Basic Course in Ornithology
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Lecture -11
Mating and Breeding Behaviour

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Hello everyone and welcome to the basic course in ornithology. Today's lecture is about mating and breeding behaviour in birds. I am Manjari Jain from IISER, Mohali. Darwin and Wallace co-proposed the theory of evolution by natural selection and the crux of the theory rests on differential reproduction and survival of individuals. Individuals that do not survive long enough to reproduce or those who survive but do not reproduce will leave fewer copies of their genes in the next gene pool.

Thus, reproduction determines an individual's fitness. Birds are sexually reproducing animals and they are the only class of vertebrates that are exclusively oviparous which means that they lay eggs and do not give birth to live young. Sex determination in birds is also different from some other vertebrates such as us humans who have a XX and XY system where male heterogamety occurs. In case of birds however female heterogamety occurs wherein females are ZW and males are ZZ.

Birds are also special from the point of view of the extraordinary courtship rituals that they exhibit and the diversity of mating and breeding behaviour that they have evolved making them an excellent model system to examine the evolution of mating systems. So, let us talk about the love lives of birds how they find and woo their mates. The various factors that may determine who gets to mate and who does not get to reproduce. And finally, let us talk about how do they provide care to the young ones.

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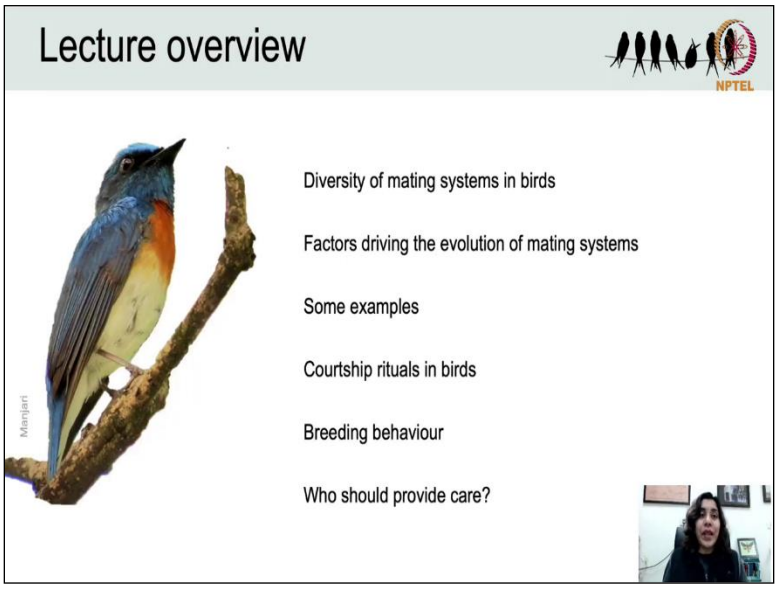

We will discuss in this lecture the diversity of mating systems and birds then we will go on to discuss various factors that drive the evolution of mating systems in general. So, conceptually we will discuss these and then discuss some examples from birds. We will then talk about male strategies to find and impress females in so, we will learn about some extraordinary courtship rituals that birds exhibit. And this is a phenomena that has captured the interests of scientists and birders all over the world.

It has for generation inspired art, theater, film, poetry, song and dance. It is a delight to our senses with different species of birds exhibiting elaborate acoustic or visual displays. From the carefully woven nests of the weaver birds to the elaborate bowers made by the bowerbirds. From the complex songs produced by the songbirds the spectacular dance of the peacock. Birds provide examples of courtship rituals making us humans appear incredibly unimaginative in our own courtship.

In this lecture we will also discuss breeding behaviour and nesting behaviour in particular the kinds of nests that birds make. Last but not the least, we will talk about who should provide care to the young ones and we will see how this will connect back to mating systems in birds.

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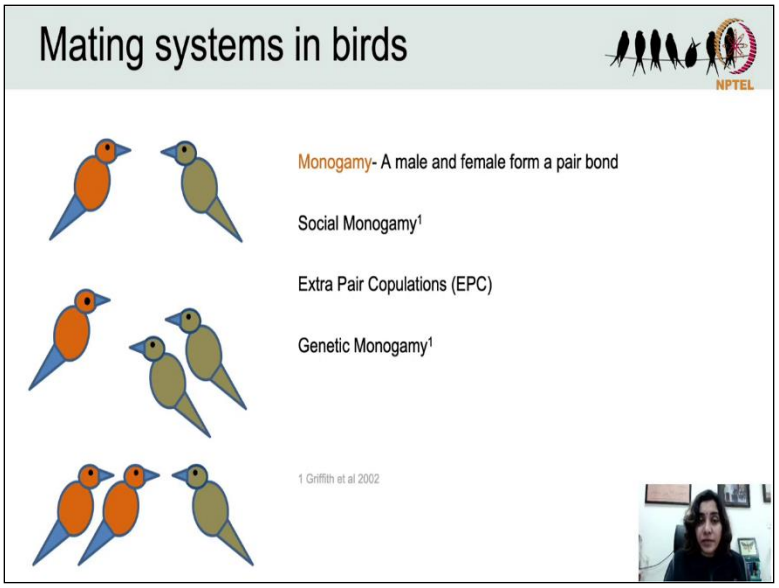

So, let us start with an overview of mating systems in birds and for that let us start with monogamy. Monogamy is a mating system in which a reproductively active male and a female of a species forms a pair bond. Monogamy is the most common mating system in birds especially in song birds. About 90% of bird species are believed to be monogamous. The same however is not true for mammals.

Now why should that be? For now, I will leave it to you to think about it and I hope that by the end of the lecture things will become a little more clear. Monogamy can be of two types - social monogamy or genetic monogamy. Social monogamy means that a pair is together socially but there is a possibility of what we call as extra pair copulations or EPCs which is when a member of the pair bond seeks copulations with other potential mates outside of the pair bond.

Genetic monogamy however implies that the pair is truly monogamous and no extra pair copulations occur. Thus, the offsprings of genetically monogamous species will have the same mother and father. Again, within monogamy itself an entire spectrum exists a pair can be

monogamous for a single nesting event or the entire breeding season. Some birds are monogamous even for successive breeding seasons yet others wear for life.

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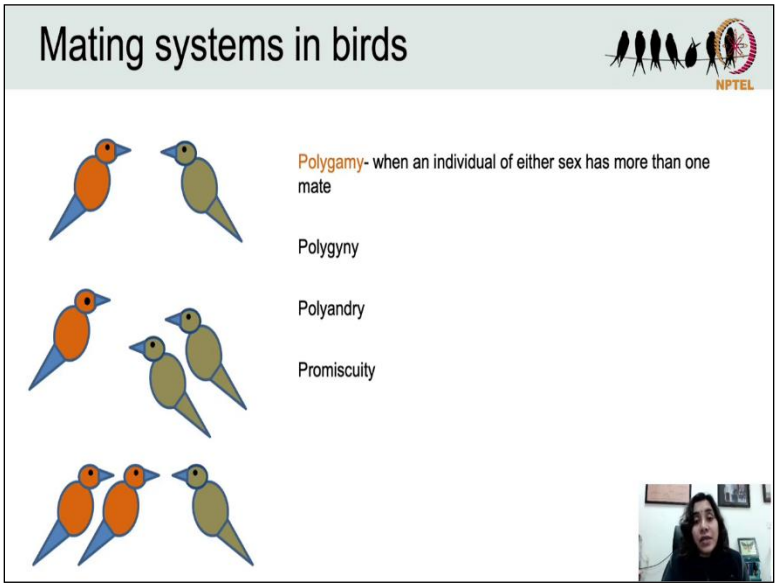

The other mating system is polygamy and polygamy refers to a mating system wherein one of the sexes has multiple partners. Polygamy can be of three types- polygyny, polyandry and promiscuity. A mating system in which a male mates with multiple females but a female mates with only one male is called a polygynous mating system. There are different types of polygyny depending on various factors that drive the mating system and we can discuss these later in the lecture.

Polyandry on the other hand is a mating system in which a female mates with multiple males but a male mates with only one female. Polyandry is uncommon in birds and is mostly seen in shore birds. Promiscuity on the other hand is where both the males and the females mate several times with different individuals.

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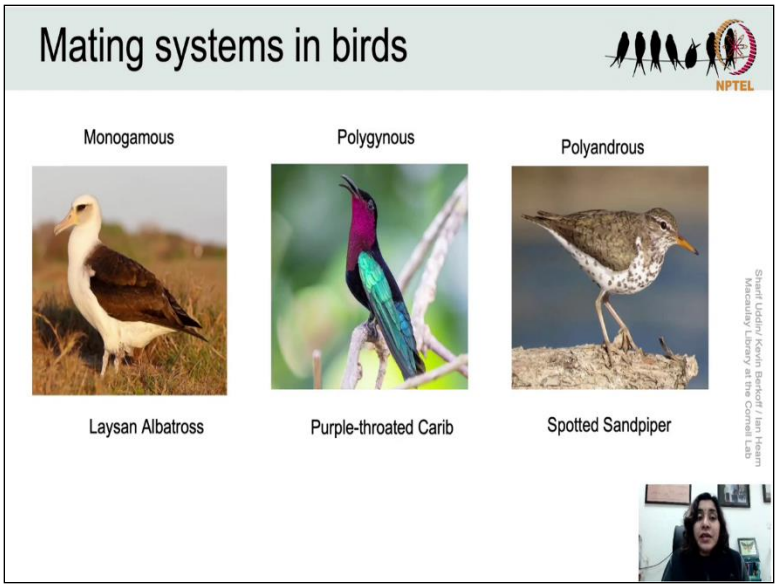

Here are some examples of birds with different mating systems. For monogamy, I have given the example of a Laysan Albatross. For polygyny, I have given the example of the Purple-throated Carib and polyandry is, one of the species in which this has been most extensively studied is the Spotted sandpiper.

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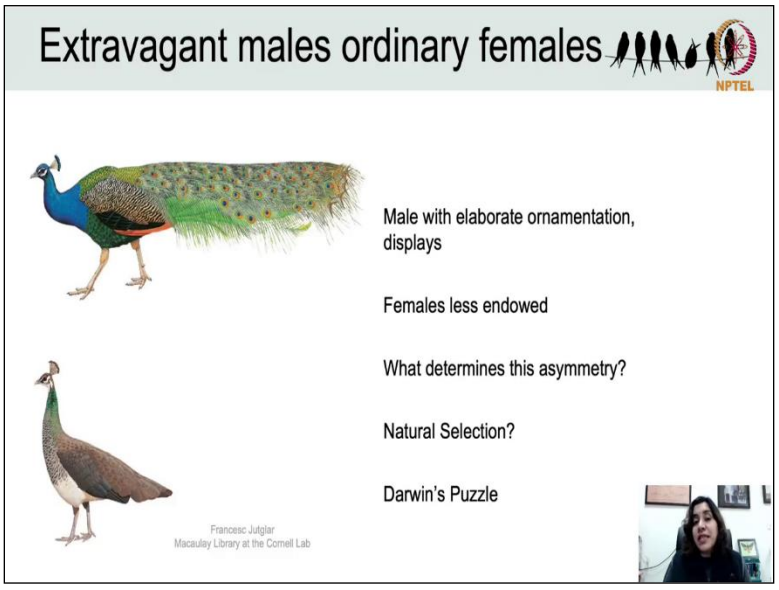

Now, let us look at the factors that influence the evolution of mating systems. You all must have seen a peacock and peahen. The most striking feature is the sexual dimorphism in the species wherein the males are flashy, brilliantly colored and have a very long and conspicuous plumage which they employ in their courtship displays that can only be described as a spectacle of nature.

