Basic Course in Ornithology
Dr. Manjari Jain
Indian Institute of Science Education and Research, Mohali

Lecture -13
Social Behaviour

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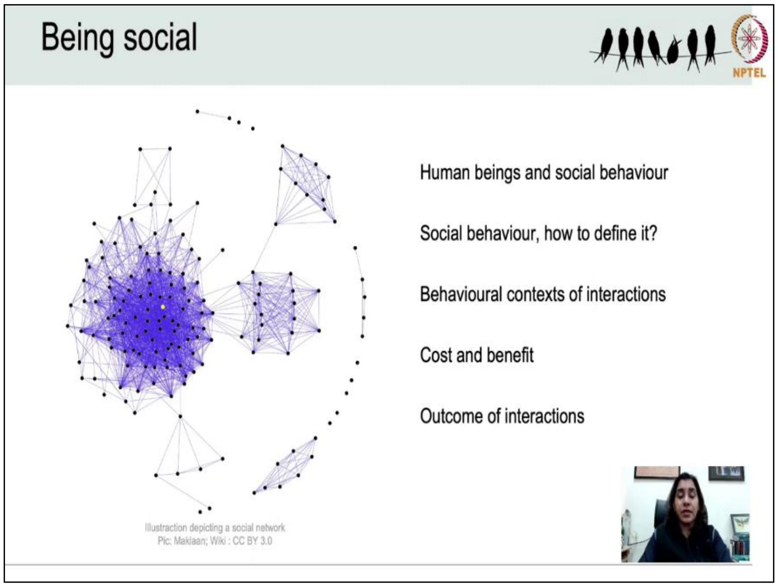

Hello viewers and welcome to the basic course in ornithology. Today's lecture is on social behaviour in birds. I am Dr. Manjari Jain from IISER, Mohali. Humans are known to be a social being and we live in well-developed societies with complex interactions between members of the group, which is commonly referred to as social behaviour. Social behaviour is a diverse set of behaviours and can span from temporary interactions that last just for a few moments to lifelong associations.

It can be exhibited between conspecifics or heterospecifics and is a fascinating subject of study in biology and has been studied for decades in diverse animal taxa. Birds too display a diverse array of social behaviour and mating and breeding behaviour is just one form of social behaviour wherein individuals belonging to the same species and typically of opposite sexes interact with each other in order to mate, reproduce and take care of the young ones.

After breeding is over these individuals may go back to their solitary existence meaning that they pair only for the purpose of mating and otherwise live solitary lives. Some other birds however continue to live and interact in stable social groups even when they are not breeding. So, the question arises of course what do we mean by being social. Social groups can be defined as aggregations of individuals in order to derive some benefit through social behaviour exhibited by these group members.

And it broadly refered to interactions between members of such a group of individuals in a manner that the actions of one individual affects another individual but also the actor itself. The behavioural context in which such interactions occur could be affiliative or agonistic and to understand social behaviour we need to understand how these groups are formed, the dynamics of interactions within a group and the costs and benefits of being a group member. We also need to understand the variety of social behaviour including the ones that benefit both interacting individuals and some in which neither benefit.

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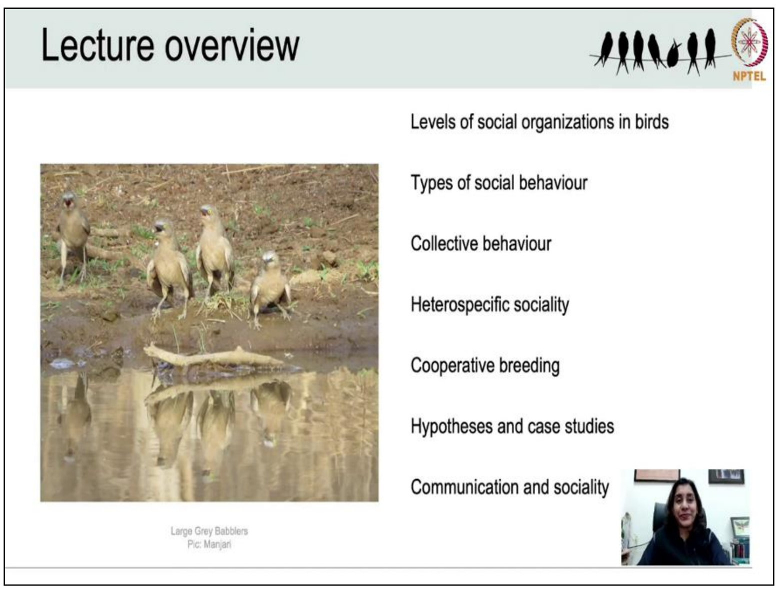

