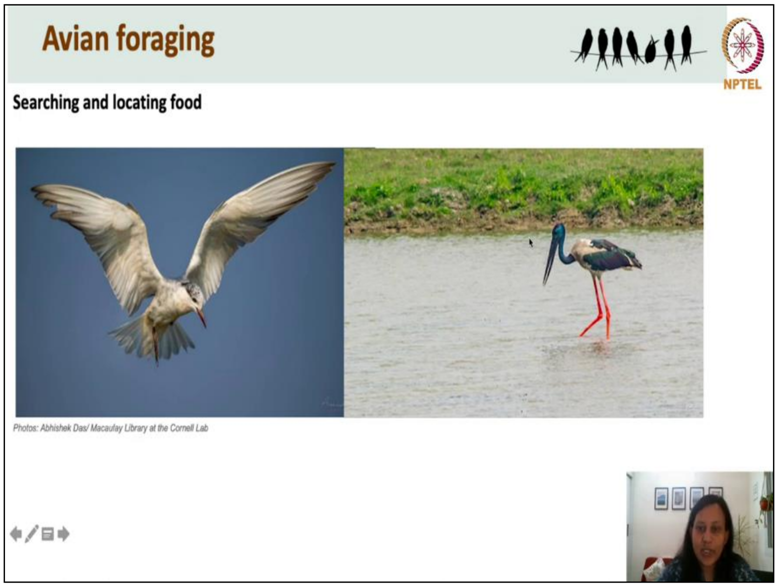

There are multiple stages associated with how birds acquire and ingest their food. It starts with how birds search and locate their food. Birds might scan from the air like this tern in this example, search for aquatic prey in the water like the stork or search the vegetation in search of insects or edible fruits.

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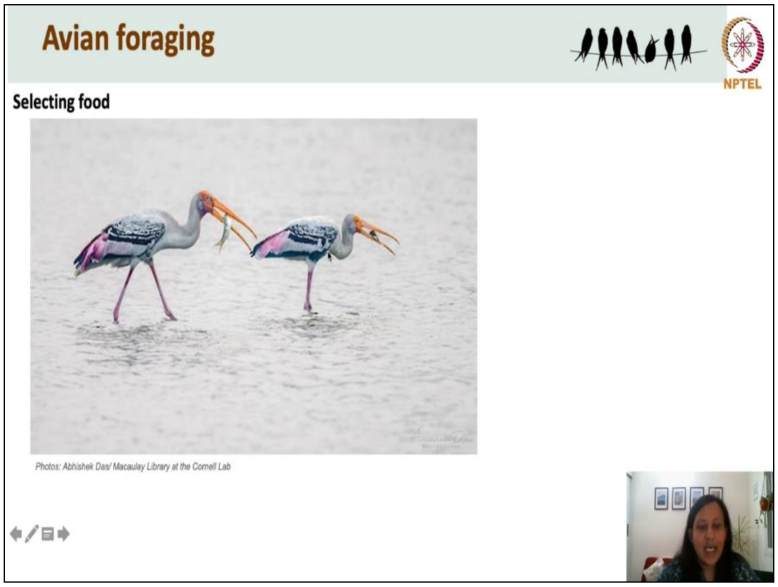

Once they locate their food they make a decision about which food to select. For instance, should they try catching a bigger fish or a smaller one as seen here for these two Painted storks.

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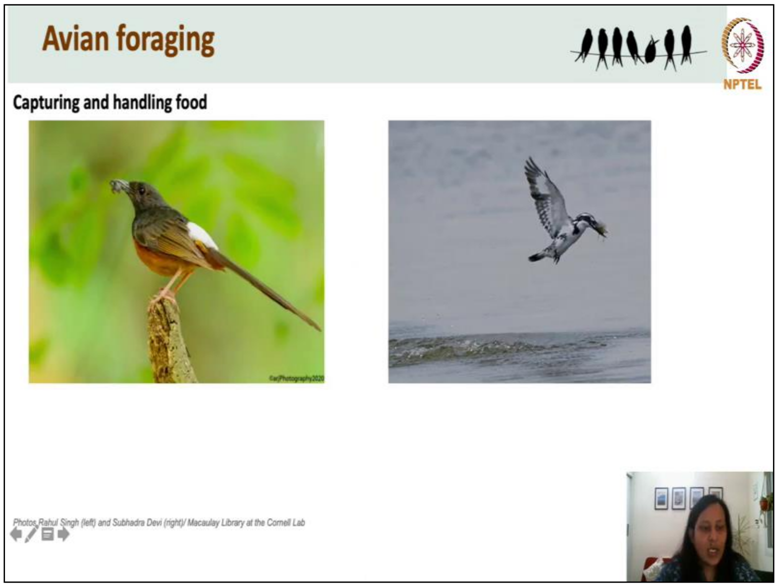

Once that decision is made, they must capture the prey using some foraging maneuver. We see a wide range of such maneuvers to catch prey among birds and these play an important role in determining the habitat a certain species is able to occupy and exploit for resources as we shall see later in this lecture.

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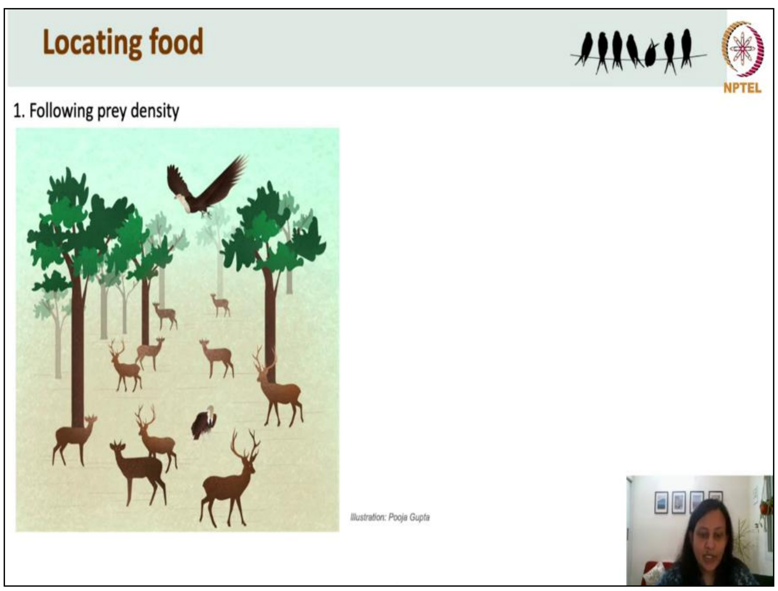

Let's see now see the different ways birds use to search and locate their prey. For large raptors such as vultures which feed on ungulate carcasses, it has been seen that they use a range of tactics since these are not constantly available in their environment. They tend to concentrate over areas which have higher ungulate densities. When ungulate density is low they fly at higher altitudes to surge over larger areas,

but when there are more ungulate available, they fly at lower altitudes. Carcasses are located rapidly and the food consumed quickly in high ungulate density areas while in low ungulate density conditions carcasses can take a long time to be located. For griffon vultures, it has been seen that to ensure more consistent food supply, they track migrating ungulate herds through the year. Their adaptations for gliding flight enable this behaviour.

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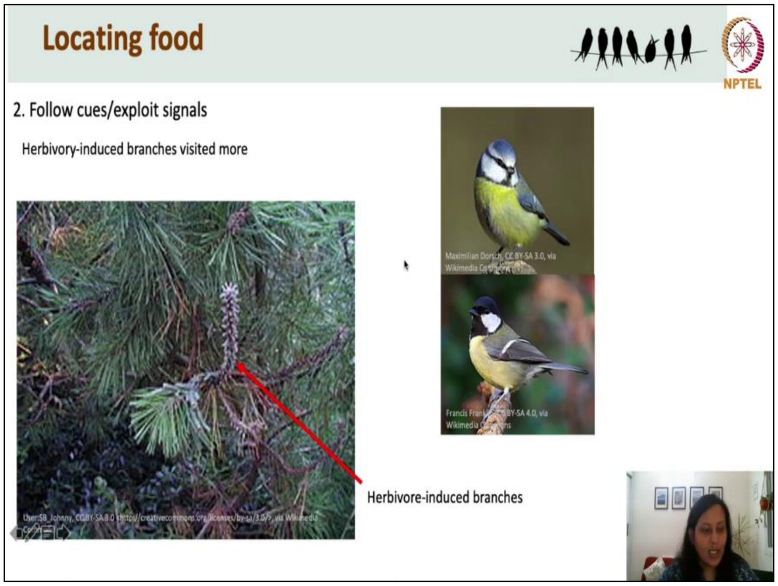

Sometimes birds use certain cues or signals to locate their prey. In a study with insectivorous tits feeding on saw-fly larvae, it was seen that they are able to differentiate between branches that have been affected by insect herbivory and those that have not been similarly affected.