Males have extravagant plumage with an extraordinarily long tail whereas peahens are more modestly dressed.

In fact, in many birds males possess elaborate ornamentation and the females are less endowed. Now why do males and females of the same species differ so starkly in many birds? Why do males exhibit extravagant behavioural and morphological traits whereas females look and behave more ordinary? In fact, in many groups of birds males of closely related species differ greatly morphologically but the females, not so much.

What determines this inequality? How could such extravagant and seemingly wasteful traits evolve via natural selection? Now, this puzzled Darwin as well and unlike Wallace he saw the problem in explaining the evolution of extravagant secondary sexual characters in males through natural selection and proposed the theory of evolution by sexual selection.

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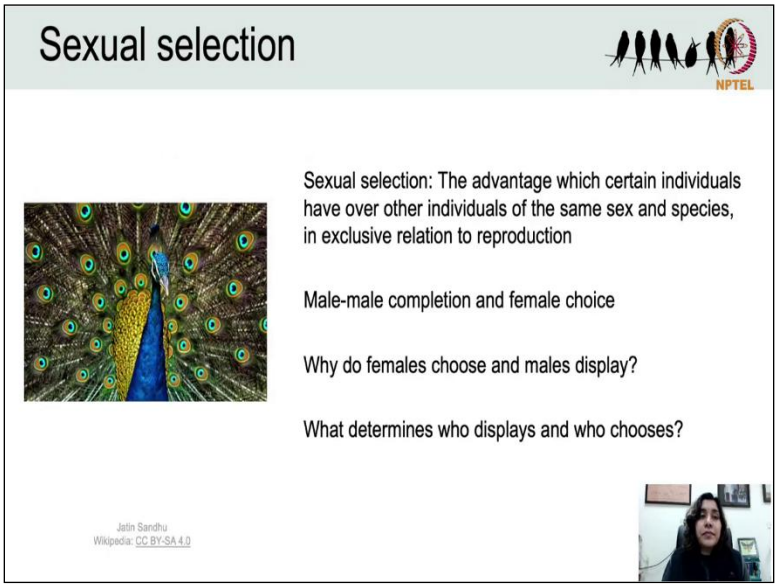

Darwin found the theory of natural selection inadequate to explain the evolution of such seemingly wasteful extravagant secondary sexual characters. And in his book “The Descent Of Man And Selection In Relation To Sex” he even argued that such extravagant traits such as the long train of the peacock may even be cumbersome and may attract the attention of predators thereby potentially making the trait bearer more susceptible to predation.

For those of us who have seen a male peacock take flight we will know why he felt so. So, he proposed an alternative theory of evolution of traits by the means of sexual selection. Sexual selection as Darwin termed it is the advantage which certain individuals have over individuals of the same sex and species in exclusive relation to reproduction. Now, this may come about why a male-male competition wherein males compete for access to resources or mates and the winning male secures most of the matings. However sexual selection may also act via female choice wherein males display, such as the peacocks dancing, and the females choose amongst the displaying males. Why do females choose and males display? Why isn't it the other way round? What determines who will display and who gets to choose? Do animals have a sense of beauty? Many such questions arise, of course. And the scientific world during Darwin's time and even much later strongly oppose the idea of evolution by sexual selection including Alfred Russel Wallace, who co-proposed the theory of evolution by natural selection. And almost for a century this debate remained unaddressed. Today of course sexual selection is not only an accepted theory, but is an active area of research in ecology, behaviour and evolutionary biology. So, let us understand how it acts.

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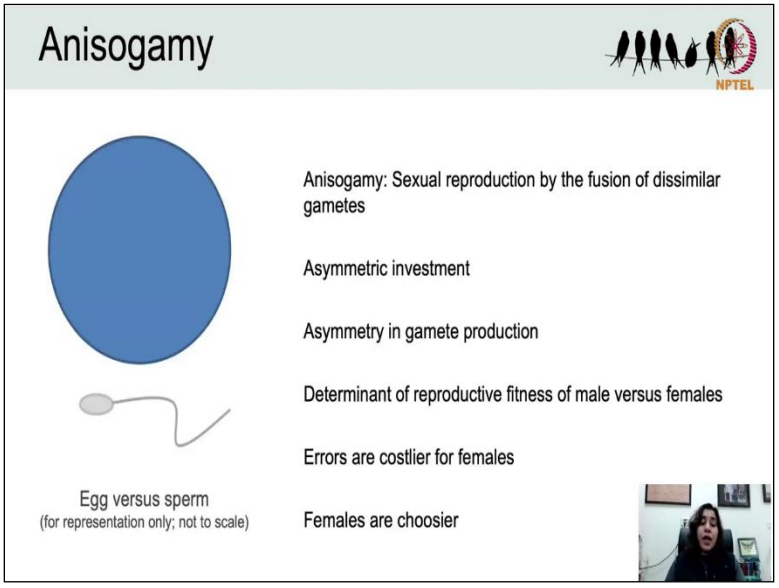

In sexually reproducing animals, the two sexes produce distinctly different gametes in which the males produce sperms and the females produce eggs. Sexual reproduction by the fusion of these dissimilar gametes is known as Anisogamy. In the schematic, observe the difference in the size of the egg and that of the sperm. This represents the asymmetric investment in the developing embryo

by the two sexes with respect to the nutrition that an egg can provide versus what is contributed by the sperms.

The difference is there in many sexually reproducing animals but in birds this is especially pronounced where the eggs of birds are large and visible to the naked eye whereas the sperms are microscopic. Further there is an asymmetry in gamete production itself between males and females wherein female birds like many other sexually reproducing animals produce a limited number of eggs and the males out number them by producing far more sperms in a single event of reproduction than the number of eggs a female can produce in its entire lifetime.

So, the females are limited by the number of gametes they can produce whereas the males are limited by the number of matings they can secure. Given the high investment per gamete and the limited number of gametes produced by the females, errors in mate selection have higher fitness cost for females than for males and that is how it is the females who get to choose.

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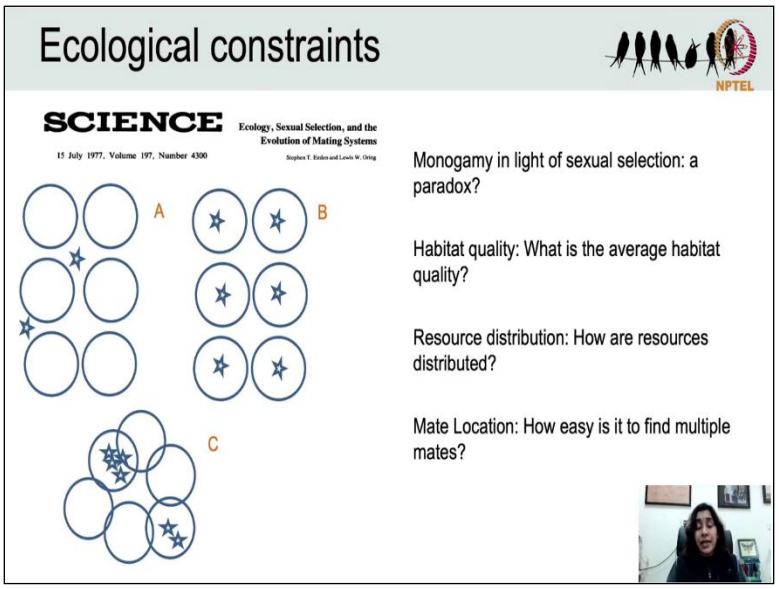

All right. So, sexual selection drives mating behaviour in birds and typically the females get to choose who gets to mate. But then given that male fitness increases with maximizing the number of matings, how can monogamy evolve at all? On the face of it, monogamy seems paradoxical when seen in the context of sexual selection. Well, it is because there are many other factors that need to be accounted for and that includes ecological constraints on the species.

In the figure given here the stars depict resources and the circles represents the territories of males of a species of birds let's say. Firstly, the habitat quality will matter if resources are overall poor in quality in a given habitat, then it may take both parents to raise a successful clutch then there is going to be limited potential for polygamy. This is depicted in figure A. Now let us lift this rationing and imagine a resource-rich habitat as depicted in figure B and C.

In both cases, there are six stars depicting roughly the same amount of resources present in the habitat. But between figure C and B, the spatial distribution of resources is different. If females are likely to be found where resources are distributed you can understand how access to multiple females will vary if the resources are clumped versus if they were spread out more or less evenly, even if resources were abundant.

It is also important to consider how easy is it to find multiple females to begin with. This will determine the potential for polygamy. This itself may be dependent on resource distribution but on other factors as well such as predation pressure availability of nesting sites or other resources, the population age structure determining the number of reproductively active females in the population at a given time period.

Thus, this will determine how many females per male is available at any given point of time and space and this is referred to as the 'operational sex ratio' or the ratio of receptive females to males that are in a mating pool seeking mates.

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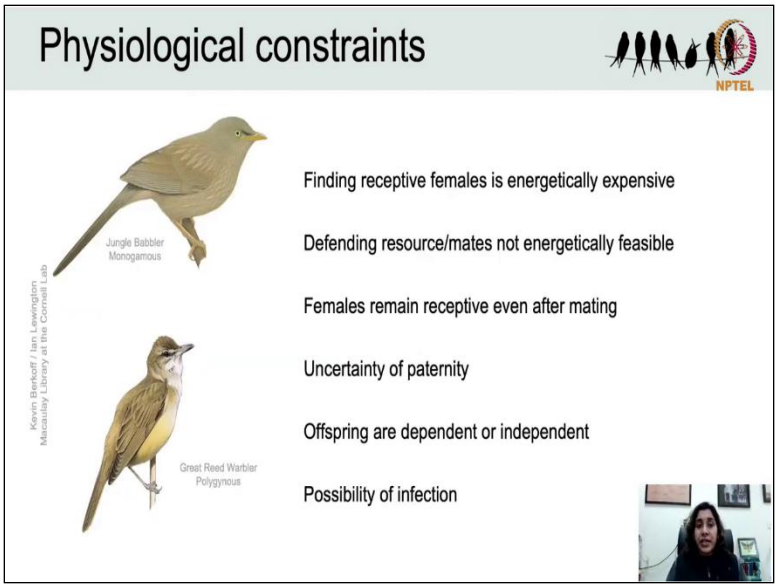

Energetic constraints also need to be considered. If many females are likely to be found in a resource rich patch it might be energetically more efficient for males to occupy a territory in such a patch defend it against intruders and have exclusive access to all the females visiting the patch. The potential for polygyny is higher in this situation as opposed to a situation where female location is unpredictable or if females are too scattered.

Further resources spread over a large area may not even be defensible. If resources are sparse and scattered then it will take much more effort to guard territories that must be very big to cover enough resources. Similarly, when defunding multiple males it might become energetically uneconomic. Hence male-male competition and thus the degree to which sexual selection can operate can be determined by such energetic constraints.