So, in this lecture we will discuss the different levels of social organization in birds and the various kinds of social behaviour that birds exhibit. We will then talk about collective behaviour in birds using the example of murmuration in starlings, touch upon a less studied but fascinating subject of heterospecific sociality as seen in mixed species flocks, and then move on to sociality in single species including those that live and breed in social groups.

We will also discuss the various hypotheses that have been proposed to explain the evolution of social behaviour specifically cooperative breeding and the costs and benefits of group living. We will also discuss case studies that have tested these hypotheses. Last but not the least, we will talk about communication and how it mediates social behaviour in birds.

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So, let us begin with understanding the levels of social organization in birds.

Some birds lead a solitary existence for most of their life and only pair during the breeding season. This includes several predatory species and other birds as well such as the solitary sandpiper. The solitary sandpiper only pairs during the breeding season and it even migrates alone. Some bird species gather in large numbers for a particular behavioural context, as in the case of these starlings who are flocking against a predator that you can see in the second image in the slide.

These temporary aggregations could also be at a given time of the year, for instance migratory birds that come together for the purpose of migration or could be temporary spatial aggregations as in the case of roosting birds. Sociality has traditionally been examined within a single species even though many animals including birds can also gather in what is known as mixed species social groups. In the case of birds, these are called mixed species flocks and typically this happens in the context of foraging where individuals belonging to two or more species can gather together on foraging grounds, as you can see in the third panel on the slide. Finally, some birds stay in conspiracy groups not only during a particular time of the year or for a particular behavioural context or in a particular location but throughout their lives. Typically, these are family groups and they can be called as truly social groups and we will discuss in greater detail about such groups in the lecture.

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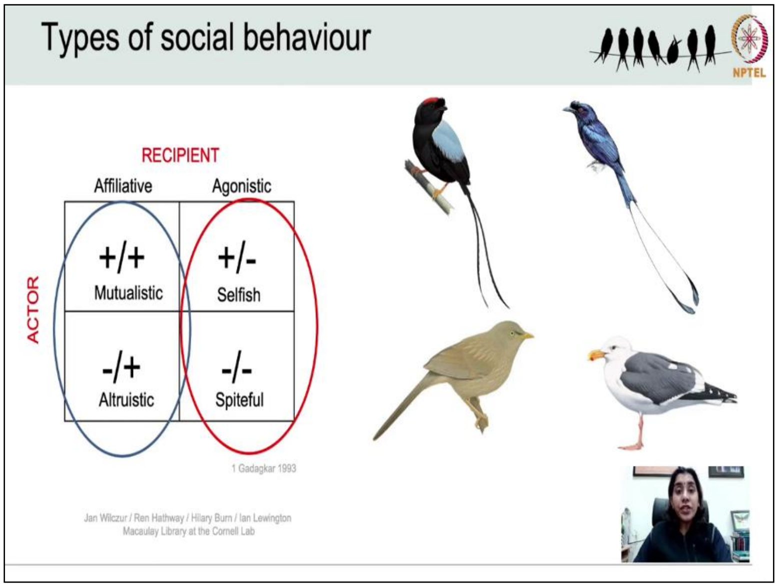

Social behaviour can be both affiliative or agonistic. Affiliative social behaviours include mutualism and altruism - an interaction in which both the actor and the recipient of an action benefits is called mutualistic. All forms of cooperation are mutualistic and this can occur between kin as well as non-kin. For an example of mutualistic social behaviour, let us look at the Long tailed Manakin behaviour.

Two or three male Long tailed Manakin form long-term partnerships for courtship displays in a lek exhibiting a cartwheel display in which the males hop over each other in order to quote the female. Although two or three males are involved in the display only the alpha male amongst these partners gets all the matings. So, how is this mutualistic? It was shown in a study that the beta male becomes the next in line for all matings in the future through his long-term partnership with the alpha male.