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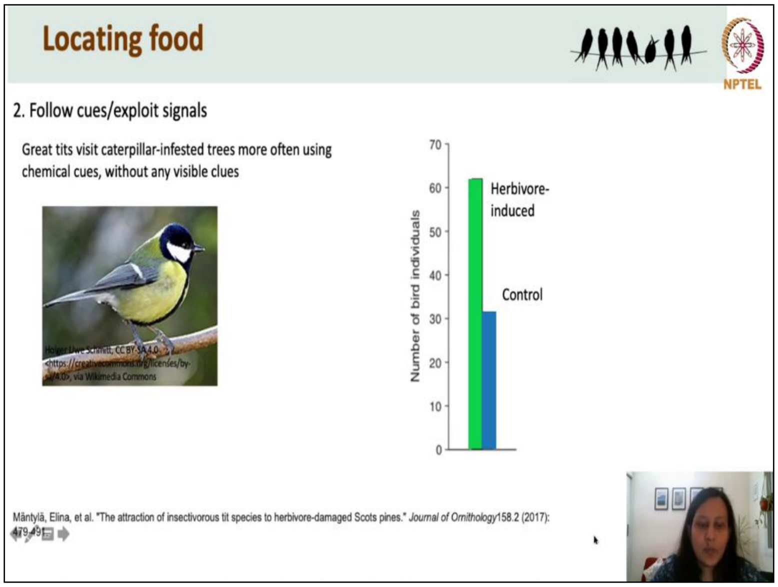

The result showed that more great tits visited her before induced branches than the control. They also noticed that the birds were attracted to trees infested by lepidopteran larvae, even when they were removed and their feeding damage was also removed just before the experiment. This allowed them to exclude the option that birds could use the larvae or their feeding damage as signals. Thus, the preference for infested trees was not due to the visible damage caused by the larval feeding on the leaves or by chemical cues associated with the larvae such as silk or faeces.

Instead, what they found was that the birds were using volatile chemicals released by the damaged branches as cues to find their prey. In fact, 21 out of 29 such volatile compounds were released in higher amounts by branches affected by herbivory.

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For group living or roosting species, it is suggested that such congregations serve as information centers where individuals exchange information about potential food sources. For instance, in this particular study they baited sheep carcasses with coloured beads at varied distances from a roost used by non-breeding juvenile ravens. It was seen that from the day that a pellet with a bead was discovered at the roost suggesting a bird has visited the baited carcass most of the birds leaving the roost increasingly visited the discovered carcass. This suggests that such roosts do seem to serve as information centers.

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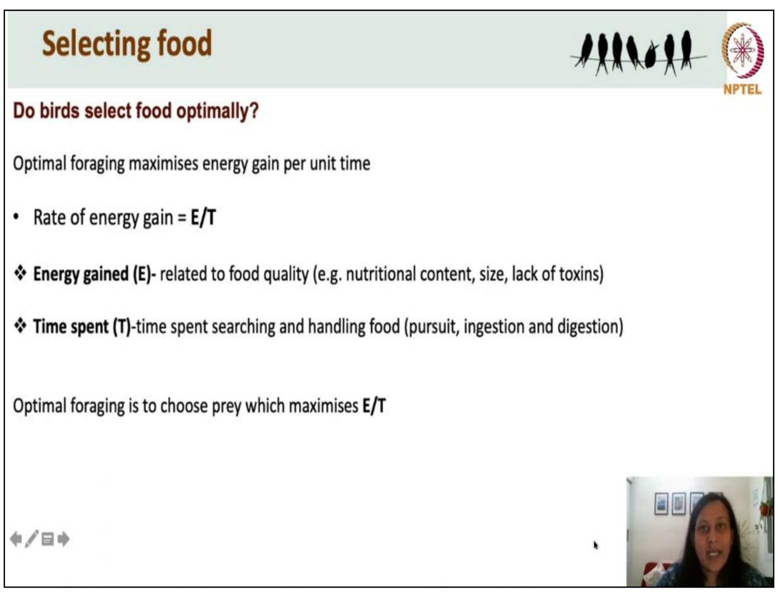

Once food is located the bird selects a certain foraging patch or food item. And the question we need to ask is do birds select food optimally? Let us first see what do we mean by optimal foraging. By optimal foraging, we mean a method of acquiring food that maximizes the energy gained per unit time spent in capturing or handling the selected food item. We denote this rate of energy gain by

$$E/T$$

where E or the energy is related to the quality of food in terms of its size nutritional content or absence of toxins.

The T or time spent is the amount the individual spends in pursuing the food its ingestion and digestion. So, essentially the optimal forager will try to select food that maximizes this E/T ratio.

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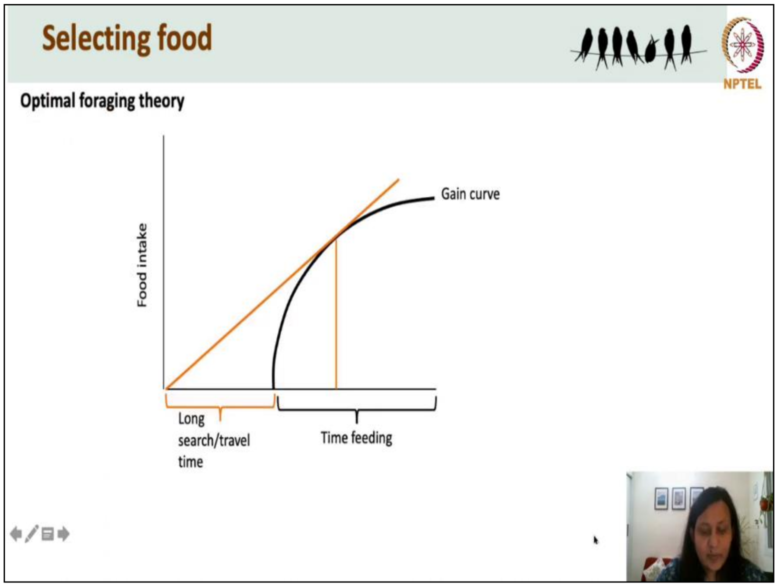

Optimal foraging theory predicts that an animal will forage in a patch of food until it reaches the highest instantaneous rate of ingestion of food, at which point it will switch to a different patch. The assumption is that the gain curve is not linear but saturates. So, that increasing foraging time results in smaller and smaller benefits over time. The time of greatest benefit depends in part on how long it takes to reach or search for that patch.

If the travel time is large, it benefits the forager to stay in the patch longer. But if the travel time is short as indicated by this green line it makes more sense to spend lesser time in the patch and then moving on.

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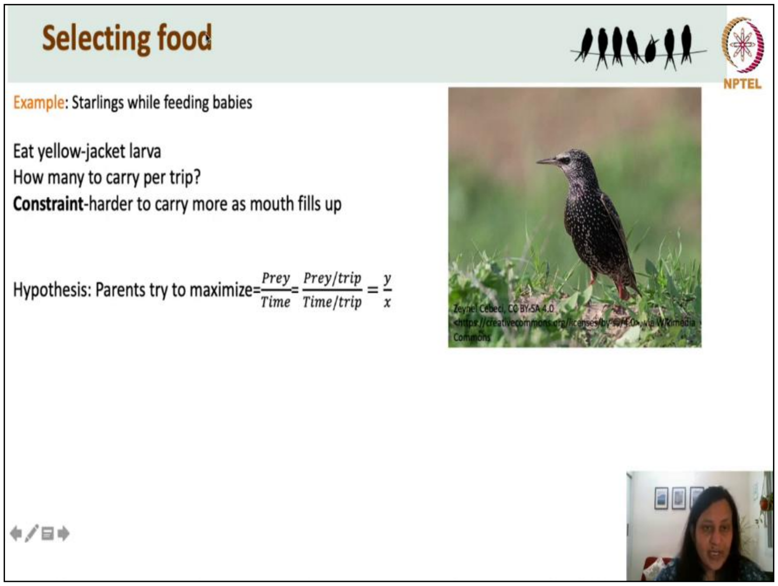

Let us look at an example of optimal foraging happening in nature. European starlings feed yellow-jacket larvae to their young ones. The question to ask here is how many larvae should they carry during each foraging trip. Given the constraint that the mouth can only fit so many. Hypothetically starlings should carry as many prey as possible to maximize the E/T ratio. But starlings that carry a large prey load also pay a metabolic and an energy and a time cost.

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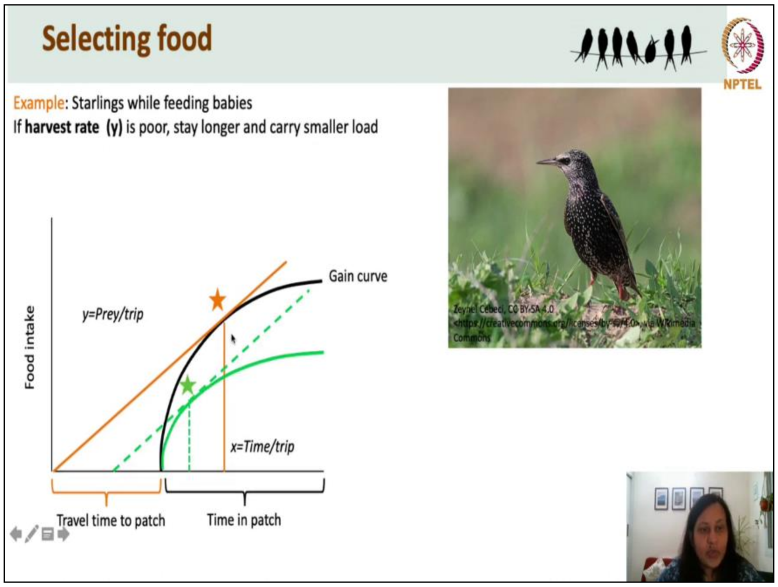

The slope of the curve indicates that the optimal foraging load in this figure. In case of starlings seven larvae seem to be the optimal load to carry given their usual travel time. Accordingly, the relationship between the load size and the time taken to do the round trip to collect the load seems linear and it plateaus off at seven. It has been seen that when the travel time is longer it seems more profitable to stay longer and carry a bigger load.