If females remain receptive even after mating then the female may mate with other males and this may influence the chance of a male to father the offsprings. This is compounded by the fact that in birds unlike several fishes, fertilization is internal and therefore paternity is uncertain. In this case it might be better for a male to stay back with the with the female in order to increase the certainty of his paternity and thereby reducing the polygyny potential.

And so you can see how monogamy can indeed evolve given such kinds of physiological constraints. We should also consider when offsprings need extended care from the parents then it

might be too costly for the male to desert a clutch and seek other mates. Here again, we expect the males to stay back with the female and help raise the offsprings so that they can reach the age of reproduction. Last but not the least, we should also consider the possibility of infection due to multiple matings.

So, taken together sexual selection, ecological constraints, physiological considerations of a species these together pose different selective pressures that together determine the evolution of mating systems.

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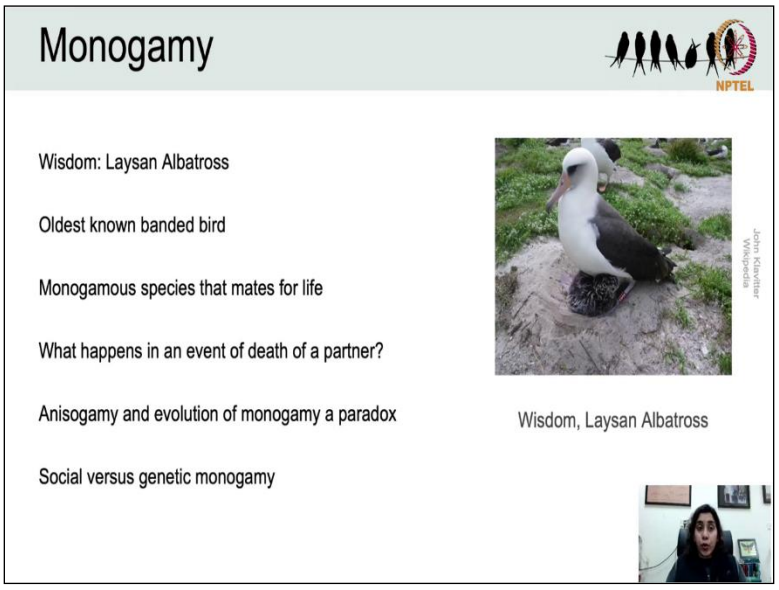

We know that 90% of bird species are monogamous. In the picture here you can see a female Laysan albatross wisdom who was first banded in 1956, that makes her the world's oldest known banded bird. She has had over 30 chicks and the most recent one is with her long-term mate Akeakamai in the spring of 2021 at the incredible age of 70 years. Laysan Albatrosses are known to be monogamous species that pair for life. If a mate dies a new mate may be acquired, but the question about the paradox of monogamy given that males must maximize mating still arises. In order to address this we must understand that monogamy in birds can be social or genetic as we discussed. Now, let us look at these mating systems using some examples.

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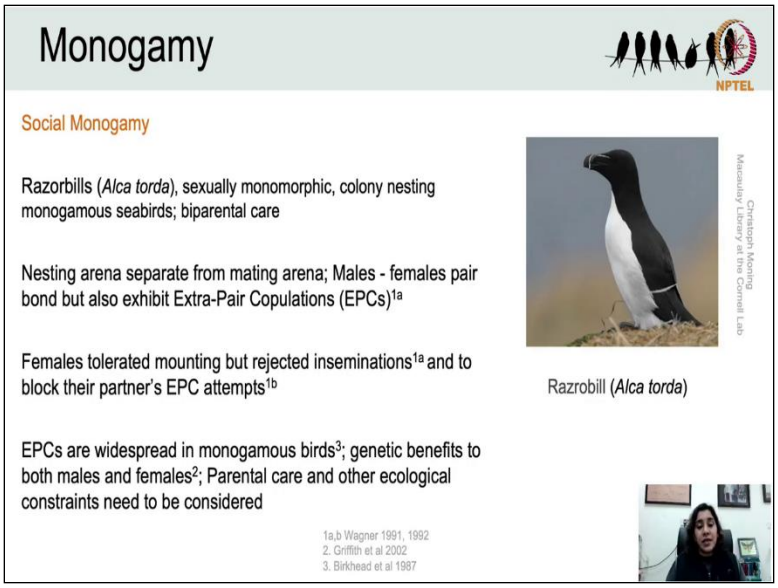

In this picture you have a Razorbill and Razorbills are sexually monomorphic colony nesting monogamous sea birds in which both males and females participating in providing care for the offsprings. In these sea birds, the nesting arena is separate from the mating arena and all the matings occur exclusively in the mating arena. Since, there are no resources in the mating arena any male or female arriving at the mating arena can be safely concluded to be seeking mates. Unpaired males and females visit the mating arena seeking partners but occasionally males and females belonging to a pair bond may also visit the mating arena. Studies have suggested that the pair-bonded males visit mating arena seeking extra pair copulations whereas females visit the mating arena to block their partners extra pair copulation attempts. However, when pair-bonded females arrive in these mating arenas males approach these females to attempt to mate with the visiting females.

In a study conducted on Razorbills by Wagner it was found that while the pair bonded females tolerated mounting by males, but they rejected insemination. This was especially true for females that had already laid the egg. Data from the study suggests that 22 out of 107 extra pair copulation attempts that were recorded on pre-laying females were successful whereas 0 of the 55 extra pair copulation attempts recorded on post laying females were successful. So, for post laying females, males who tried to copulate with these females did not result in mating. Now, we can ask that how do the females resist or stop insemination if they tolerate mounting how do they stop insemination?

Well, females can resist insemination from mounting males by stiffly pushing down their tail and not allowing the males to make cloacal contact. Further, there is evidence that the females can even eject the sperms of males in this species. This implies greater control over extra pair copulations by female Razorbills than one would assume. This also highlights the importance of behavioural studies in understanding the ecology, behaviour and evolutionary biology of mating systems.

Visiting females were found to block extra pair copulation attempts by their partners in this species. Now, extra pair copulation is widespread in monogamous birds providing the opportunity to maximize mating for males and offering genetic benefits by matings with better quality males and insurance against infertility of social partner for females. A study by Griffith at al. conducted genetic analysis on more than 150 bird species and it shows evidence of extra paternity in 86% of the species examined and that is a very large number.

So, these birds were socially monogamous but not genetically monogamous. Despite this social monogamy still offers advantages. For instance, birds breeding with former partners show reduced aggression and better synchronization between the breeding pairs this allows them to breed more rapidly and efficiently thereby in enjoying higher reproductive success. It also insulates against stochastic ecological conditions resulting in not being able to find any mate in a breeding season.

Also mate fidelity becomes important when the energetic burden of parental care and the duties towards taking care of the offspring needs to be put in consideration.

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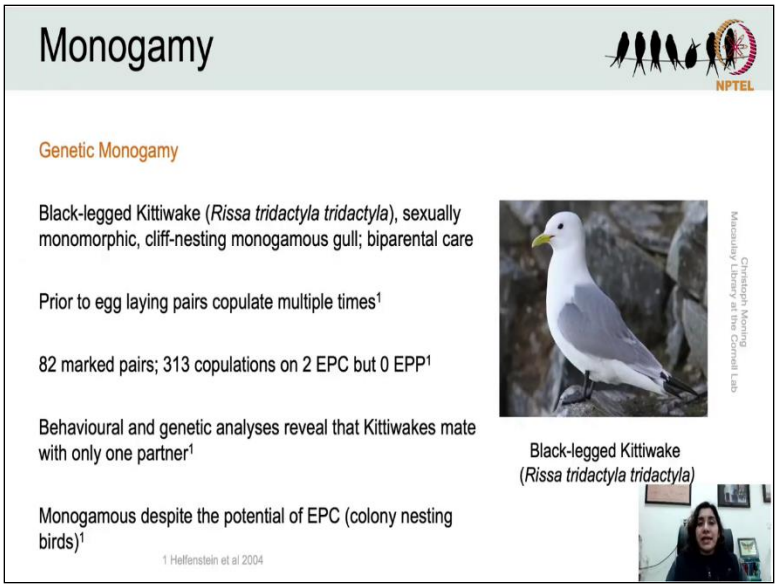

Now let us take the example of a species that is genetically monogamous. In the picture, the species presented is the Black-legged Kittiwake and these are sexually monomorphic cliff nesting gulls who are monogamous. Here again both males and females provide care to the offspring. In a study conducted on the species 82 pairs were marked and studied to examine their mating behaviour and it was found that prior to laying eggs, pairs copulate multiple times: about 14 times per clutch on an average. Further, of the 313 recorded copulations across 82 marked pairs only in two instances extra pair copulations was recorded. Last but not the least, paternity analysis in the species revealed that of the 119 offspring recorded in the study not even one provided evidence for extra pair paternity. Thus, both behavioural and genetic analysis revealed that kittiwakes mate with only one partner and are genetically monogamous species despite the potential of extra pair copulations given that they are colony nesting birds, which has a good potential access to mates outside of the pair bond, because there are nesting females and males in close proximity.

It has been proposed that the high level of parental care requirements in combination with paternity assurance by multiple copulation may have driven the system into one of the best known examples of genetic monogamy.

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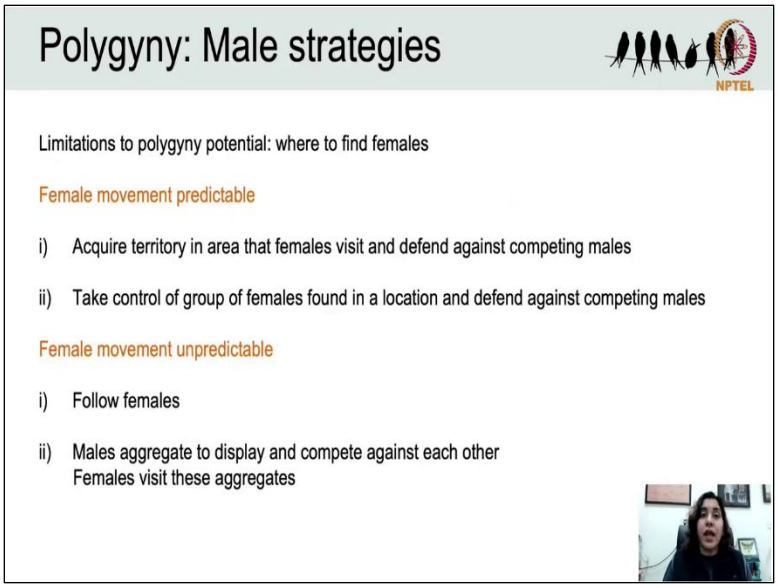

Now, what strategies can the males adopt in order to maximize their chances of matings? It really depends on many factors and one of the most important factors as we discuss is where to find the females. Suppose that the female movement is predictable in relation to the location of say critical resources like food or nesting sites or roosting sites. Now, females will arrive at these locations individually in search of these resources and if they arrive in an asynchronized manner, not necessarily together in a large number, then what a male can do is simply acquire a territory in that area where the females visit and defend that territory against competing males and wait for the females to arrive.