If the alpha male dies or disappear the beta male will take his place and the alpha and will become the alpha thereon and receive all the matings with the same set of long-lived females. So, the alpha male benefits immediately through this partnership with the other males but this partnership is beneficial for all other males in the long run as well. In a mutualistic interaction both parties benefit however altruistic social behaviours are behaviours in which the recipient of an altruistic act is benefited but the actor is harmed.

Birds provide several examples of altruism and the best examples come from cooperatively breeding birds such as the jungle babbler. In cooperatively breeding birds, members of the group forego their own reproduction in order to care for the young ones of the breeding pair. On the face of it, the behaviour seems paradoxical and the question arises how could such seemingly self-harming behaviour evolve. We will talk about this in greater details later in the lecture.

Among agonistic social behaviours there are two types - selfishness and spite. Social behaviour in which the actor benefits but the recipient is harmed is called selfish and this too is fairly common in the animal kingdoms and so in birds too. Kleptoparasitism is one such behaviour where some bird species such as the Greater racket-tailed Drongo steal food from other birds during foraging with other birds.

The Racket-tailed Drongo is a great vocal mimic and it can mimic the alarm calls of other species listening to which the foraging birds drop their meal and fly for cover and the mimic swoops in to steal their grub. Spiteful behaviour is when an individual risks harm to itself in order to harm other individuals by its action. A weak example of spite comes from the western gull in which pairs that have lost their eggs or their chicks have died were observed to attack other breeding conspecifics even killing their chicks.

The risk of injury or even fatality due to this combat incurred by the attacking gull is the fitness cost to the gull that attacks, and the gull pair who are attacked also bear the likelihood of injury and of course dead to their offspring for no apparent reason. However, such examples are uncommon in animals and so also uncommon in birds. Professor Raghavendra Gadagkar articulates this elegantly and he said that “..conventional wisdom has it that to be spiteful is the prerogative of us humans alone”, and that unequivocal examples of spiteful interactions in the animal world is lacking. You can read more about this in his article called ‘Can animals be spiteful’.

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While pairwise interactions also qualify as social behaviour much of our understanding of social behaviour in birds comes from observing birds that join groups. So, let us first look at how these collectives form and why do birds join these large collectives. One of the most awe-inspiring behaviour in birds is the murmuration of starlings. It is a form of collective behaviour when the birds move around at dusk for roosting.

The fluid and synchronized movements is a result of interacting individuals that are part of a large group and these group members need not be related. In fact, for collective movement relatedness is irrelevant. It is mesmerizing to watch the starling flocks effortlessly take limitless forms in the backdrop of a melting sun. The large scale pattern seen in murmuration is a result of coordinated movements which are bound by a set of decision rules in a manner that individual members cannot completely behave independently.

Collective movement thus is a result of simple rules of interactions that are followed by the participants resulting in spectacularly complex patterns that are emerging properties of the group but not of individual members of the group per se. The obvious question that comes to our mind

of course is how are these decisions made and who makes these decisions. This is relevant because members of the group are not kin. So, their interests may diverge and not converge.
For instance, in which direction should the flock turn; some members may want to go east while others may want to go north even if the destination is not debatable but what path should the flock take from the position of every individual the shortest path to the destination will vary. The answer of course to these questions will vary from system to system.

In some forms of collective movement animals may simply follow a leader and in stable social group this is typically the highest ranked individual or the most dominant individual. In other cases, individuals may follow the individual that has the most directed movement. So, can single individuals direct or lead murmuration? The question has got biologists and physicists as well as computer scientists all charged up.

In fact, a study published in the journal PNAs in 2010 examined this phenomenon in particular asking the question if the velocity fluctuations of birds are correlated to each other in startling murmurations. What they found was that the relationship was not constant and instead scaled with the linear size of the group such that the behavioural correlations were found to be scale free. So, irrespective of the size of the group the behaviour of an individual affects other members of the group and that individual is in turn affected by the behaviour of group members. So, we can safely conclude that starling murmurations at least cannot be directed by single individuals.

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Somewhat surprising given the amount of work that has gone into understanding the mechanism of murmuration, we know little about the adaptive value or what factors affect the size and duration of murmuration. Several hypotheses have been put forward to explain why birds may join such large groups and thereby provide a functional explanation of such collective behaviour. First is the safer together hypothesis that posits that murmuration are an anti-predator strategy.