But when the harvest rate is lower due to say lower food availability, it makes sense to carry smaller loads during the optimal time to be spent for that travel time.

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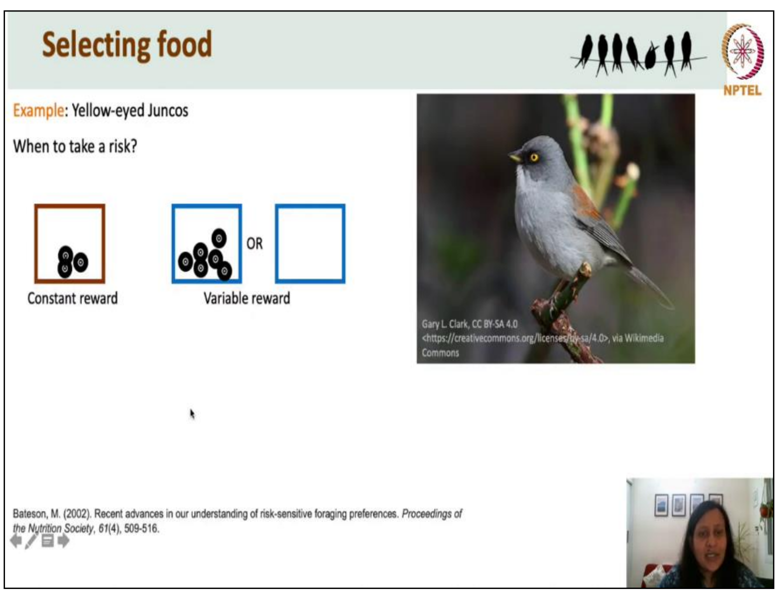

Recent studies such as the experimental study done by Mellisa Bateson on Yellow-Eyed Juncos show that animals are sensitive to variants associated with alternate food sources. By this we mean that if a bird is offered a constant reward of three seeds versus a variable reward of no seeds or six seeds, what would they prefer? The experiments show that given the average reward for constant and variable options are equal, the birds were either found to be risk prone or risk-averse.

Whether birds are risk averse or risk prone appears to depend on a range of factors including the energetic status of the forager. Let us see what we mean by this. The researchers found that when the temperature is warmer at 19 degrees mimicking when birds are warm and fat, they prefer the constant meal without variation. But when the temperature falls to one degree simulating cold and hungry birds, they prefer to gamble on variable means. But why does this happen?

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We can understand this by using utility functions. A utility function is simply a graph of a resources utility to an animal plotted against that resources abundance. In case of the concave down functions as seen here, the more units of resources the organism consumes the less valuable those units are. This is a common occurrence when foraging on a batch of prey. After a certain point eating another one is not at all beneficial which is what is happening when it plateaus out.

In the process of such foraging, risking the current morsel and losing costs more than the gain from the next one. Birds faced with this kind of situation tend to be risk-averse. In the case of juncos, the well-fed birds that chose the stable tray had a concave-down utility function; each seed was basically less valuable than the previous seed. So, there was more to lose.

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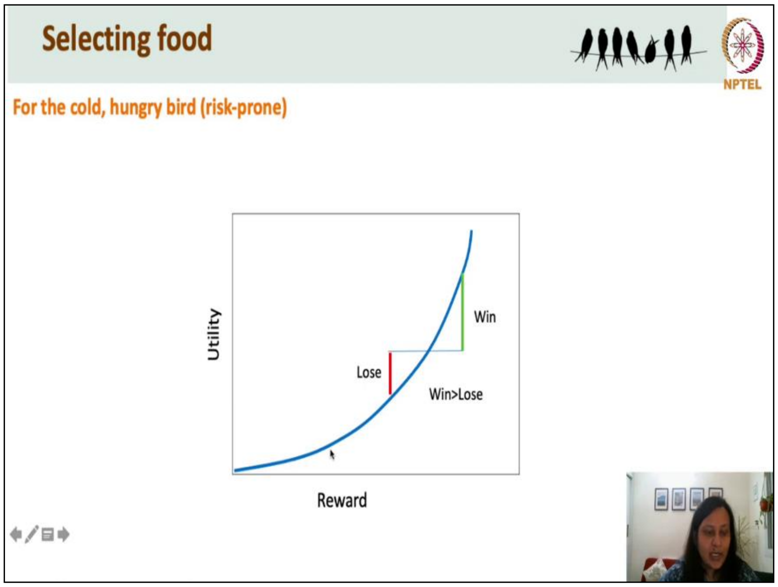

The next curve shows the opposite situation: each unit of resource is more valuable than the last, a situation that often occurs when some threshold must be attained before the resource can be useful. In this case, a bird is likely to risk losing a unit because the loss is less in order to gain more, because the potential gain outweighs the possible loss. Such animals are risk prone. The cold hungry, juncos had a concave-up utility function because each additional seed for them was more valuable.

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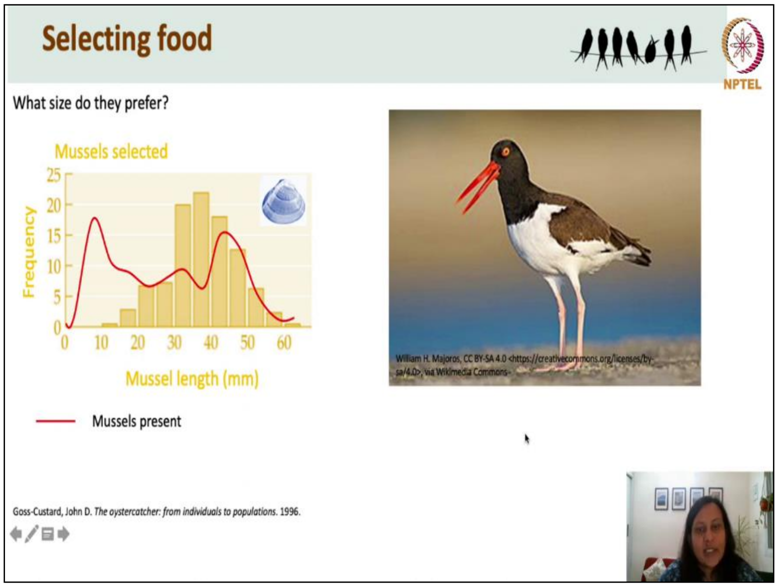

The optimal foraging theory also applies to the size of prey as seen amongst Oystercatchers selecting mussels. The first hypothesis says that the bird should opt for the largest mussels to maximize energy gain but the alternate hypothesis suggests that there should be an optimal mussel size somewhere in between before they become too large there by requiring longer handling time to break them open. The data suggests that this is indeed the case. When we plot the sizes of available mussels, we see that the ones chosen do not reflect the availability.

There is a distinct choice for mussels in the 30 to 40 millimeter size category, most probably since they strike the best balance between the energy gain and the costs incurred to handling time.

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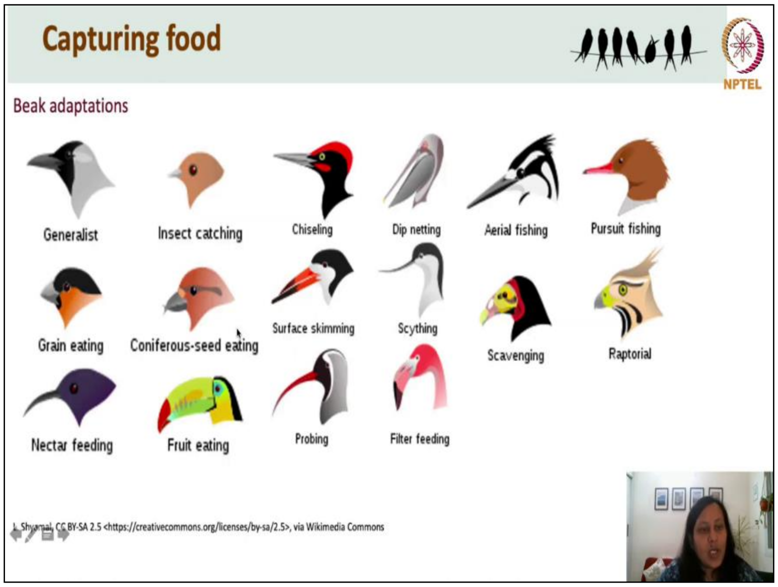

Coming to how birds capture and ingest their food, we see a wide variety of beak adaptations to accommodate the food types and the methods used to capture them. We find smaller slender beaks amongst insectivores but smaller and stouter beaks amongst granivore. We have specialized beak shapes for feeding on fruits, hooked beaks for tearing flesh among raptors, dip netting beaks amongst pelicans and a very highly specialized one for opening pine cones found in crossbills amongst many others such interesting adaptations. Changes or variation in beak shapes explain many interesting ecological and evolutionary phenomena.