Alternatively, if females are gregarious and gather in large numbers in a specific location which could be unrelated, (this gathering could be unrelated to reproduction) then the male has the opportunity to access a large number of females together in a single location, gaining mating privileges by keeping rival mates out. Now, if female movement is not predictable then what does the male do? The male can simply follow the females instead of waiting for them to arrive or the males can gather and display in a certain location and wait for females to visit. Now let us take a look at each of these different strategies in birds using some examples.

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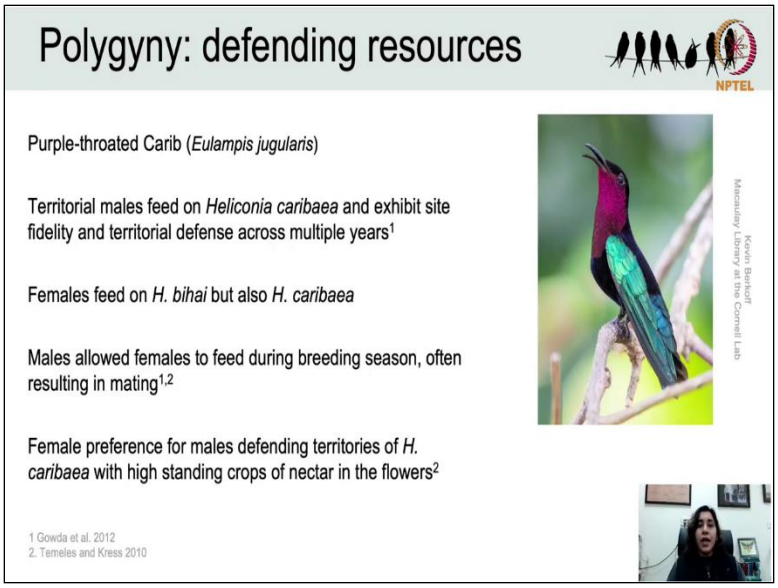

The Purple-throated Carib is a sexually monomorphic hummingbird native to the mountainous islands of the eastern Caribbean. However, males are larger than females and studies have found that males feed on *Heliconia caribaea* whereas females feed on heliconia species, a different *Heliconia* species, *Heliconia bihai* but they also feed on *Heliconia caribaea*. Males defend their territories which includes rich source of nectar from flowers of these *Heliconia* plants and they exhibit high levels of site fidelity defending the same plant across multiple years as found by Dr Vinita Gowda.

Males defend these plants against conspecifics and heterospecifics during the breeding season but also during the non-breeding seasons even when the plants are not flowering. During the flowering season, the nectar produced by the flowers within the territory of male is in far excess of the energy requirements of males. Yet, males defend these plants aggressively against intruders even when they have satiated themselves. So, why do they so?

So, researchers have found that males defend their territory aggressively against intruders during the breeding season but they allow conspecific females to gain access to the flowers to draw nectar. They have also found that when females visit to feed on nectar from these flowers it provides mating opportunity to the males. So, the males who have access to these nectar-rich flowers also end up having access to females who arrive to his territory in search of nectar, after the nectar levels of flowers from undefended plants have diminished.

Thus, males who could better defend the nectar-rich flowers against other males not only preserve the nectar for their own consumption but also make it available to females thereby securing mating opportunities for themselves. In fact, females in the species were found to prefer males who own richer territories with higher standing crop of nectar in the flowers. Here, defense of a resource allows the males to access multiple females and thereby maximize its number of matings.

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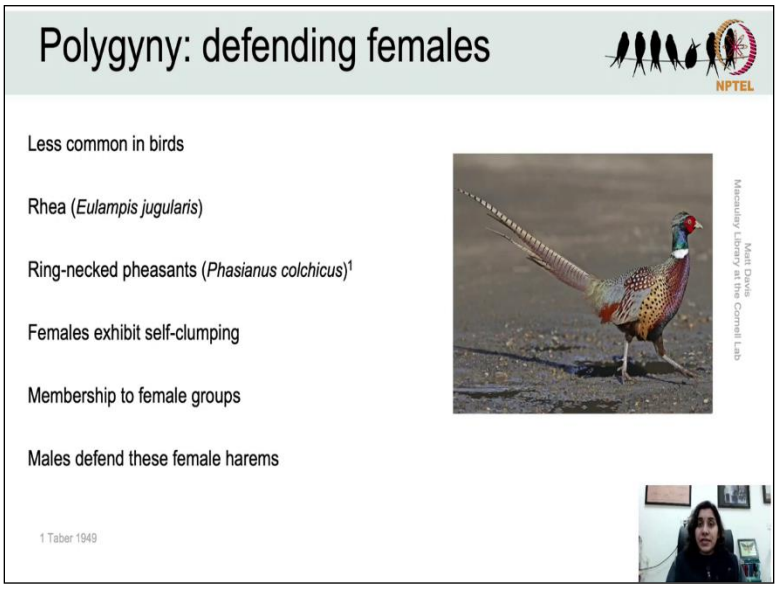

Female or females of Ring-necked pheasants on the other hand, exhibit self-clumping and membership to this female group is variable. Now, new individuals join throughout the summer to these female groups and the gregarious females are known to arrive at male territories together thereby allowing the males access to multiple females. Now, here the difference is that the females are clumped or are gregarious for a completely different reason and these groups of females arrive to male territories together as a large group. And now the male will have access to this entire group of females that have arrived to its territory.

Now, breeding is staggered or asynchronous in the species which means that not all females are reproductively active or receptive together during a small period of time, it is staggered. This allows a single male to mate with multiple sexually receptive females in the female group at any given point of time at another point of time another set of females will become sexually active and the male continues to have access to these females.

A large number of females, if they are reproductively active together, then it becomes harder for the males to defend all the females from rival males. Now, remember energetic constraints to mate defense is also important. So, the males can defend these large harems of females and mate with the females who are receptive at a given point of time and mate with the others who become receptive at a different point of time.

This is female defense polygyny and this is less common in birds and known for certain only in certain species of pheasants and in the Greater rhea.

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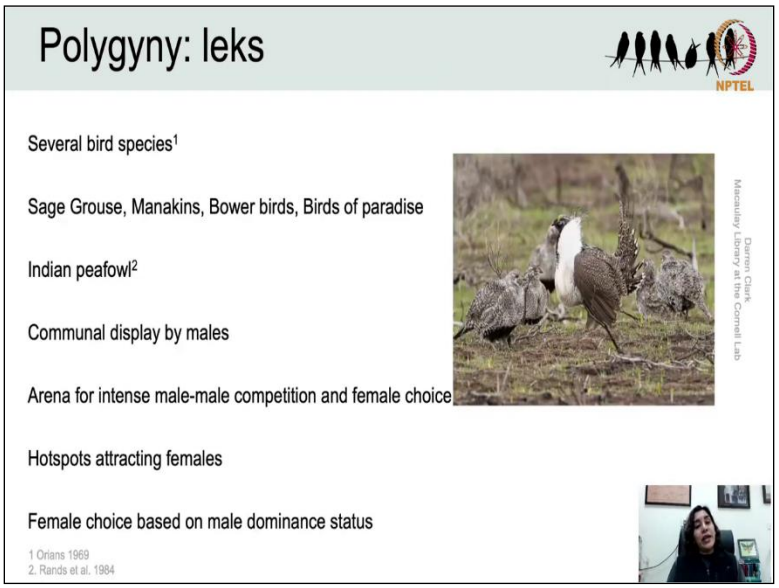

Now, let us look at lekkig behaviour in polygynous species. Lekking behaviour is known in several species of birds such as Sage grouse, Manakins, Bower birds, Birds of paradise and of course the Indian peafowl. What is a lek? Basically, a lek is a resource-free arena that provides grounds for communal display where males and females congregate for exclusive purpose of reproduction. The males display and the females choose. Here the males do not directly defend the females, as in the case of the Purple-throated caribs and the Ring-necked pheasants. On the other hand, what the males do is to compete against each other thereby establishing a dominance hierarchy within males and females then choose males based on their relative status in this dominance hierarchy. Thus, leks are considered to be arenas for intense male-male competition and female choice. Lek mating system is known to increase the variance in reproductive performance in males wherein a

very small fraction of displaying males secure most of the matings. As males join these aggregates, the leks themselves become hot spots which attract females looking for mating opportunities.

This explains why it makes sense even for lower ranking males to join these leks even though most of the mating will be secured by the higher ranking males because if the lower ranking males join these leks, they simply increase their chance of reproduction with females who would be visiting and would be otherwise very hard to find. When would such a situation arise? Such a situation can arise if the resources are very widely scattered and it is not economic to defend such resources.

In mammals, one of the most well-studied example of lek mating system comes from the studies on a species in India, the Blackbuck through the studies of Dr Kavita Iswaran from the Center for Ecological Sciences. IISc, Bangalore.

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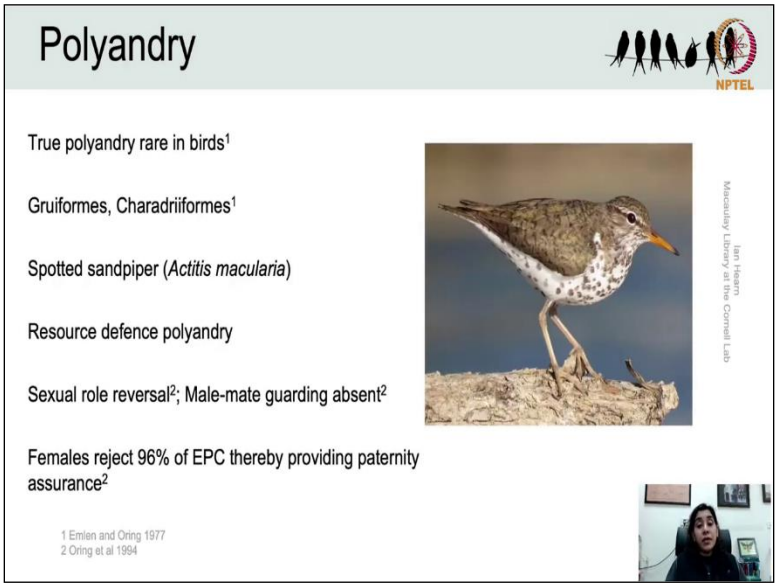

Polyandry is the other major mating system in birds. True polyandry is extremely rare in birds and is known to be found in less than 1% of the birds that have been studied so far. Most documented cases are restricted to the avian orders Gruiformes consisting of crane-like birds and Charadriiformes, consisting of waders and shorebirds. Only three polyandrous bird species have been studied extensively - the spotted sandpiper being one of them.

In the image here in the slide you can see a Spotted sandpiper. In this species males primarily provide parental care and they do not re-mate till the current clutch successfully completes. Predation is also extremely high in the species but females are known for their ability to replace failed clutches rapidly, which means the physiological constraint of multiple clutches is reduced in this species.

Given that this physiological constraint of multiple egg-laying is sufficiently relaxed in females, they have a very high reproductive output which far exceeds available males. This in combination with the fact that the males invest heavily in parental care explains how polyandry can exist in this species. Females exhibit resource defense polyandry wherein females compete with each other for and defend critical resources that are fairly clumped spatially allowing females to monopolize them. Thus, this species also provides an excellent example of sexual role reversal. The degree of polyandry in the species is limited by the availability of males. The males do not guard the females even though there is great chance for cuckoldry. Part of the reason could be because female, to an extent, provides paternity assurance to a male for a given clutch by rejecting 96% of the extra pair copulations that the female has access to.