It has been proposed that murmuration may reduce predation risk in several ways. First, there is a dilution effect of joining a large group, if n is the group size then the probability of a particular individual of a group being preyed upon in a prediction event is

$$1/n$$

So, as the group size or n increases, individual predation probability values decrease. For the more individuals in a group offer higher vigilance and this in itself increases safety of group members.

Lastly, it has been proposed that the fluid collective movement of prey in a group as in the case of starling murmuration confuses the predator and messes the predator's ability to target specific individuals. Given that starlings are potential prey for a wide variety of avian predators, especially hawks and falcon, it is tempting to consider the possibility that joining a large flock may be a means to secure one's safety.

Second, the warmer together or thermal hypothesis posits that these large gatherings serve to advertise a roost site to attract more birds to a communal roost which will become warmer as more birds join it. The hypothesis predicts that murmuration size and duration should be inversely correlated with temperature as the need for roost advertising should be far more crucial in colder conditions. Given that murmuration occur immediately before roosting and during late autumn and winter months mostly, the hypothesis certainly warrants investigation.

Ward and Amotz Zahavi had proposed that roosts are centers for eavesdropping on information about feeding sites and the birds assemble in the roost to gather such information. This of course has more to do with roasting behaviour than with murmuration per se. However, the first two hypotheses have been tested empirically in a 2017 study in which researchers use citizen science data to test the safer together and warmer together hypotheses.

The study found that birds of prey were the birds of prey were found to be present in 30 percent of all murmuration observations that were found recorded worldwide. They also found that the presence of a predator was positively correlated with both murmuration size and how long the murmuration lasted. However, temperature was not significantly related to murmuration size and duration. So, they concluded that murmuration is likely to be an anti-predator strategy and thus upholds the safer together hypothesis.

Irrespective of why murmuration occur in nature they are certainly one of the most spectacular collective behaviour in nature. And Darwin would have said they literally represent “endless forms most beautiful and wonderful”.

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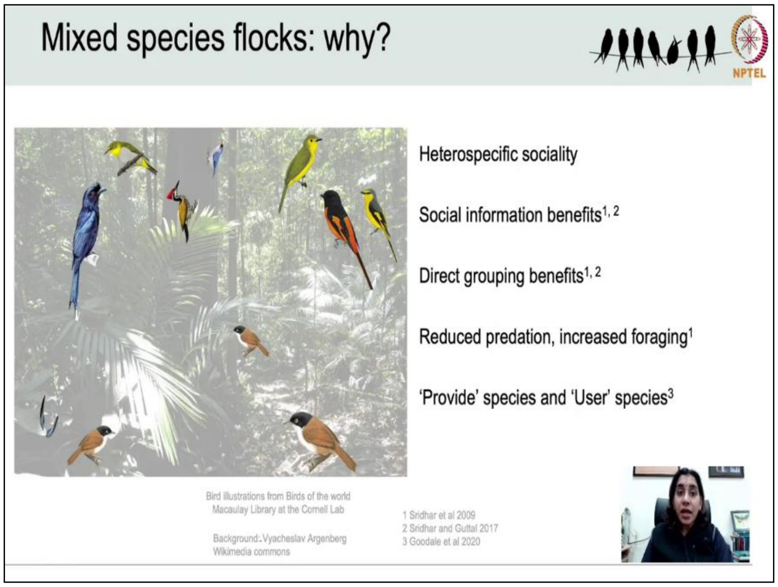

Research in animal sociality has largely focused on conspecific social groups even though many animals including birds may occur in what we call as mixed species social groups. In birds, such groups are called mixed species flocks or mixed species hunting parties because these species come together for foraging. Much less research has gone into understanding heterospecific animal sociality and mixed species flocks are heterospecific bird groups comprising of two or more bird species that forage and move together.

The advantages of such group membership are two-fold. First is the social information benefit wherein fitness benefits are in the form of information about food predators roosting or nesting site gathered from social partners within the flock. The other kind of benefit is called direct group benefit wherein direct fitness benefit is derived from social partners, which is not mediated by access to information, which could include reduction in predation probability, deriving warmth by being in a group, reducing wind resistance by flying in a group etc.

Reduce predation risk by being a member of a mixed species flock can come through social information or via direct group benefits by increased vigilance. It was found by Dr Harish Sridhar and colleagues in a global analysis of mixed species flocks that species susceptible to predation, follow those bird species whose vigilance they can exploit thereby reducing their own vigilance effort and increasing their foraging rates.