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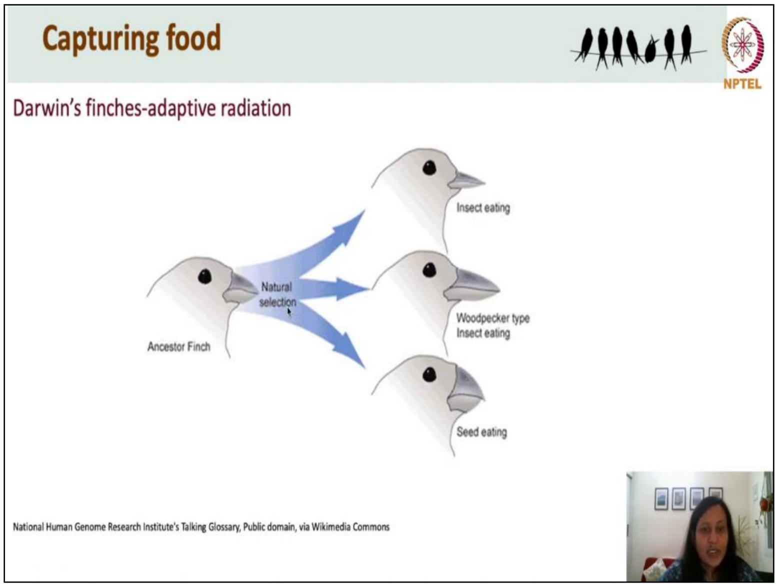

Consider the birds called finches that Darwin studied on the Galapagos islands. All of the finches probably descended from one particular bird that most probably arrived from on the islands from South America. Until the first bird arrived, there had never been birds in the habitat. The first bird was a seed eater, it evolved into many finch species. Each species was adapted for a different type of food. This is an example of adaptive radiation. This is the process by which a single species evolves into many new species to fill all available niches.

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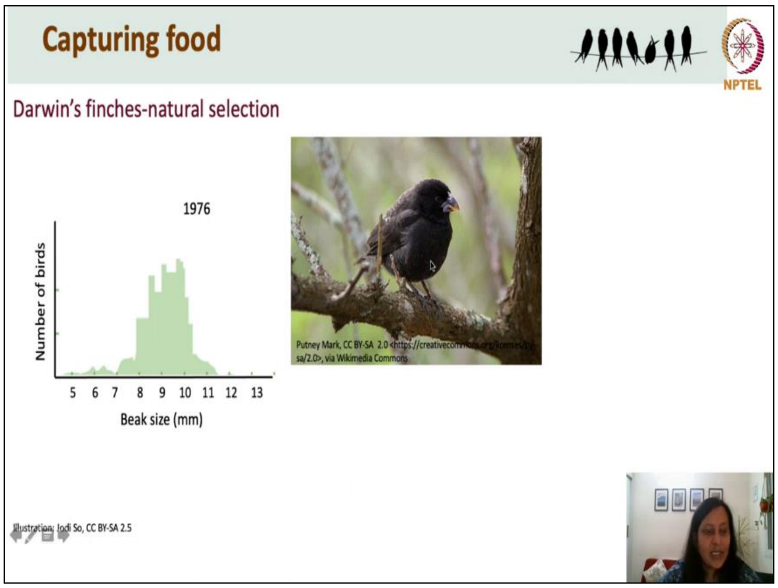

These finches are also an example of natural selection happening in a really short span of time, something which is very hard to come across amongst larger life forms such as birds particularly during our lifetimes. It was recorded in Daphne Majo, which is a volcanic island. The medium ground finch shown here is a resident to this island and this was a distribution of beak sizes in 1976. In 1977 an extended drought happened. Dry conditions resulted in plants producing larger seeds with tougher seed casings.

This meant that the birds with larger beaks did better and produced more offspring subsequently. Between 1976 and 1978 there was a change in average beak depth within the finch populations. Finches with larger beaks were better equipped to feed on the seeds and thus produce more offspring with larger beaks.

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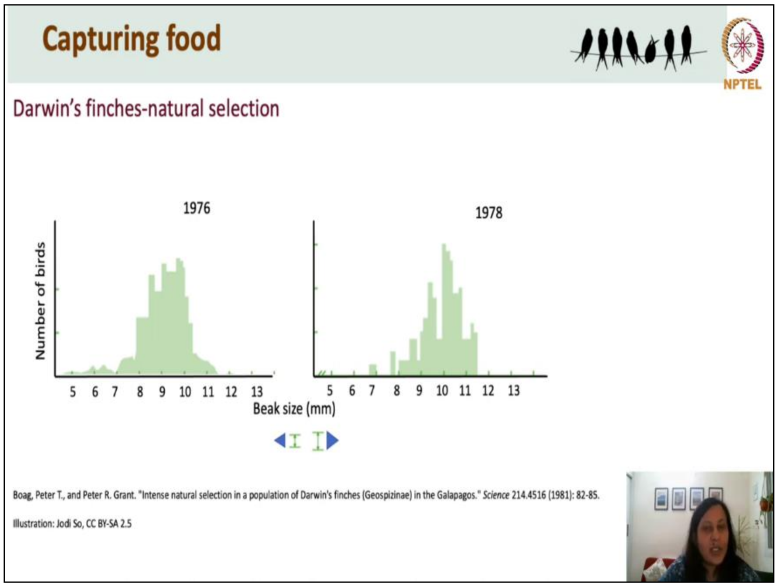

Within two years, the average beak size in the finch population increased due to this natural selection induced by drought.

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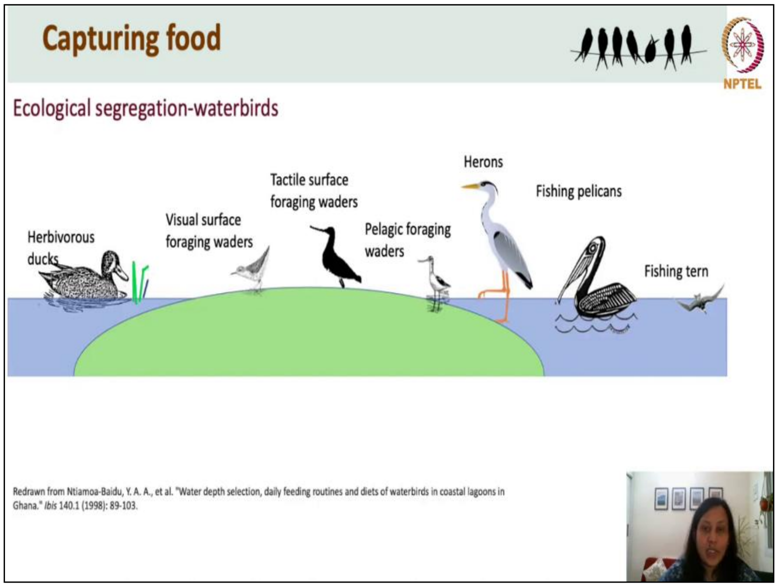

The variation in beak morphology and foraging behaviour also helps species within a community achieve ecological segregation, as seen among these waterbirds. They are able to coexist by using different resources but… facilitated by the different feeding preferences and behaviour.

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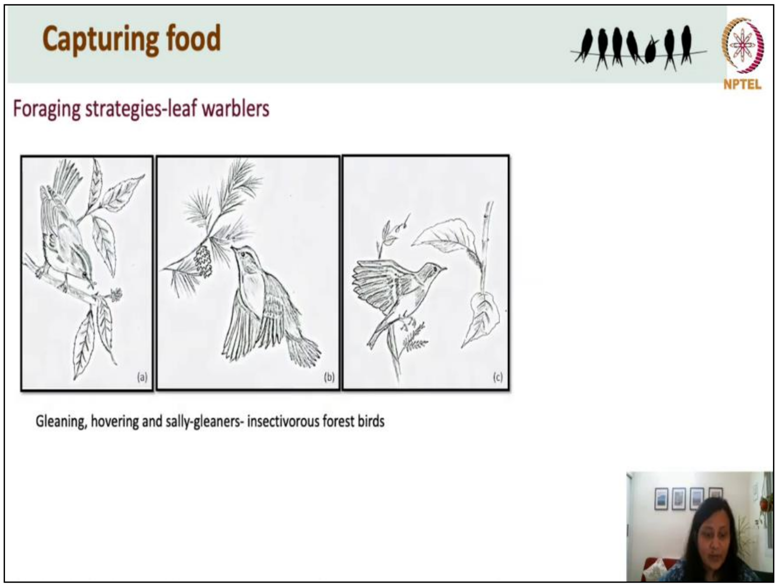

Closely related species may show finer segregation in their foraging behaviour. For example, these Leaf Warblers differ in how they use these three different feeding strategies. Standick when they pick an insect while hopping on branches, hover picking when they search while hovering and sally-gleaning is when they fly to capture a stationary insect.

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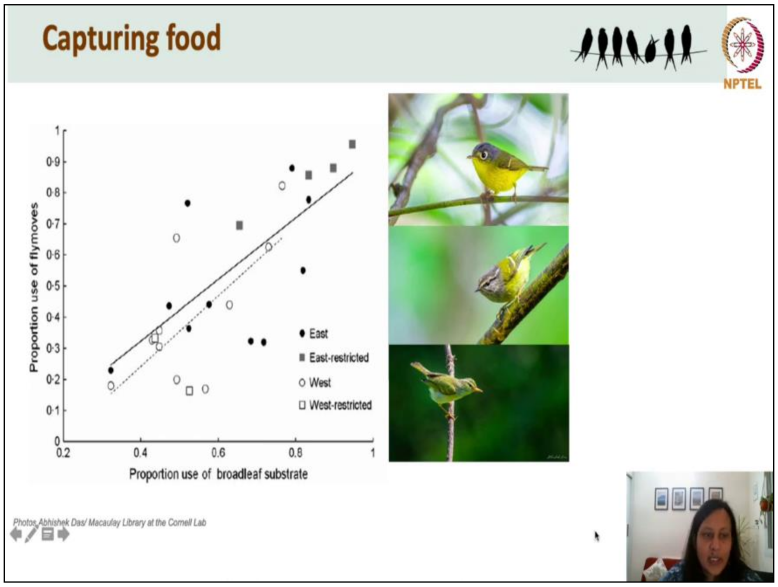

These behaviours are often intricately associated with the habitat that the bird occupies. Among these Himalayan leaf Warblers, species in both east and west Himalayas use more flying moves that is hoverpicks and sallygleans combined when they use broadleaved vegetation.