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Now let us look at various courtship rituals in birds. Birds provide extraordinary examples of courtship displays and a lot of work has been done in this area over the many decades. Courtship displays are a result of generations of choosy females who select males based on the displays,

which could comprise of songs or dances or both, or building structures or other kinds of performances and rituals that the male birds have evolved to exhibit in order to secure the approval of females.

Let us first look at one of the most fascinating forms of courtship rituals in birds which is giving nuptial gifts. Now, the most common nuptial gift that is given by male birds to females is food. Male courtship feeding is one of the most fascinating subjects and a lot of work has been done in this in relation to mating and breeding behaviour in birds and it is found commonly in several species of kingfishers, bee-eaters, kittiwakes, fly catchers. But one species in particular has been studied extensively in relation to courtship feeding and that is the Common tern.

In this image you can see Common terns which are exhibiting courtship feeding and the function of this behaviour has been debated and many possible hypotheses have been proposed to explain the evolution of this behaviour. Many of these hypotheses have actually been tested in the Common tern and I have given reference to some of the studies which have examined courtship feeding in the Common tern.

One of the hypotheses suggests that courtship feeding provides vital nutritional contribution by males to the females towards the energetic expenditure of egg production. In fact, it has been shown that female Common terns that were experimentally supplemented with food, laid more number of eggs and higher quality of eggs than those females who did not have additional food given to them. Another hypothesis suggests that courtship feeding gives the males prolonged access to the female or may even enable them to prolong copulation while the female feeds.

This could then be a strategy for the males to increase the probability of fertilizing the female's eggs or as a means of mate guarding ensuring that no other male gets to copulate with the female, thereby assuring paternity for itself. Finally, it has also been proposed that courtship feeding could be a means of male quality assessment by the females.
In Common terns it has been found that courtship feeding is correlated to the rate of chick-feeding by males. Thereby, it is proposed that this could be an indicator of a better quality males who is capable of gathering sufficient resources for its offspring.

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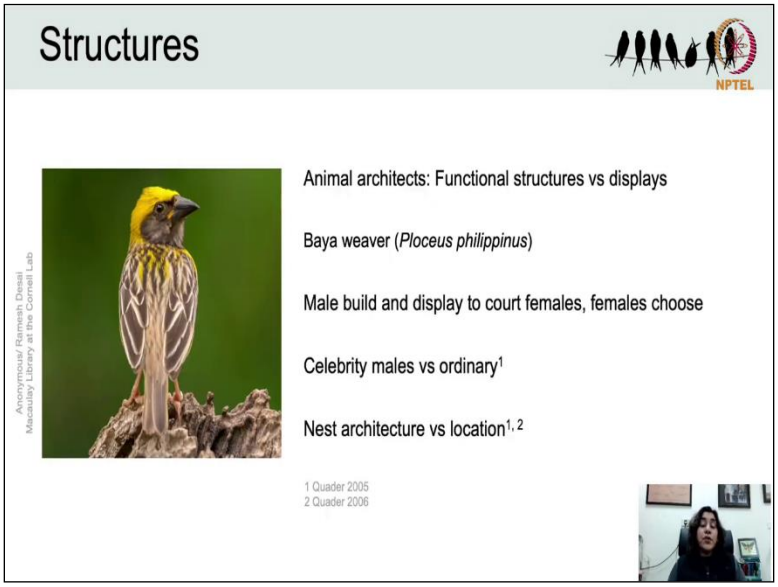

Birds can also rival the most skilled architects when it comes to building elaborate structures. These structures include nests which can be used in courting females to mate with the male and to lay eggs in the home that the builder has built. Or, these structures could simply be display structures with little or no functional value. In this case these display structures are meant to signal superior quality of the male. Typically, it is the males that build the structures and it is the females who give the verdict on whether the male structure is good enough or not. And now we understand how this works via sexual selection.

Let us take the example of the Baya Weaver. These birds are common in the agricultural landscape of India and males as you can see.. sport a yellow-brown breeding plumage during the monsoon which coincides with their breeding season. Unlike many bird species in which both sexes or only females build the nest, in the case of Baya Weavers. males exclusively build specialized pendulous nests in order to attract females.

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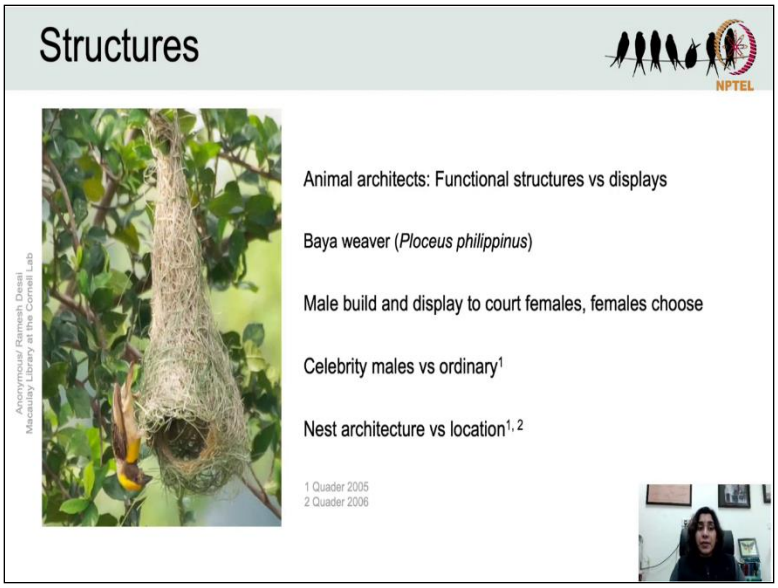

Many males may build their nests on the same tree, although each defends a small territory around its ownness. Now the males after building this nest display on top of these creative extravaganzas to woo incoming females. Females who come to visit inspect the nests and upon satisfaction may copulate with the male. The male then completes the nest by giving the brood chamber a floor and also builds an entrance tube. Parental duties however are left to the females and it has been shown that some males are far more popular with the females and receive far more visitations from females who also stay longer with these males than with other males. Now clearly the males are investing in building these elaborate structures, on which they display and which is attracting the females, but what exactly do the females base their final mate choice decision on? It is tempting to believe that it is the nest architecture on which the females makes the mate choice decision. However, studies conducted by Dr Suhel Quader in great details on this species have shown that in fact it is not the nest architecture but it is likely the location of the nest that finally secures the mate choice decision by the females. This could be due to safety considerations of the nest locations and this is not surprising.

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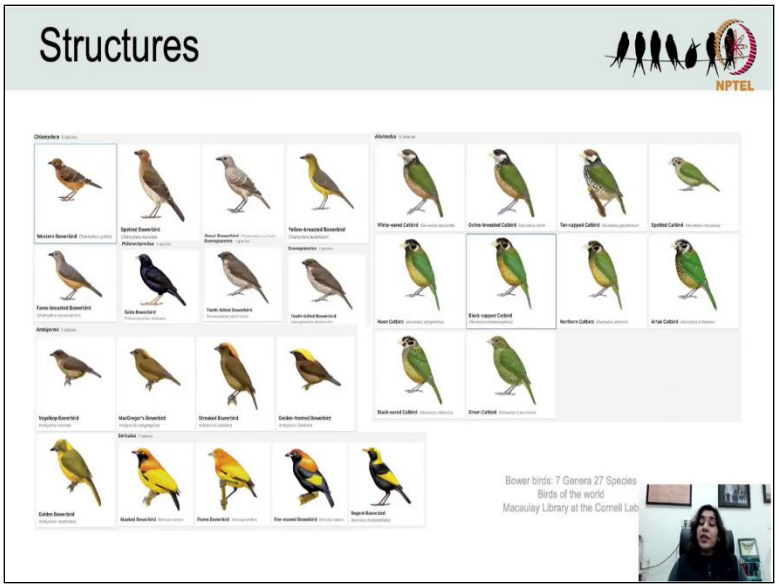

On the subject of building structures to attract females, one has to mention about Bowerbirds. Bowerbirds include 25 or 27 species belonging to seven genera and these birds live in the tropical rainforests of Papua New Guinea and Australia. Male Bowerbirds build a bower or a shady enclosure enclosing a display arena which serves to attract and court receptive females. The males meticulously decorate the bowers with a variety of items including fruits, flowers, bottle caps, snake skin, feathers etc. The bowers are actually exquisite creations that are no less than art galleries, if you like, and require a great deal of effort to build, maintain and defend. Often the bower items include objects of a particular kind of colour that the females may prefer and each species seems to have its own notion of what item will be put on exhibition. Some Bowerbirds do not build bowers, instead maintain only a decorated display arena. Members of this group provide excellent model system to understand how sexual selection can drive the evolution of extravagant male displays in particular building structures.

You can see some excellent videos on youTube on the courtship rituals of Bowerbirds that can put us humans to shame.

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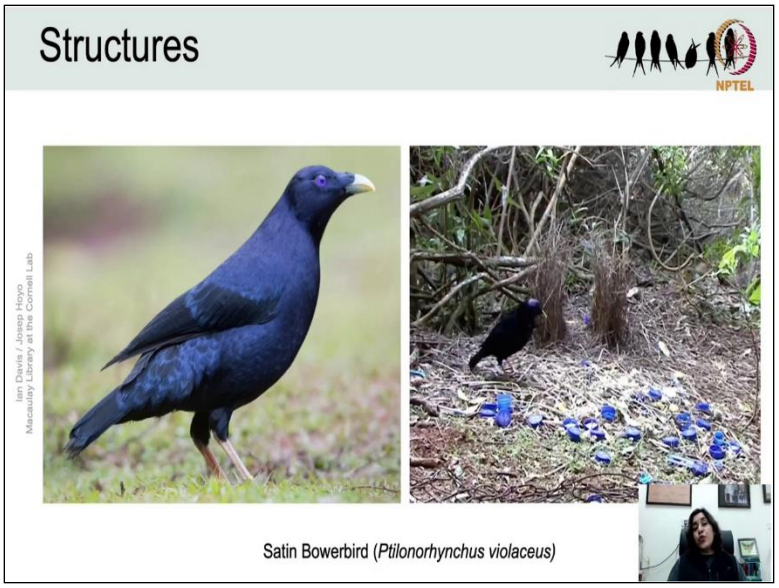

Now bowers can be of two broad categories Avenue Bowers and Maypole bowers. Avenue bowers are made of two parallel walls made of sticks that are arranged vertically and the area on the either side of the bower can be used as a display court where the bird displays items that it has collected to decorate its bower. Now of the 27 bowerbird species what I am showing right now here is a Satin bowerbird.

Satin bowerbirds construct avenue bowers with sticks that are densely packed together and the walls of the bowers are thicker towards the base and bulge out at the base and curve back in towards the top. This one as you can see has a liking for blue and Satin bowerbirds are also known to steal items from the bowers of rival males and sometimes they even destroy the bowers of their rivals.