Members of a mixed species flock can be viewed as ‘providers’ or as ‘user’ species. Providers are species whose individuals provide greater proportion of benefits to the flock on an average than other species members of the flock. For instance, a sentinel species or those bird species that beat the foliage flushing out insects that other birds can consume would be provider species. Member species that on an average derive more benefit then providing benefit to group members by being part of the flock are called ‘benefit users’ or simply ‘users’.

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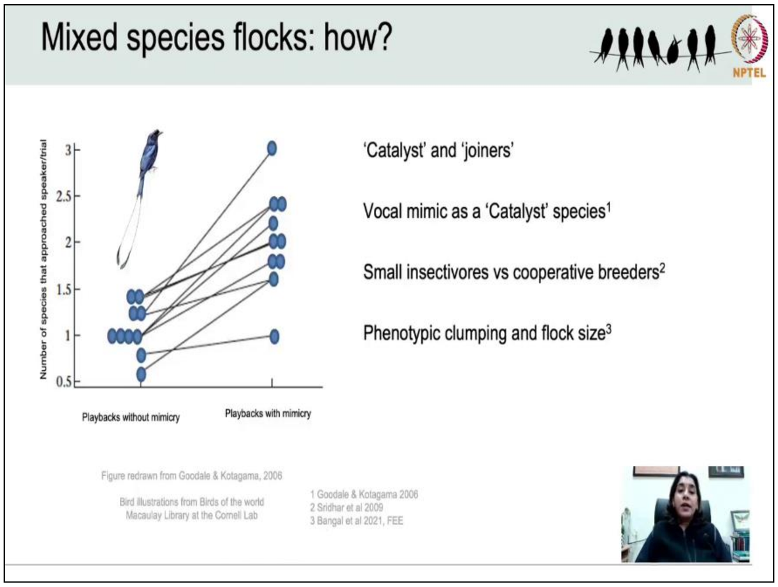

Clearly, joining the mixed species flock has demonstrable benefits and since the why question has been worked on extensively. The key unanswered questions are - how are these mixed species flocks initiated and how are they maintained? Some species in such flocks are called ‘catalyst species’. These are flock initiators and also play a key role in flock maintenance whereas those that join subsequently are called joiners. Eben Goodale along with Sarath Kotagama studied mixed species flocks in Srilankan birds and found that the Greater racket-tailed drongo, a known vocal mimic initiates mixed species flocks.

To understand how the initiation is mediated by the Greater racket-tailed drongo, they conducted playback experiments in which they used two kinds of playback stimuli. One in which the playback included the song mimicry of the Greater racket-tailed drongo and the other stimuli in which the playback lacked the song mimicry. They found that the playback that included the song mimicry of the drongo were more than twice as attractive to birds of other species than those that lacked them.

Dr Hari Sridhar and colleagues used a comparative global analysis of mixed species flock studies to find that small size and insectivorous species are more likely to be joiners. And cooperative breeders tend to be leaders of mixed species flocks. In a subsequent study using a null model approach Dr Priti Bangal and Dr Harish Sridhar at the Center for Ecological Sciences and other colleagues found that small flocks are more phenotypically clumped for body size than expected by chance. And as the flock size increased the phenotypic assemblages became more random.

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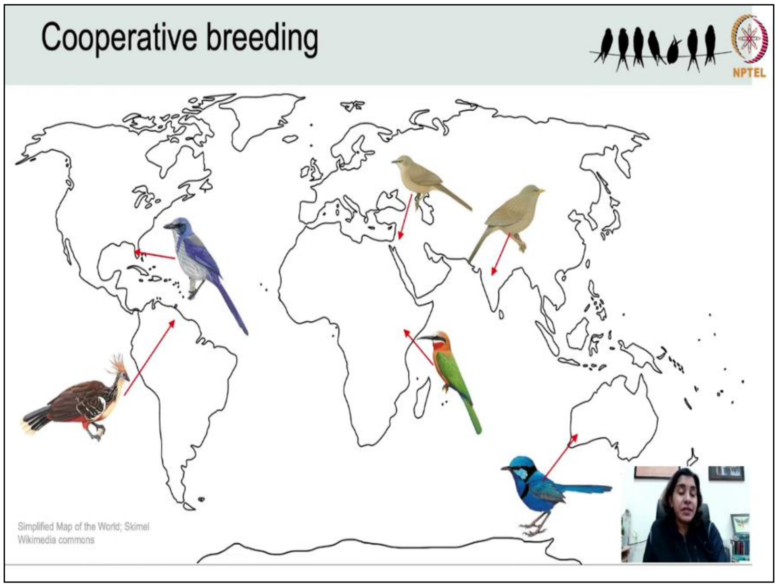