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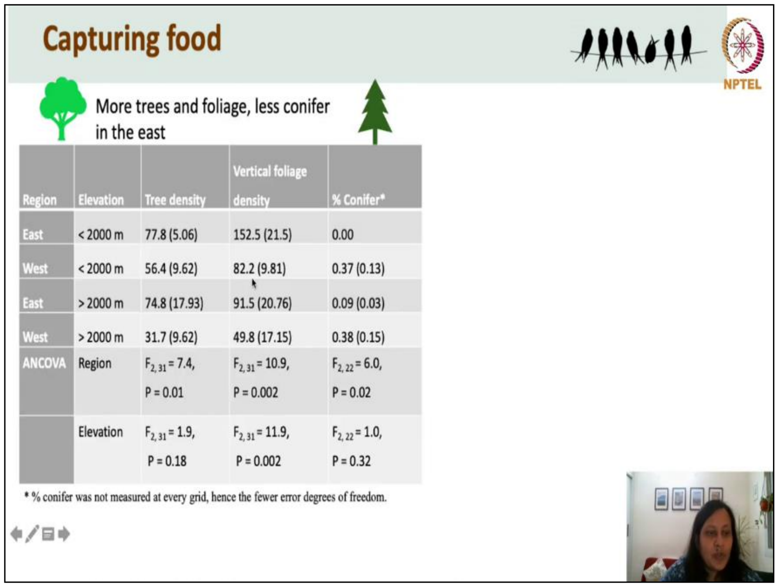

Region	Elevation	Tree density	Vertical foliage density	% Conifer*
East	< 2000 m	77.8 (5.06)	152.5 (21.5)	0.00
West	< 2000 m	56.4 (9.62)	82.2 (9.81)	0.37 (0.13)
East	> 2000 m	74.8 (17.93)	91.5 (20.76)	0.09 (0.03)
West	> 2000 m	31.7 (9.62)	49.8 (17.15)	0.38 (0.15)
ANCOVA	Region	$F_{2,31} = 7.4$, $P = 0.01$	$F_{2,31} = 10.9$, $P = 0.002$	$F_{2,22} = 6.0$, $P = 0.02$
	Elevation	$F_{2,31} = 1.9$, $P = 0.18$	$F_{2,31} = 11.9$, $P = 0.002$	$F_{2,22} = 1.0$, $P = 0.32$

But when we move from east to west Himalayas and look at the vegetation, we see that there is an increase in both overall and broad-leaved tree density. But west has relatively more coniferous vegetation.

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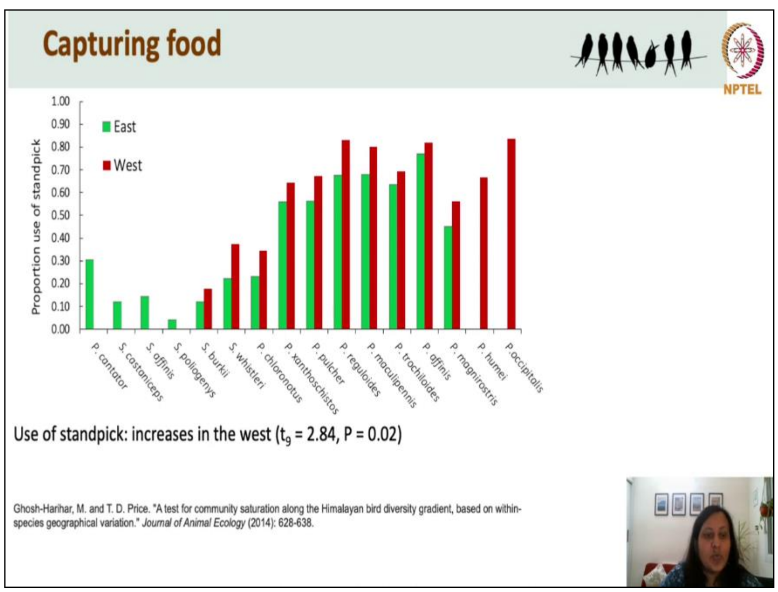

To adapt to this change in vegetation structure, all species use more stand picks when they move from east to west as indicated by these longer red bars in this figure. The eastern species for example the Chestnut-crown warbler which specialized in using flymoves, are therefore not able to move into the west because of this drastic change in vegetation.

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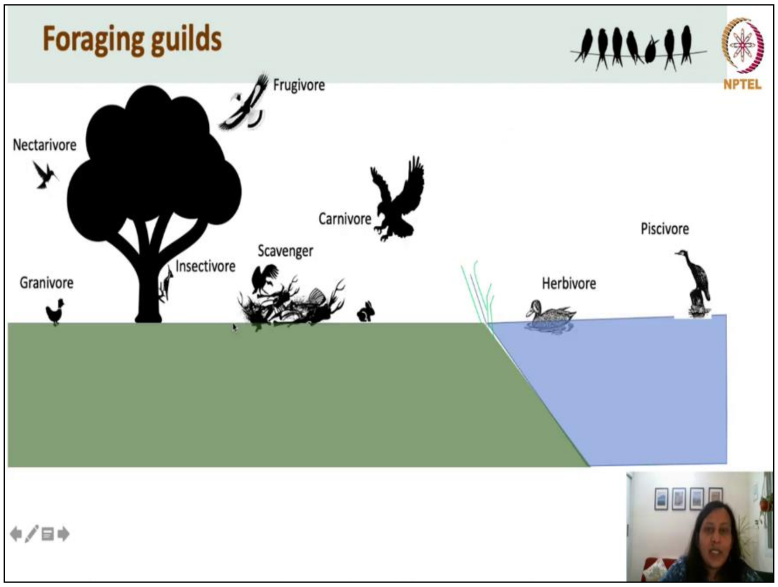

Given each foraging behaviour is associated with specific morphological adaptations and similar relationship with their environment, we often group species feeding on similar types of food into the same guild. Since habitat changes or threats might affect functionally similar species in a similar manner, clubbing ecologically similar species make such investigations simpler. Some of the often-used categories when we deal with foraging guilds are these nectarivores for the ones who feed on nectars of flowers,

granivores for grain consuming birds, insectivores, frugivores, scavengers that feed on carcasses, carnivores that feed on vertebrate prey, aquatic herbivores such as ducks. Then there is of course there is land herbivores as well which are represented by geese. And there are many piscivorous species such as cormorants which use the aquatic habitat.

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You can see one such example of feeding guilds in the state of India's bird report released last year. Here there is a chart that shows how different feeding guilds have been faring over the past few decades. While, we see a general trend of decline across feeding guilds, we find that the carnivorous species or raptors are declining more than the others. Since this group shares similar traits such as large body size, long generation length, low clutch size and dependence on vertebrate prey.

It might make it easier to narrow down the factors to look at for those interested in looking behind the reasons for this decline.

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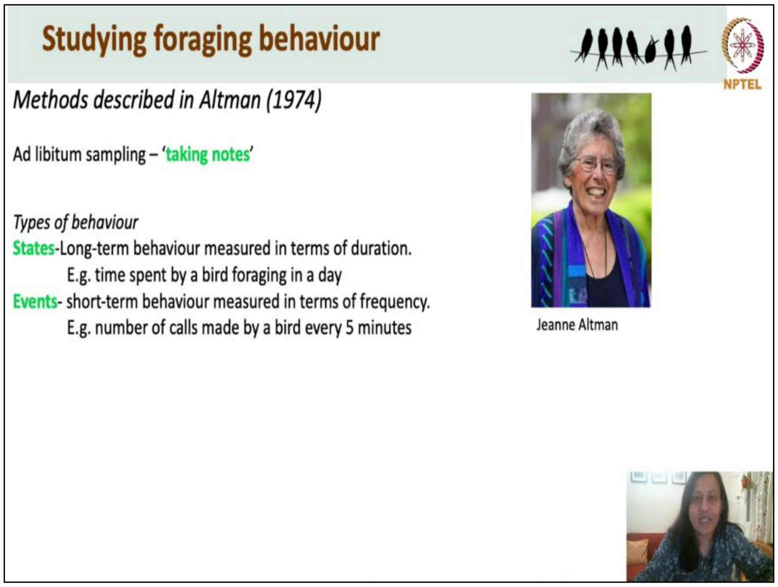

So, now we understand in what ways is foraging behaviour an important aspect to consider when we study birds. But how do we go out and carry out such studies in field? The first step when starting any kind of behavioural study is making observations or taking notes to learn to identify and describe the behaviours of interest. This is done through a process called Ad libitum sampling. Ad libitum literally means as much or as often as is needed or desired.