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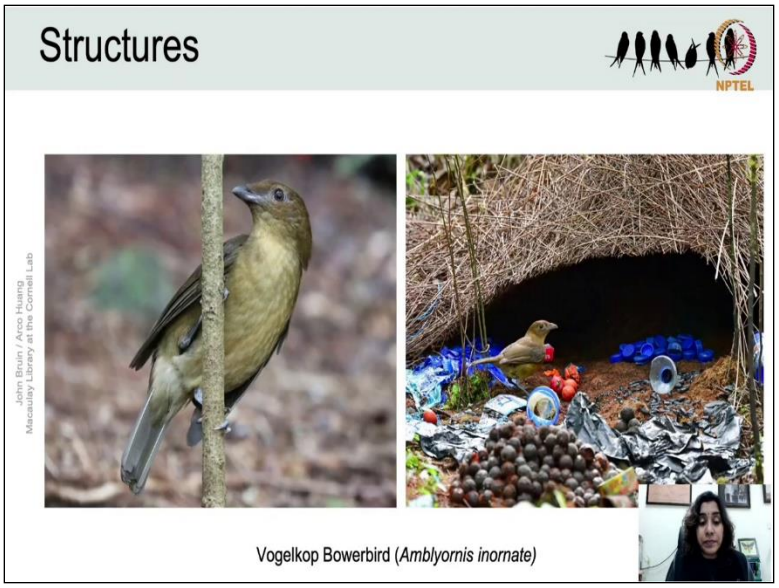

This one, on the other hand, is a Vogelkop bowerbird. As you can see the main in this case is less flashy than the Satin bowerbird. But it compensates for that with its very coloruful and beautifully decorated bower that it has constructed as a maypole bower. Maypole bowers are structures that are built around a plant sapling, that acts like a pole. It consists of a circular display court with sticks stacked around the pole sometimes resembling a hut-like structure as in the case of this species.

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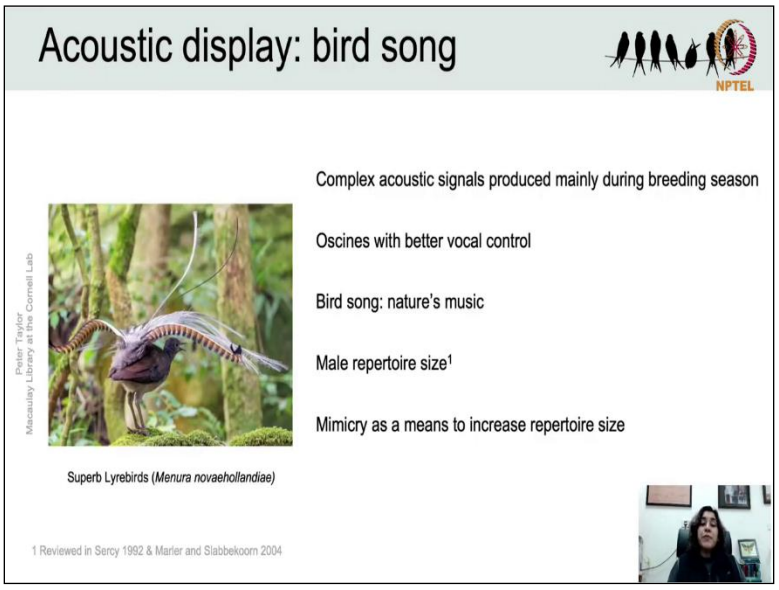

Many species of birds court females by elaborate songs which are complex acoustic signals produced mainly during the breeding season. The group of birds that especially excel in song

production are called Oscines. They belong to the order Passeriformes and have better vocal control than sub or signs that too belong to the same order but to a different suborder. So, extraordinary is the ability of birds to produce sound that even great music composers like Beethoven use birdsong as an inspiration in their composition.

Some birds have a single species-specific song although there may exist variation between males, on the other hand, some other species have males singing a variety of songs and the collection of this variety of songs sung by a bird is called its repertoire. Some species incorporate the sounds of other birds and of sounds in the environment of the bird into the repertoire in order to increase their repertoire size.

The Lyrebird as shown here is one such example but there are many other examples of mimicking species in the avian world. Conspecific females use the repertoire size to make mate choice decision and this has been tested using manipulative experiments in the lab and using observations in the field. It is known that female birds prefer to mate with males that have larger repertoire size. Why should that be? One possibility is that a larger repertoire size is an indicator of a better-quality male.

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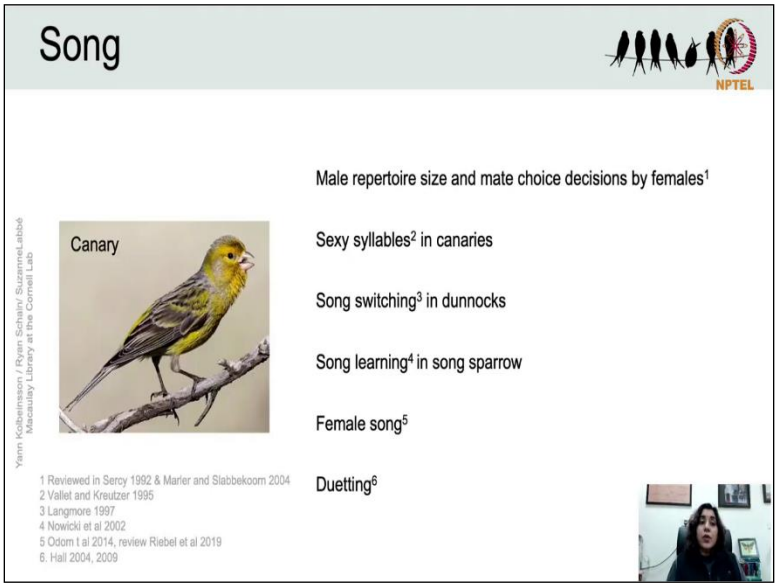

Now, what do the females look for in the song of the male? Like we said ,it could be many things: it could be the repertoire size, but it could also be other features of the calls such as the ability of

the males to produce certain kinds of complex patterns wherein the notes of two different frequencies are uttered very rapidly. It has been argued that such notes are very hard to produce as they test the song production limits of the birds and males who can produce such notes are likely to be of superior quality. Such studies have been conducted on Canaries and we have found support for this in canaries.

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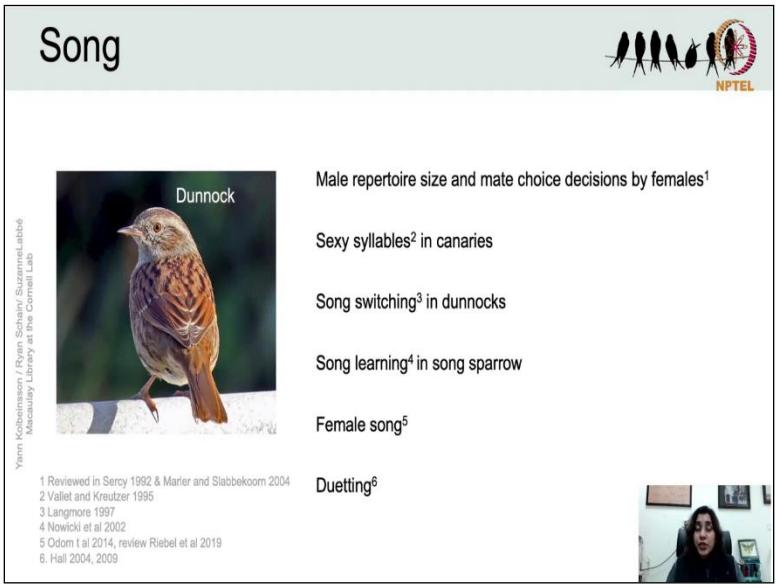

Another feature that some females may like is song switching. Males can switch from one song type to another song type during the courtship display as well as during their territorial displays. Females are likely to get habituated to a repeated song which would be monotonous whereas a song which is less monotonous in which different song types are being switched from one type to the other will increase the male's ability to attract the female's attention or retain the female's attention. This has been shown and studied in Dunnocks wherein female Dunnocks prefer males who exhibit high rates of song switching and the males increase their song switching rate in the presence of breeding females. I have given the references to the relevant studies in the slide itself.

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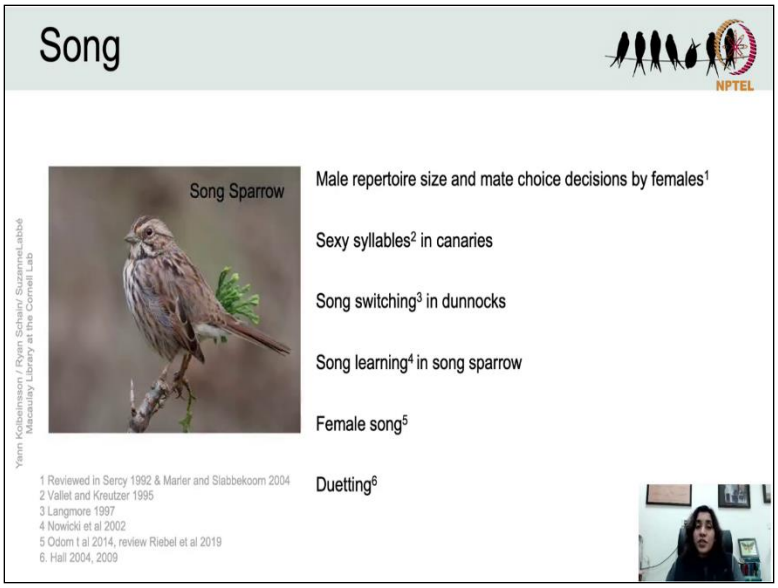

Song sparrows are amongst the most widely studied species on various aspects of bird song. A study conducted by Nowicki et al. showed that female song sparrows assessed the males based on their song learning ability and preferred males who were better learners. But in all of this the focus has squarely been on male song and the possibility of female birds possessing songs and using it in mating behaviour was largely ignored in the scientific community. Only recently researchers have found that female song is far more common in birds than previously thought. It was also shown in a separate study that female researchers were more likely to be authors of papers that researched female bird song. Bird's song was historically thought of as a male trait but women scientists proved this to be wrong. Thus, we must remember that while scientists try their best to be as unbiased as possible, after all they are all humans and this highlights the importance of diversity in science.

Anyway, last but not the least, several bird species are also known to engage in what is known as duetting behaviour where males and females sing together in a collaborative fashion. Avian duetting is not uncommon and has been reported in more than 400 species and various hypotheses have been put forward to explain the evolution of avian duetting but some of the important ones revolve around forming and maintaining partnership in mating pairs.

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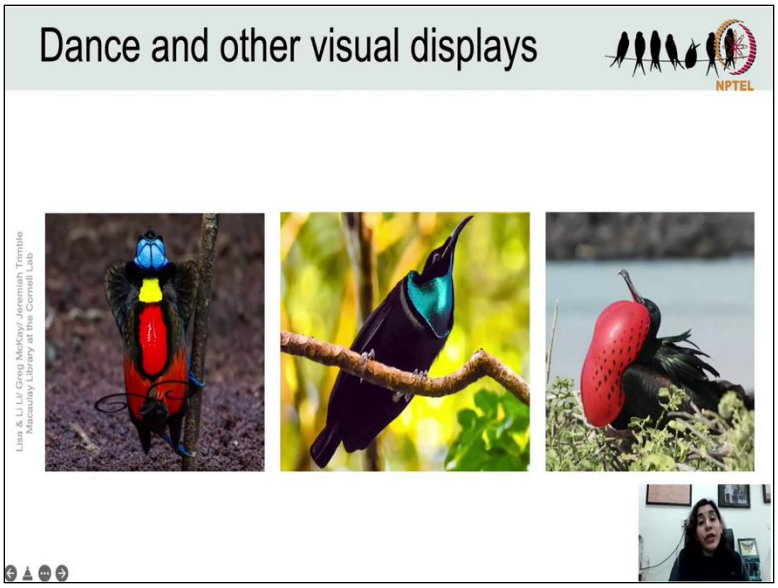

However not all birds are gifted singers. Those who lack the vocal artistry, compensate for that by their looks. Shown here is a Wilson's bird of paradise a Magnificent riflebird and the Greater frigatebird. What do they have in common? Their flamboyant plumage coloration, of course. These birds are certainly more glamorous looking than the dunnocks and the song sparrow that we saw earlier. Many birds employ visual signals such as plumage coloration, contrast, patterns, postures, monotonous body movements to complex dances to woo females.