From heterospecific social groups of birds, let us now move to single species social groups in birds. Cooperative breeding is a reproductive system in which a social group has a single breeding pair called as the breeders. And other group members forego the opportunity to breed independently and instead provide care to the young ones of the breeding pair and this system, the cooperative breeding system is the most fascinating system of a single species stable social group and has been worked on many different species of birds.

Now, these group members who help are called helpers and helpers may aid in many different ways including providing territory defense, nest building, incubation in some species, defense against predators but most importantly by providing food to the young ones. It is not a common breeding system and is exhibited in less than 10% of the bird species of the world. Some of the species that exhibit cooperative breeding include the Florida scrub jay from, well, Florida: belonging to the family Corvidae.

The Hoatzin of Venezuela belonging to the family Opisthocomidae, the White fronted bee-eaters from Kenya belonging to the family Meropidae, the Splendid fairy-wren from Australia from the family Maluridae. In fact, Australia is home to many different species of cooperative breeders and the Splendid fairy-wren is just one of the many found in Australia and the Jungle babblers from India and the Arabian babblers from Israel belonging to the family Leiothrichidae.

Now, this assortment of species that I have shown you here is simply to cover cooperatively breeding species found from different avian families and from different continents. And this is just to tell you how diverse bird species belonging to diverse avian families are cooperative breeders and they are found from all over the globe. Yet this is not a common breeding system.

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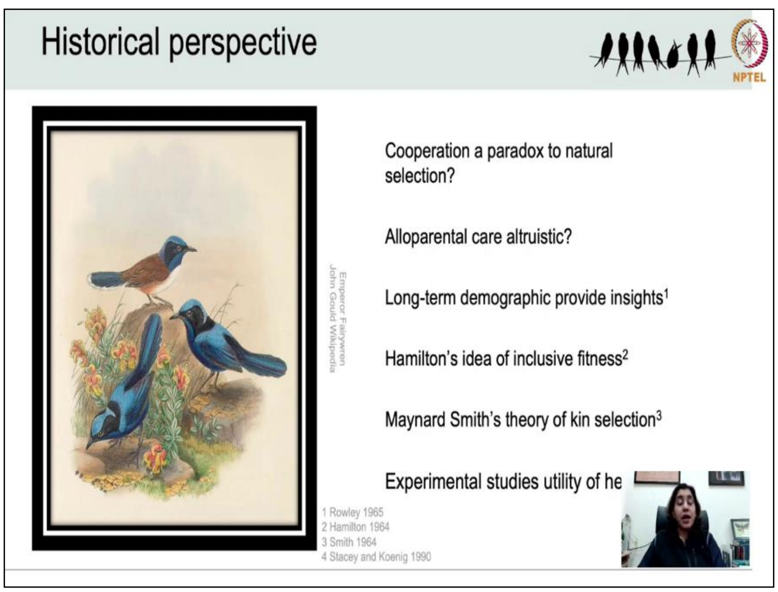

A major difficulty in understanding the evolution of cooperative breeding was to reconcile the fact that helpers are essentially forgoing their own reproduction to care for someone else's young. Now, how can this kind of maladaptive system have evolved through natural selection that favours individuals that maximize their own reproduction? Sacrificing your own reproduction to raise the offspring of another breeding pair seems like a huge cost to pay in.

So, alloparental care which is to care for someone else's offspring at the cost of one's own reproduction seems altruistic. We have learnt about what do we mean by altruistic behaviours. Long term demographic studies on banded and individually marked cooperative breeders belonging to many different species have provided insights that helpers are often offsprings of the breeders who have stayed back at the nest.

Yet, the benefit of staying back and helping raise your parents' offspring or helping raise your siblings is not apparent. Except for the opportunity to delay your dispersal until the conditions become favorable for helpers to leave the nest and become breeders themselves. Even so, why not simply stay back and not provide care? The lack of a theoretical framework explaining this apparently altruistic behaviour of helpers resulted in studies in cooperative breeding receiving much less attention of researchers despite its promise of revealing novel understanding in evolutionary biology.