So, basically you just go out and watch birds in the wild and take notes in a way that helps you identify and classify their behaviour. Much of how we study behaviour comes from this study by Dr Jeanne Altman titled "Observational study of behaviour: sampling methods" published in 1974. She describes two main types of behaviours in behavioural sampling. 'States' which are long term and measured in terms of duration.

For example, how much time does a bird spend foraging in a day. The other type is called 'event', which is basically short-term or instantaneous behaviours which are best measured in terms of their frequency. For instance, how many times did a bird call during a five minute period of observation.

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The first step in any behavioural study is to build an Ethogram. An ethogram is a record of behaviours exhibited by an animal used in the scientific and objective study of animal behaviour. For example, while studying foraging behaviour in birds. Starting with an Ethogram is particularly important when studying new some new groups of species or novel behaviour which has not been described before.

Let us see how do we go about building an ethogram. We first make Ad-libitum observations of an animal in its natural surrounding and describe a set of 'state' and 'even' behaviours with clear definitions. These are often categorized under broad classes. An ethogram describes at least eight states and two events it must also include 'other' or "out of view" as one of the states. And if multiple researchers are preparing one ethogram together it is necessary that the partners agree on the definitions.

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Here is an example showing how an ethogram looks like. This particular ethogram describes different categories of behaviour in broiler chickens, such as appetitive or those to do with feeding, activity behaviours, aggressive ones and one categorized as disturbance. As is suggested, it has a category called other to class any that do not fit the predefined behaviours.

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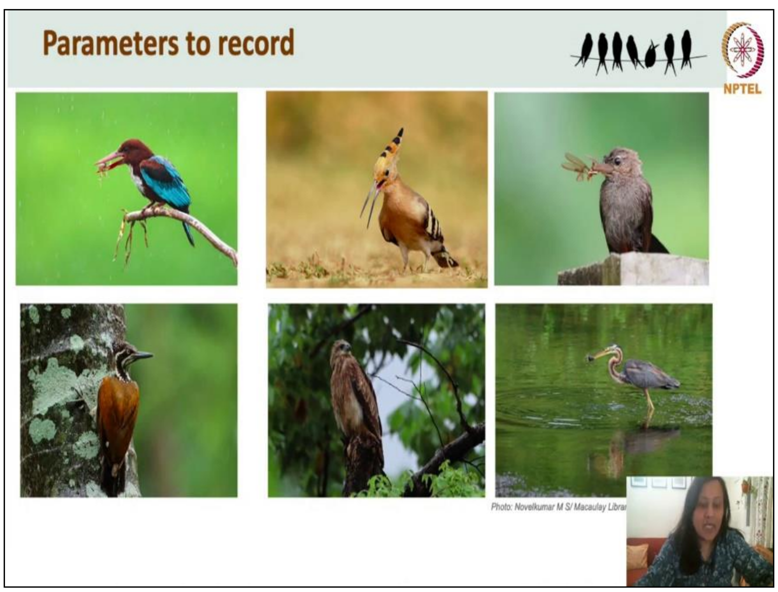

Now let us see what kind of parameters do we usually record when studying avian foraging. From these pictures it is evident that birds occupy diverse habitats and obtain their food in very different ways. Therefore, the parameters to record depends on the kind of birds we are interested in.

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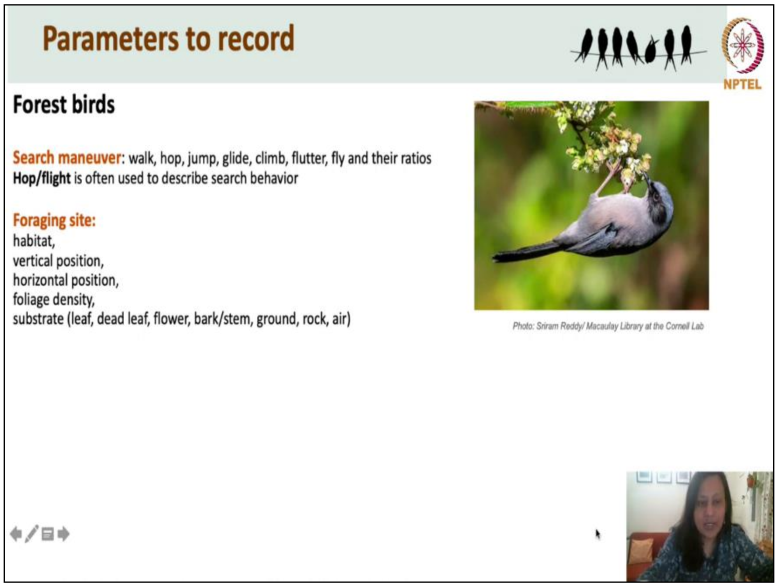

As an example, when studying forest birds, we might be interested in how they search for food in the foliage, be it insects or fruits and the kind of maneuvers they use while searching. Are they hopping or flying or perhaps hovering to locate food? You might want to record where they pick their food from…the habitat, vertical position, that is, whether it is in the understory or canopy, whether it is to the interior of the bush or tree or to the periphery, is it dense vegetation or sparse and the substrate from where they pick the food from.

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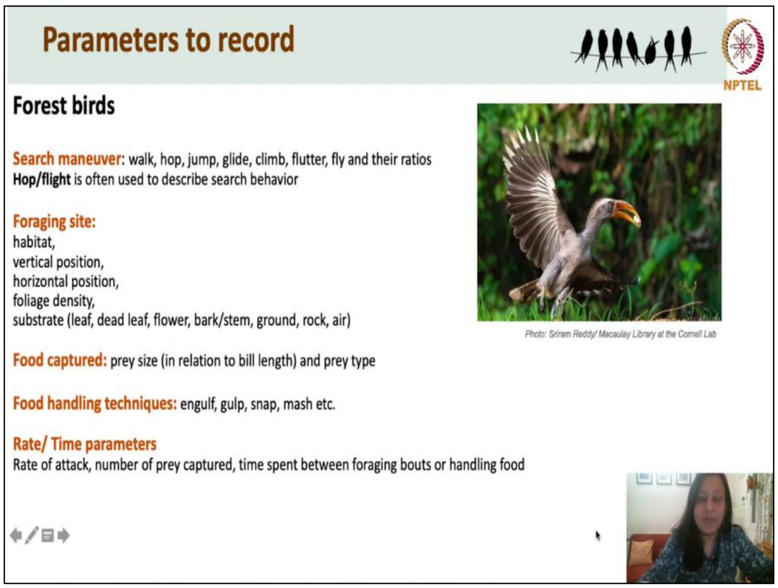

You may also record whether it is a fruit, insect or vertebrate prey and sometimes you can even attempt to measure the size by comparing it to say the beak. A food handling technique and the time taken might also be important to consider for say if you are trying to look at the relationship between food size and handling time in the 'optimal foraging' framework. Similarly, certain rate or time parameters of importance may include rate of attack, the number of prey captures, time spent between foraging bouts and the food handling time.

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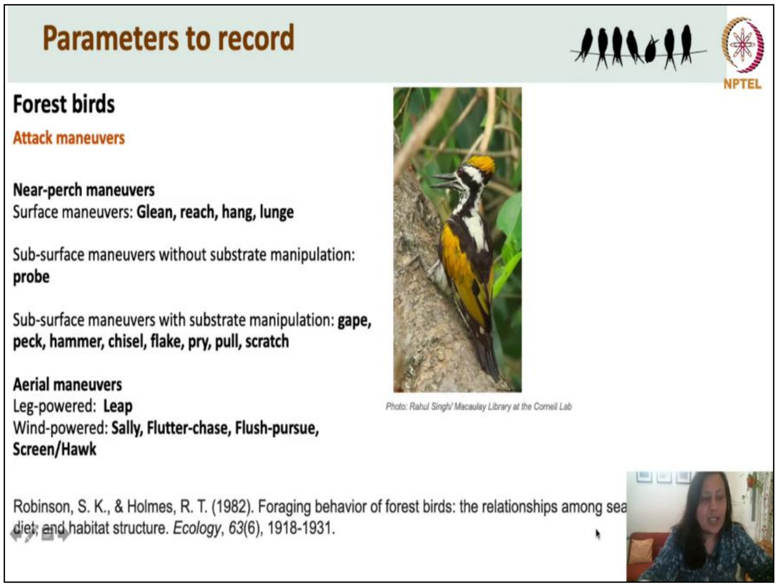

In fact, sampling foraging behaviour in forest birds is particularly well described in the study by Robinson and Holmes in 1982. Just to cite an example from the study how the insectivorous birds attacked their prey is categorized based on where they happen, that is, whether it is on the surface of leaves or below. Maneuvers performed in air are again categorized based on whether they are powered by legs or wings and each is described in great detail with illustrations. A must read for anyone planning to study foraging in forest birds.