In the animal kingdom, including birds, it is rather common to find females to be more modestly dressed than the males.

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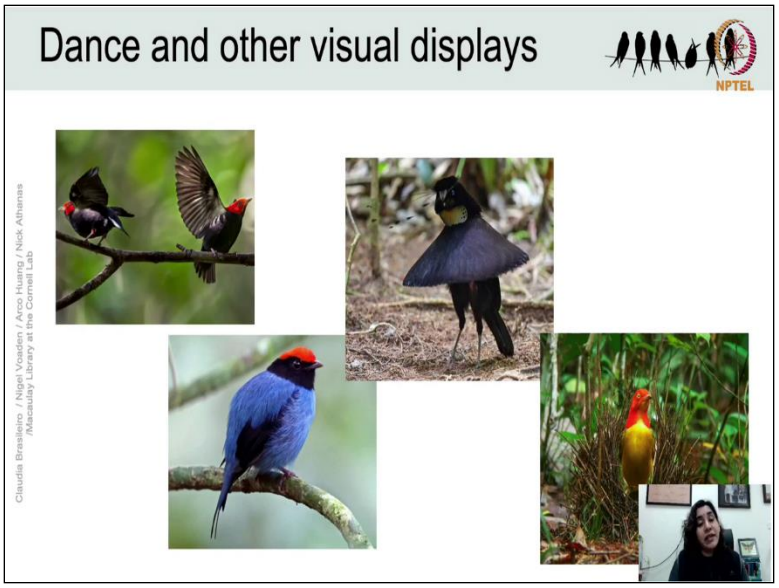

Take for instance the moon walking red-capped manakin or the synchronized carousel display of the Blue manakin; the extravagant plumage, visual display and the fancy footwork of different species of birds of paradise such as the Western parotia or the elaborately decorated bowers and choreographed dances of some of the bower birds such as the Flame bowerbird. Courtship displays through visual signaling, in fact, is unparalleled in birds.

For these magnificent visual displays, we have sexual selection driven by dull colored choosy females to thank.

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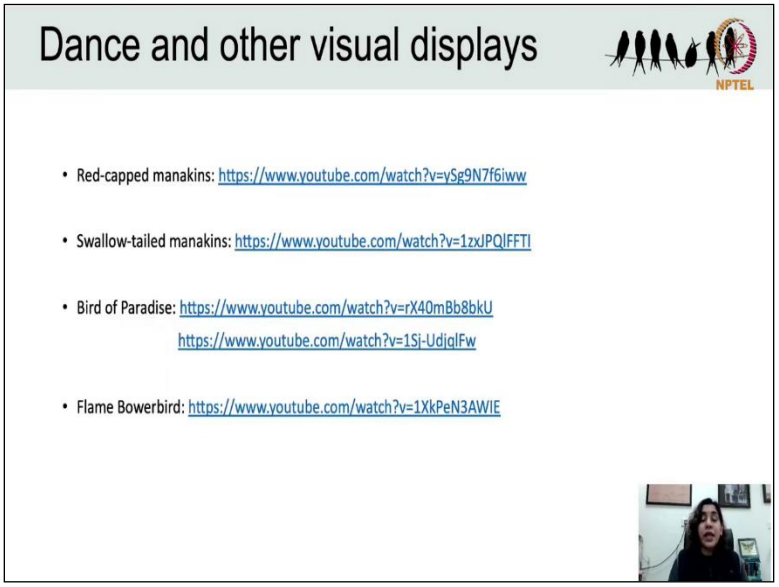

Here are some youtube videos that you can watch to get a full flavour of the dances and the moves of these birds which includes those of the red cap manakin the swallow tail manakin or the blue manakin, the western paroctia and other birds of paradise and the flame bowerbirds. These are indeed marvels of natures that make birds the undisputed masters of courtship rituals.

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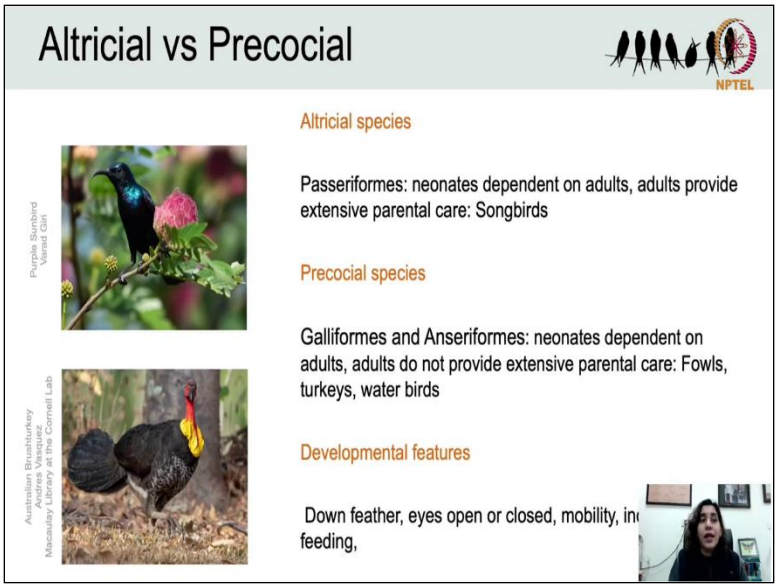

Once mating is accomplished yet another challenge begins which is to take care of the young ones. Parental care duties include building a safe nest, providing enough food and protection from predators to the young ones. Do all species provide care? If not, then what determines this? Do all species make nests? Are all nests of birds more or less alike? Who must put in the effort towards parental care duties males or females or both? Let us have a look.

In birds and mammals, there exists a gradient of developmental maturity of neonates across species. Many species especially songbirds hatch as immature, helpless young ones that take a lot of time to mature after hatching. They are greatly dependent on adults for support and care and such species are called altricial. Altricial species are characterized by sophisticated parental care that includes building complex nests, high attendance at the nests and to the offspring. And in the picture, you can see one such species which is a Purple sunbird. It is a songbird and songbirds are known to be altricial. On the other hand, many land fowls, turkeys and water birds have young ones that require minimal or even no parental care and are fairly independent of adult support and

care. Young ones that hatch out, seek their food on their own and only rely on parents for some degree of brooding and protection. Such species are called precocial.

Precocial birds are characterized by simple or minimal parental care, minimal nest attendance and simple nest structure. Megapods are super precocial and are not even present around their offsprings when they hatch. In the picture is the largest megapod of the world also known as the Australian brush turkey a precocial, promiscuous, mound-building bird. A range of developmental features of newly hatched chicks correspond to the gradient of parental care provided to neonates. And these are used to categorize the species into precocial or altricial. These include, whether down feathers are present or not, whether the eyes are open, whether the young ones are mobile upon hatching, can they feed themselves and whether they can move around on their own. If the answer to these questions is NO, then the species is altricial and if the answer is yes then the species is precocial.

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Seen here is the hatchling of an altricial and a precocial species a Tree swallow and a Spotted sandpiper. Note, the lack of down feathers, closed eyes, helpless, immobile looking neonate in the altricial species in comparison to the precocial birds. Now, if the species is altricial then the young one would require parental care this starts with nest building and here again there is an entire spectrum.

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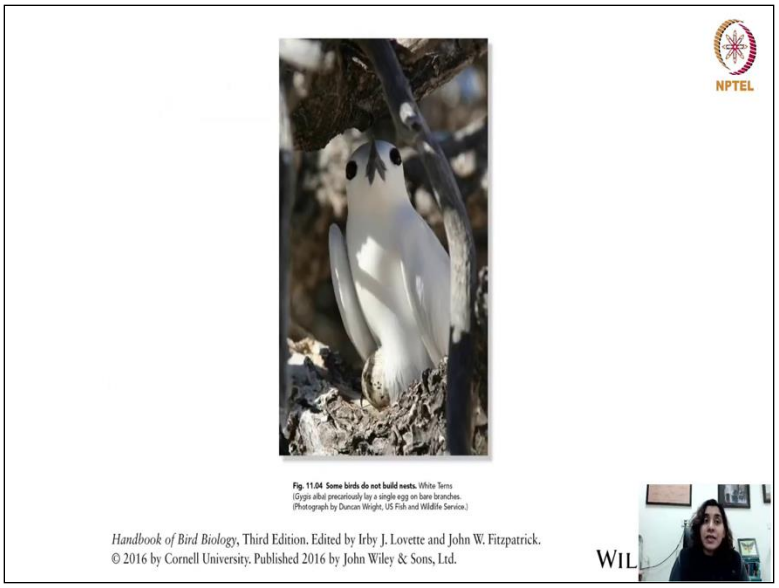

Some birds do not build nests at all as seen in this picture a white tern that simply lays its single egg, precariously on a branch of a tree.

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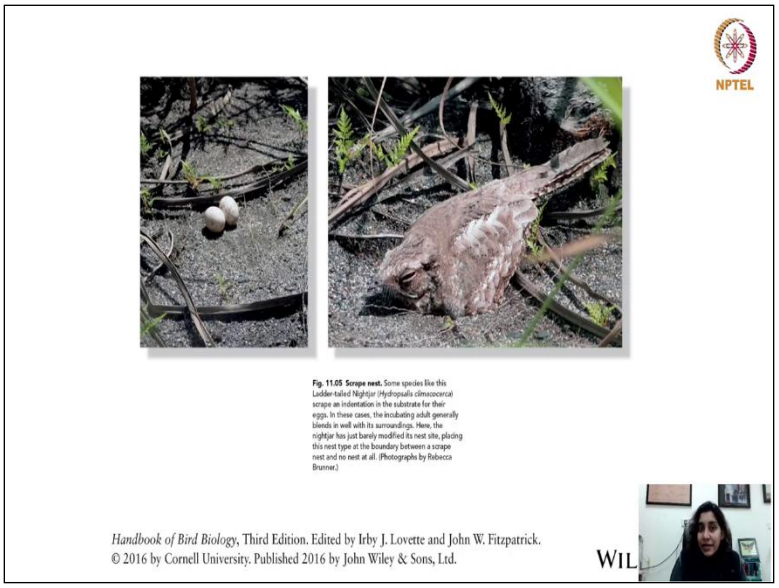

Then we have minimalist like this Ladder-tailed nightjar that make a scrape nest which is simply a small depression on the surface on which the bird will lay its egg. In this case the ground. Of course, the superb camouflage of the adult nightjar makes it nearly invisible to predators and those of you who have seen a nightjar know, what I mean by this.