In 1964 however, Hamilton proposed the idea of inclusive fitness and building on the work of Haldane and others, and Maynard Smith developed the theory of kin selection. Inclusive fitness and kin selection together provided the foundations on which much of our understanding of altruism, cooperation, social behaviour in animals rests. Soon after empirical and experimental studies on cooperatively breeding birds took off again and in the mid 70s to about 1990s we saw a boom of studies on different groups of cooperatively breeding birds in all taxa belonging to various different avian families.

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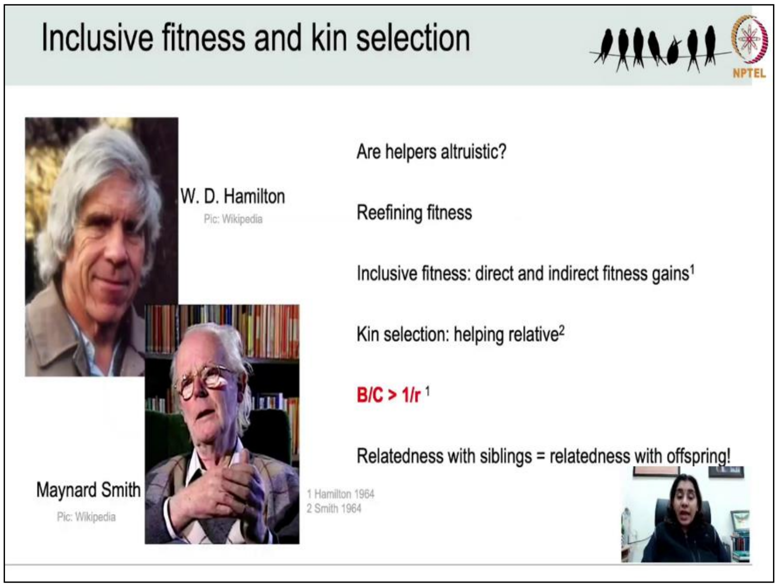

So, we need to look at the benefit of an act to the recipient, the relatedness of the actor to the recipient and the cost of the altruistic act to the actor. So, we have to look at B, r and C. As long as the recipient is sufficiently close relative of the actor and the benefit to the recipient outweighs the cost to the actor, the altruistic behaviour can still evolve through natural selection. In other words, inclusive fitness and kin selection taken together provides the foundation to understand how seemingly altruistic behaviour may evolve if they indeed increase the proportion of genes of an individual in the next gene pool via direct and indirect fitness.

Thus, an altruistic act can be argued to not be truly altruistic when viewed in this light. In other words, by helping a genetic relative say a sibling, a niece, or a nephew the helper is simply increasing the copies of its own genes that this helper shares with the relative that it is helping. Although, this was initially applied to understanding the evolution of sterile caste in social insects, it was quickly understood that helpers in cooperatively breeding birds can be viewed as individuals of the worker caste in insects who too have evolved to forgo their own reproduction to raise the offspring of the queen.

Thus, relatedness of helpers to the breeders is important and as apparent from long term studies the helpers do tend to be offsprings of the breeders. Now, since birds are diploid sexually reproducing animals, their relatedness to their siblings is the same as their relatedness with their own parents and offsprings which is 0.5. So, they share about 50% of their genes with their siblings with their parents and with their offsprings on an average.

So, I will leave you with a question to think about. If the average relatedness of a diploid individual to its sibling is no different from that with its own offspring then why is parental care far more common than sibling care?

The pressing question was why do helpers forego their own reproduction to care for the offsprings of the breeders? Does it not reduce their own fitness for this? Let us first define fitness.

Fitness of an individual can be measured as the proportion of genes present in the next gene pool or in the following generation that are identical by descent with that of an individual in question. Hamilton argued that the fitness of an individual is determined by two components - a direct fitness component which comes from one's own reproduction and an indirect component that comes to the reproduction of an individual's relatives.

Both components put together is the measure of an individual's fitness and he termed this to be inclusive fitness. In the same year 1964 Maynard Smith in a paper coined the term kin selection based on the work of Haldane and Hamilton and called it as the evolution of characteristics which favored the survival of close relatives of the affected individual. Thus, it becomes evident that such genetic selection will favor an allele that enhances the reproductive success of its carrier say the helper, but also, the genetic relative. But could an allele that reduces it carriers fitness while enhancing its relatives fitness be adaptive and would it spread in a natural population. For this, let us look at inclusive fitness and kin selection together to understand the conditions under which an altruistic act will spread in a population or a gene or an allele responsible for such an altruistic act will spread in a population due to kin selection.