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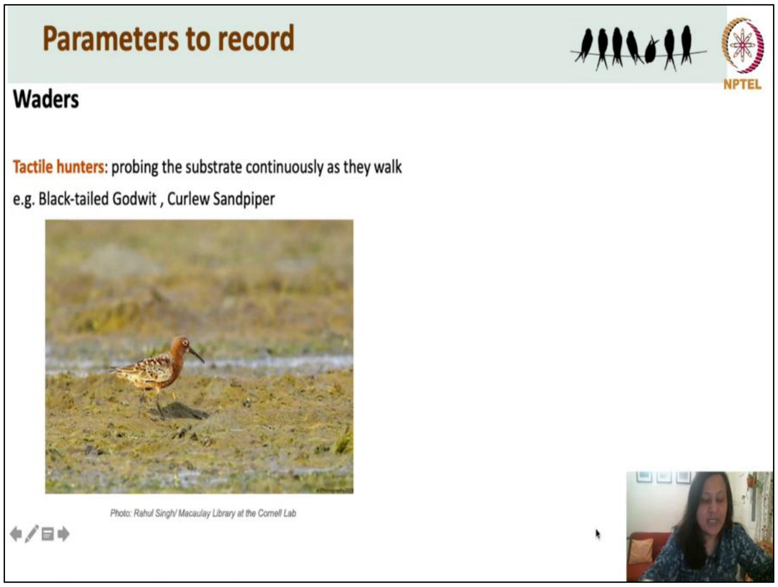

When we look at waders, which forage in an entirely different way compared to forest birds, the parameters of interest are of course very different. Firstly, we have to consider that within waders, there are some broad types of foraging behaviour. First there are the tactile hunters that locate prey by constantly probing the substrate with their beak. Examples include species like Black-tailed godwits, and Curlew sandpiper which is pictured here.

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Then we have the visual feeders that peck continuously on objects seen on the surface. Common sandpipers and Greater Sand Plover forage this way.

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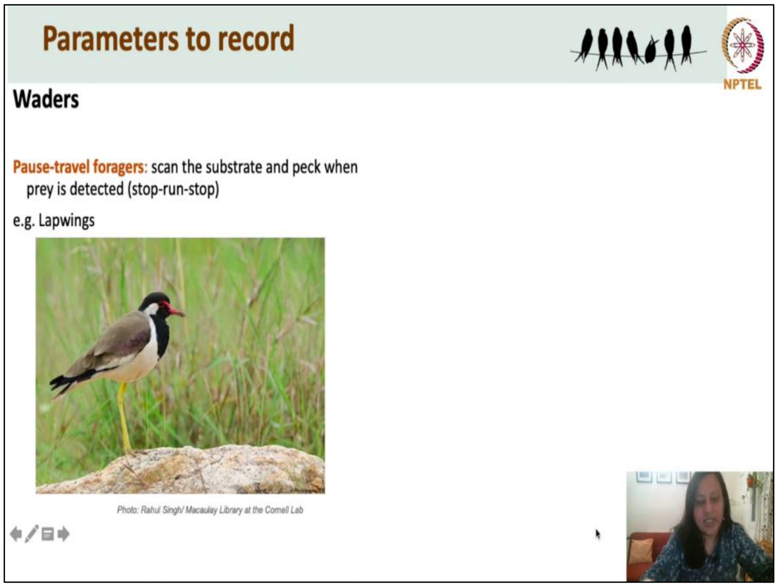

Lastly, there are the pause and travel foragers which scan the substrate as they are moving and stop and peck when they locate a prey. Lapwings forage in this manner.

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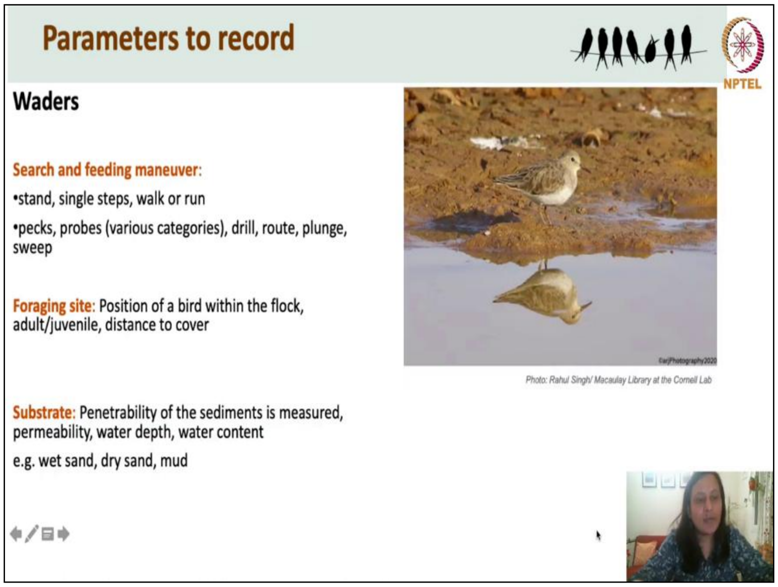

Based on these broad types we can categorize their search maneuvers as stand, single steps, walk or run. Similarly, feeding can be classed into pecks, probes, drill, route, plunge and sweep. We can similarly classify their foraging site with respect to an individual's position within the flock. This gives us clues to how the individual is situated with respect to the underlying resource distribution and the amount of threat it faces due to predators.

Finally, we might want to make note of the properties of the substrate from which the bird is picking up its prey. This is important because it might tell us about the type of prey it is feeding upon and this is also important way in which multiple species might be segregating ecologically in this habitat when they feed at the same site. For instance, some might feed on prey available on the surface while some might dig deeper into the mud using specialized beaks.

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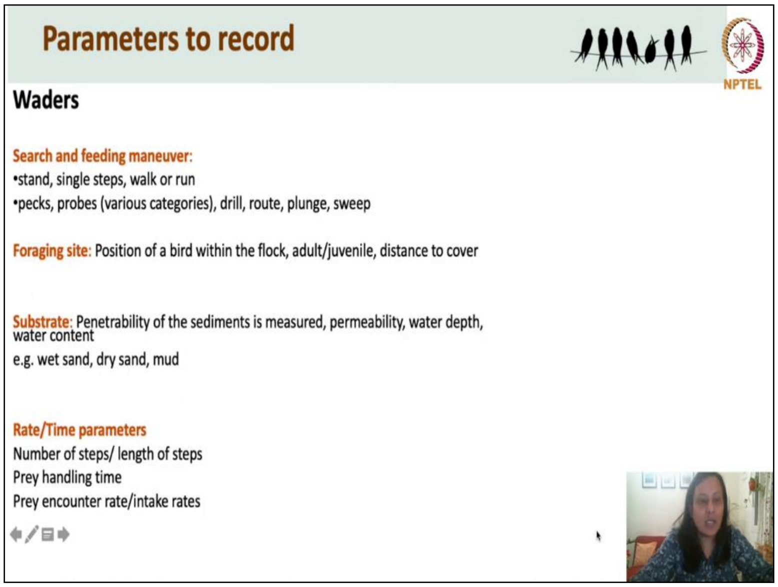

Again, we might want to record rate and time parameters when required to answer our specific objectives. Now that we are aware of the parameters of interest, let us see how such behavioural observations are made.

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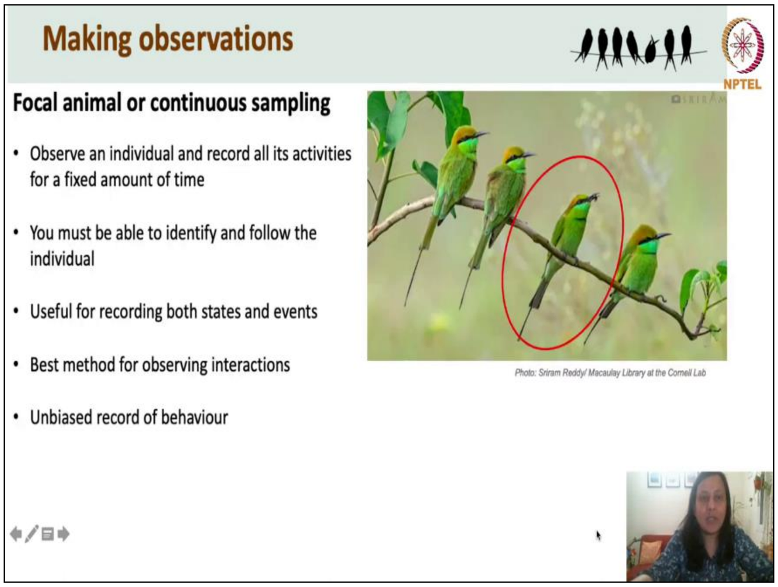

There are two main approaches in sampling methods described by Altman. First, is ‘focal animal’ or continuous sampling. Here you basically, pick an individual within a group for instance this bee-eater indicated in the red circle and record all activities or predefined behaviours for a fixed amount of time. For this, you must be able to follow the individual you have chosen, which can be challenging for fast moving birds moving inside thick foliage.

This method is useful for recording both states and events and it is the best method for observing interactions. It gives us a relatively unbiased record of behaviour. The alternate to this method is instantaneous or scan sampling where you can observe or scan all individuals in a group and record their activities at a pre-set interval like say every five minutes. The advantage is you do not need to identify and follow any one particular individual.

But it is useful for recording only states. Then again, it is really useful for monitoring larger groups of birds.