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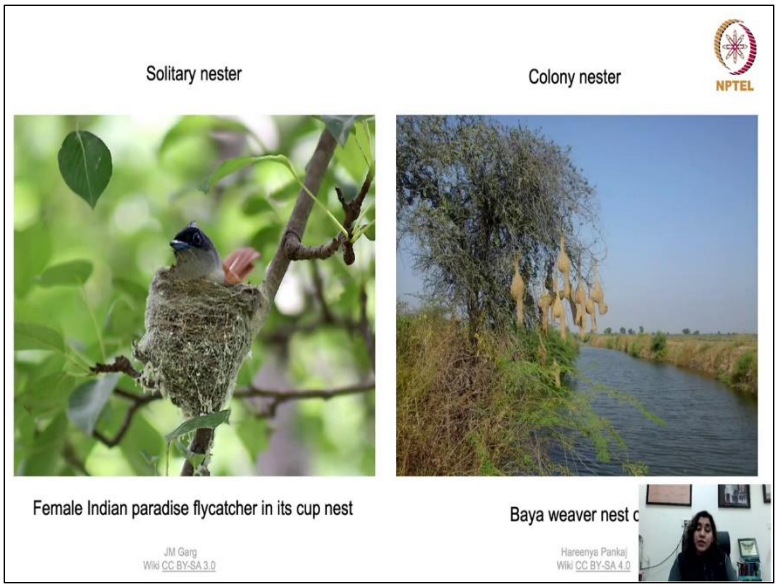

Birds can also be solitary nesters wherein a single individual or a pair builds a nest away from other individuals of the species such as the Indian paradise flycatcher shown here along with many other species of birds. Then there are colony nesters such as the baya weaver, cliff swallows, sand martins and many other species.

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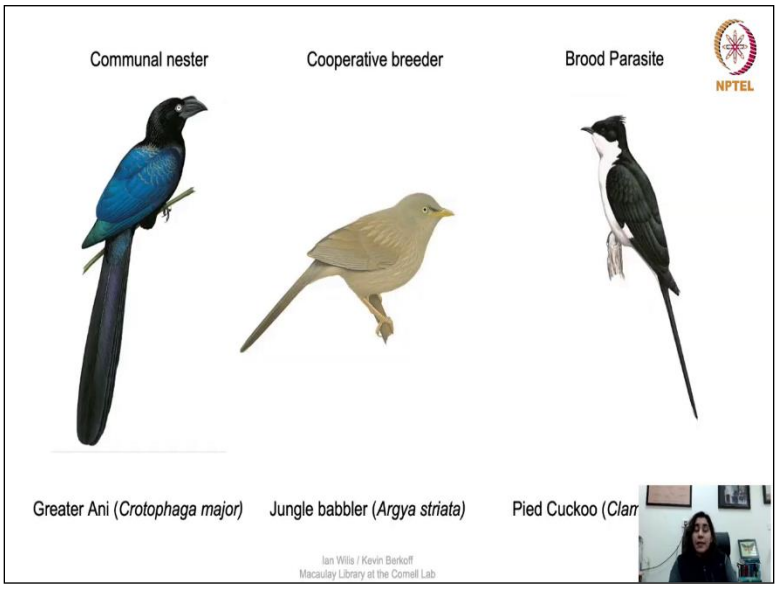

Some species are what we call as communal nesters and given here is one such example the Greater Ani. It is a cuckoo where many unrelated females form breeding groups and they lay their eggs in a single nest, sharing incubation duties. Yet other species as shown here the Jungle babbler are what we call as cooperative breeders where a single breeding pair sires all the offspring and all

other group members contribute to parental care. The Jungle babbler is a species that my lab works on and it is a cooperatively breeding species. Last but not the least, there are species which are called brood parasites. Seen here is a Pied cuckoo or a Jacobin cuckoo that is one such of the many broods parasites that belong to the cuckoo family. We know pied cuckoo as the 'Chataka pakshi' and it has important an important place in the Indian mythology.

Now, why do some birds serve as foster parents for a completely different species is something I will leave for you to think about.

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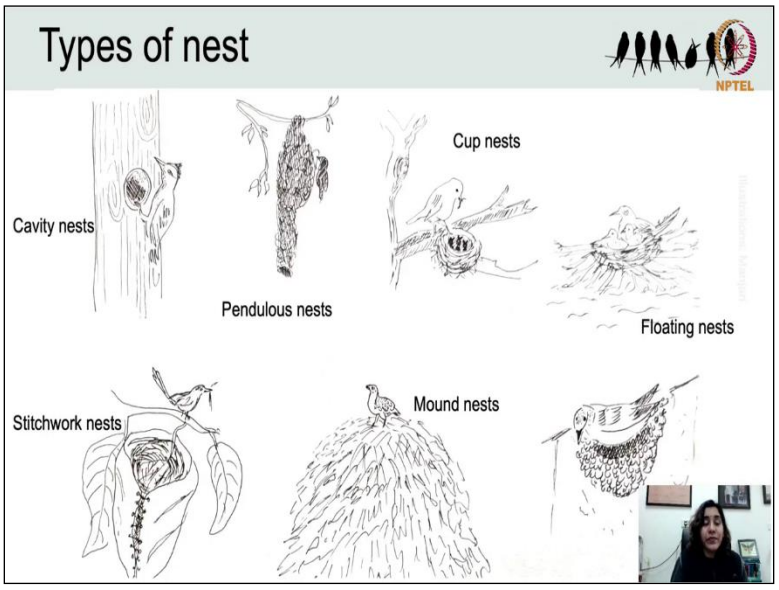

In this sketch you can see many different kinds of nests of birds and bird nest architecture is also an active field of research in itself and there are many interesting aspects to understand how how birds actually build these nests, the material that they use and how do they know how to build these magnificent structures. A word of caution to everyone here: Bird nest photography is unethical. Please do not take photographs of nesting birds as you may be disrupting months of their efforts and this may also result in nest predation causing the death of both the young and the adult. Only experienced researchers studying breeding birds should go anywhere near nesting birds and this also requires specific permits from the forest department. If you are on photography groups, please do your bid to discourage people from taking nest photos.

I have illustrated some different kinds of nests shown here is a cavity nest, pendulous nest, cup nests, floating nests which are basically made of vegetation floating on water found in several

water birds, stitchwork nest as that of the tailor bird; mound nest as that of the megapods and mud nest as that of the swiftlets.

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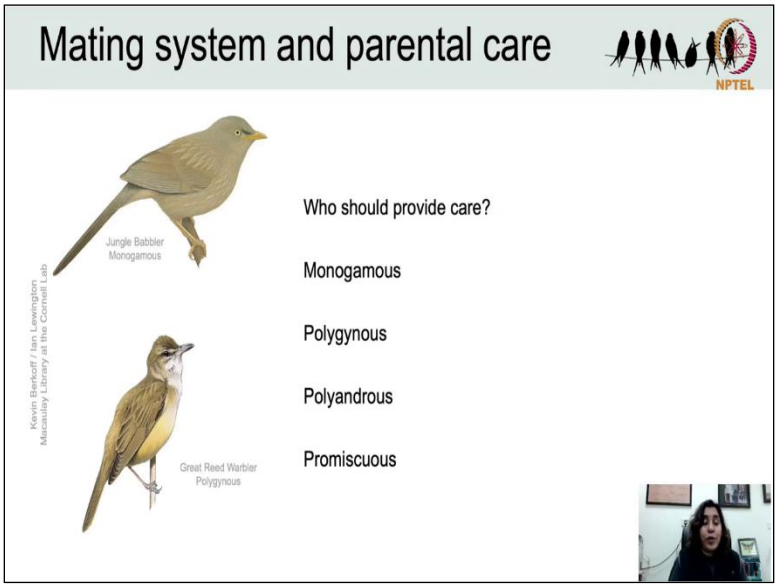

Now lastly let us ask who should provide care to the growing offspring? Given that the successful completion of reproduction includes not just mating but also providing young ones care such that they can emerge as reproductive adults, and this would impact the fitness of not just the females but also the males, the question arises who must forego their future mating prospects to stay behind to take care of the young ones?

In birds, given that they are the only vertebrates that are exclusively oviparous and the females lay eggs, naturally, the males have the opportunity to desert first and the fertilized egg is basically carried by the females who must lay it and cannot scoot off to seek other mates. So, naturally, (female) birds become more or less the primary care giver in many species of birds. But then why cannot they lay the egg and leave behind the offspring?

Turns out that there is more to this than just who lays the egg. There are many constraints that we have already discussed which are applied by sexual selection, the ecology of the species, the environmental constraints, resources available, the physiology of the species, all of which together determine not just the mating system but also the parental care system in birds.

So, for monogamous species it is expected that both parents will provide care or there is what we call as biparental care.

For polygynous species, we expect maternal care where the males maximize their mating opportunity by mating with multiple females and do not stay back to help the females to provide the young ones. So, it is the females who must provide care.

Polyandrous species where females mate with multiple males, typically it is the male that provides care therefore there is paternal care.

Promiscuous species can have either both parents providing care or neither.

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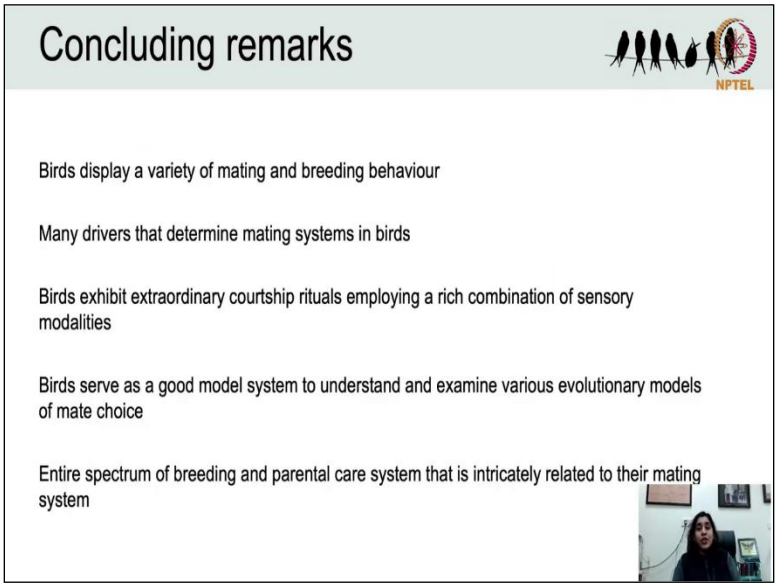

Alright, to conclude in this lecture we have talked about the variety of mating and breeding behaviour in birds. We have learnt that there are many drivers that determine the evolution of mating systems which include ecological constraints, physiological constraints, sexual selection etc. We also learned that birds exhibit extraordinary courtship rituals employing a rich combination of different sensory modalities to woo the females.

They exhibit an entire spectrum of breeding behaviour and parental care system that is intricately related to their mating system. More than anything else, birds provide an excellent model system to understand and examine evolutionary models of mate choice and test various hypotheses regarding mating and breeding behaviour.

Thank you for your attention. I am Dr Manjari Jain from the Behavioural Ecology Lab, The Department of Biological Sciences at IISER, Mohali. If you have any questions or comments I would appreciate if you would write to me, thank you.