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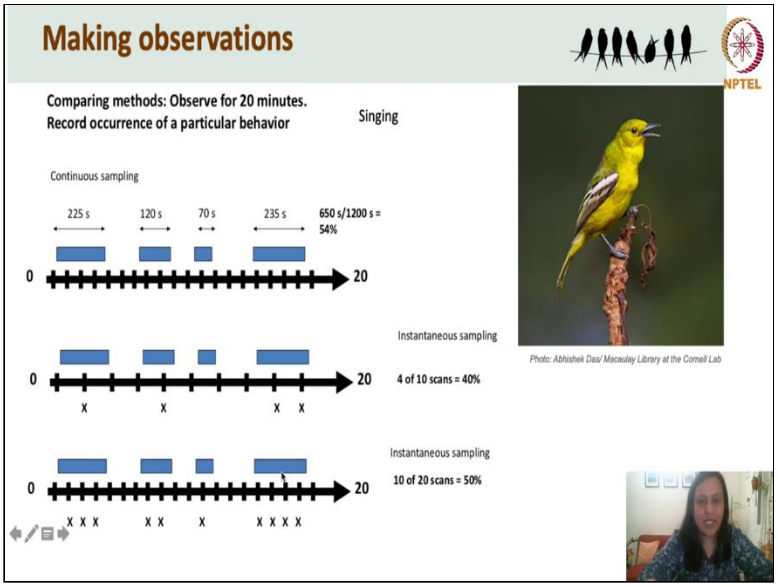

Let us see how this works. Assume we are interested in recording the occurrence of a particular behaviour like singing and observe a bird for 20 minutes to measure this. In this figure we have black bars on the horizontal line which indicate one minute each and the blue rectangles show when a bird is singing through this 20 minute duration. If you do focal animal or continuous sampling, we find that the bird does singing for 650 seconds out of the 1200 seconds or 20 minutes for which we make the observation.

And this is about 54% of the observation time. Now, let us do scan sampling, where we do 10 scans first out of the 20 minutes and record if the bird was singing when we looked at it for the same sequence of behaviour. We can see based on the overlap between the black bars and the red blue rectangles, that singing is picked up in 4 out of the 10 scans. So, we get a value of 40% through this method instead of the actual 54% that the behaviour actually occurred.

What happens… now, let us see what happens if we increase the number of scans. When we look at the sequence again by scanning 20 times instead of 10, we get a figure of 50% which is closer to the actual figure of 54%. This basically means that if we do scans frequently enough, we approximate the results that we can get out of focal animal or continuous sampling. I will conclude with an example of sampling behaviour from my own work.

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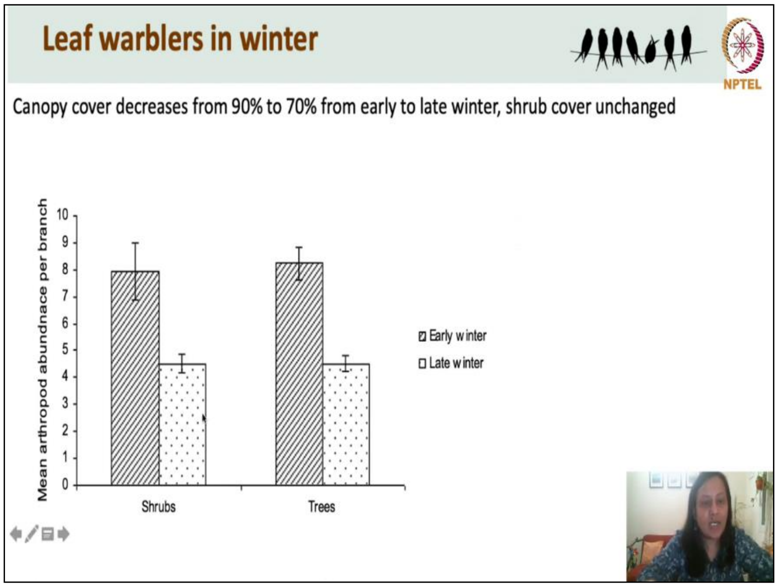

I was interested in assessing how three leaf Warblers segregate ecologically in their wintering habitat in the Himalayan foothills and if the pattern of segregation changes as conditions change in the habitat through winter. I found that from early to late winter, due to leaf fall, canopy cover decreases by 20 percent but the shrub cover remained more or less unchanged. This was associated with a decline in availability of arthropod prey in both trees and shrubs as we move from early to late winter.

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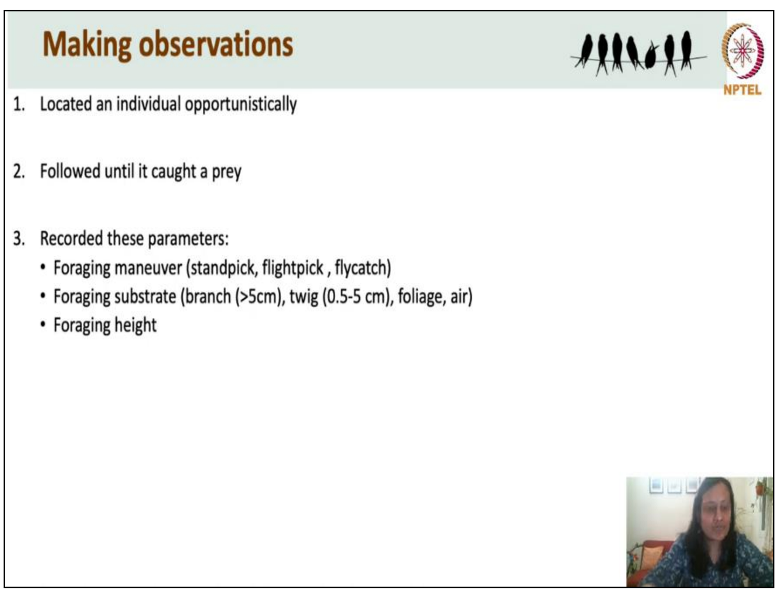

Since I was interested in how these species segregate through foraging behaviour. I made some foraging observations through this period. For this, I used to walk along existing forest trails choosing a different trail every time to avoid sampling the same birds again and again. Once I located an individual, I followed it until it captured a prey. I confirmed prey capture by seeing the prey in the bill or if it was not seen because it was too small by watching a bill wipe.

These birds wipe their bills each time after they feed. For each capture, I recorded the maneuver used the foraging substrate which I had already classified into certain categories and I also noted down the foraging height. I had these predefined categories based on some initial ad libitum observations that I did prior to starting actual sampling.

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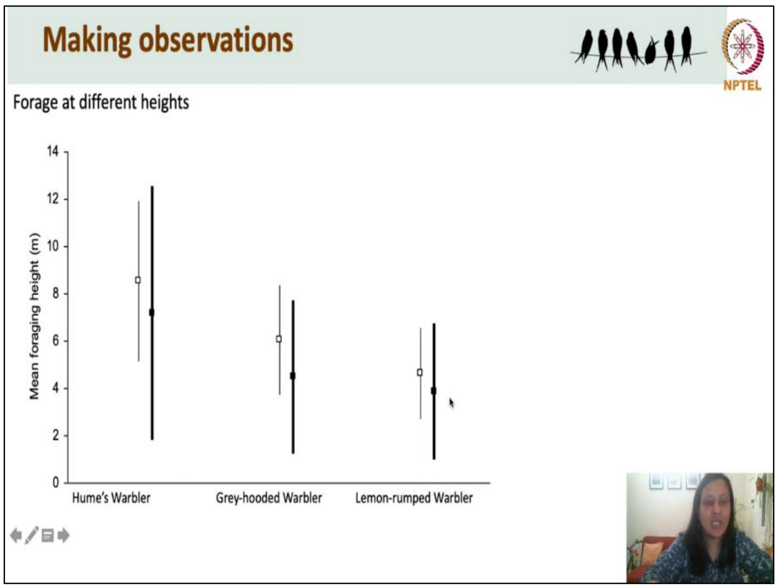

Based on the data collected, I found that these species primarily segregate by foraging at different heights in the vegetation, with Hume's Warbler preferring the canopy, Grey- hooded Warbler preferring the mid canopy and Lemon-rumped Warblers mostly foraging in the understory and I also found that this segregation was maintained from early to late winter.

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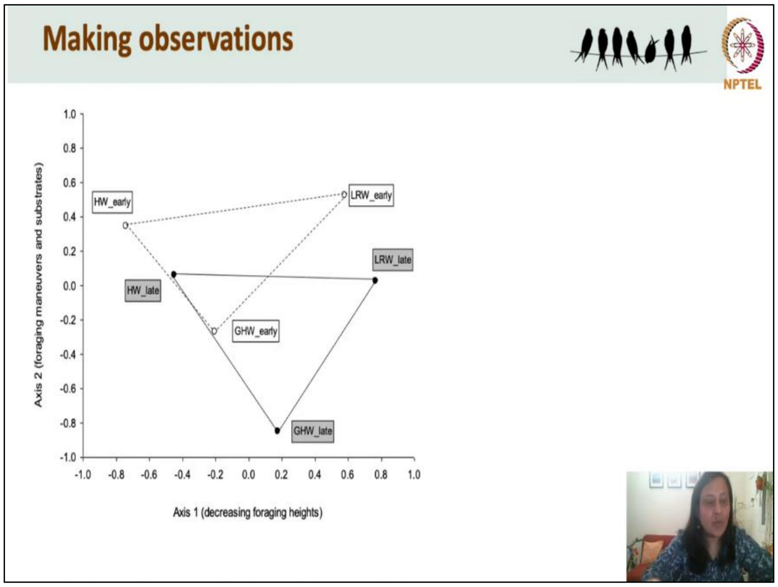

But in response to the reduction in prey availability, I found that the entire guild shifted towards the understory as we move from early to late winter, used more flying maneuvers and picked prey from branches and twigs more often as leaves fell down. This indicates how species are able to adapt as conditions change in their habitat, while maintaining interspecies ecological segregation. This brings us to the end of this lecture on foraging behaviour and how to study it. I hope this encourages you to study more about avian foraging behaviour and maybe do some research studies of your own.