Imagine an interaction between an altruist or an actor and a recipient or the receiver say the actor is helping the recipient by virtue of feeding it or giving alarm calls to alert the recipient of a nearby danger. Let us assign a cost C of this interaction to the actor and a benefit B to the recipient. Say these can be calculated in terms of the probability of survival of the actor and the recipient respectively.

Hamilton proposed through a mathematical model that if an actor suffers a cost C, for example making itself more visible to a predator by giving an alarm call or losing a food item it had found by giving it off to a receiver, then we should also look at the benefit that the recipient gains from this act and let that benefit be B as a result of this altruistic act. In this condition, the gene causing the actor to behave altruistically will increase in frequency if

$$B/C > 1/r$$

where r is the coefficient of relatedness between the actor and the recipient.

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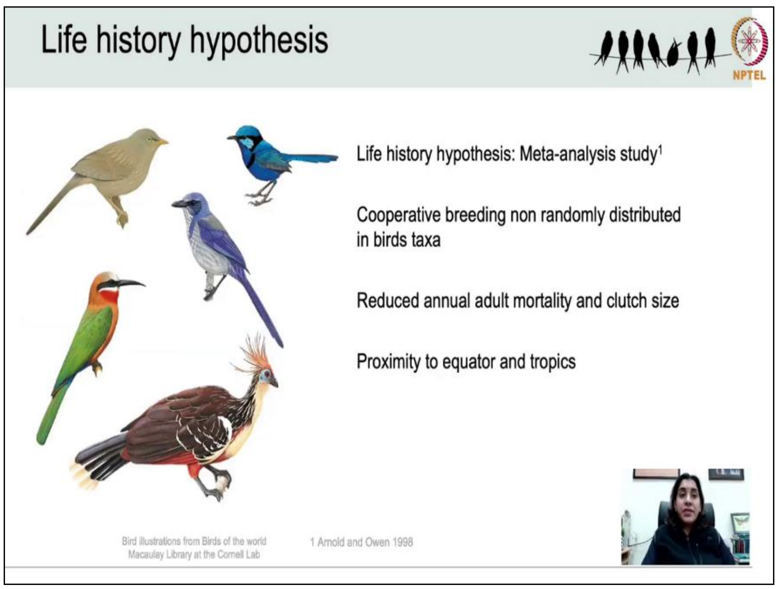

The life history hypothesis has been proposed to explain the evolution of cooperative breeding in birds. It suggests that common features of cooperatively breeding birds is their longer lifespan rather than any particular feature of their breeding ecology. A meta-analysis by Arnold and Owen tested this and the results demonstrate that: one, cooperative reading is restricted to a small number of avian families and not randomly distributed across various avian families thereby providing some support to the idea that some bird groups are likely to have certain features that predisposes them to the evolution of cooperative breeding whereas other do not. What could these features be? Well second they found that cooperatively breeding is strongly associated with a decrease in annual mortality and modal clutch size. Further they found that the proportion of cooperatively breeding species per avian family to be correlated with a low family-typical value of annual mortality of birds. Here, by family, I mean avian families and not family units. However, this does not clarify whether cooperative breeding is a cause or a consequence of reduced mortality and fecundity.

Moreover, their analysis suggests that high breeder survivorship is significantly correlated to being close to the equator and being in the tropics where the temperature and rainfall ranges are less variable. So, the environment is more predictable and reduced environmental fluctuations is likely to allow the birds to hold territories all year round. Nonetheless, despite the correlations found ecological and climatic considerations offer little predictive power beyond the fact that northern temperate zone species are unlikely to be cooperative breeders.

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One of the most well studied and cooperatively breeding bird species is the Arabian babbler. Israeli scientist professor Amotz Zahavi established the Arabian babbler project in the middle of the Arav desert in Israel in 1971.

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Over the last fifty years or so, Amotz along with his lifelong collaborator and wife Avishag Zahavi conducted research on the Arabian babblers along with researchers from all over the world.

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Male and female babblers look alike except that the males, as you can see on the top, has a yellow iris while the females have completely black irises represented in the lower image.

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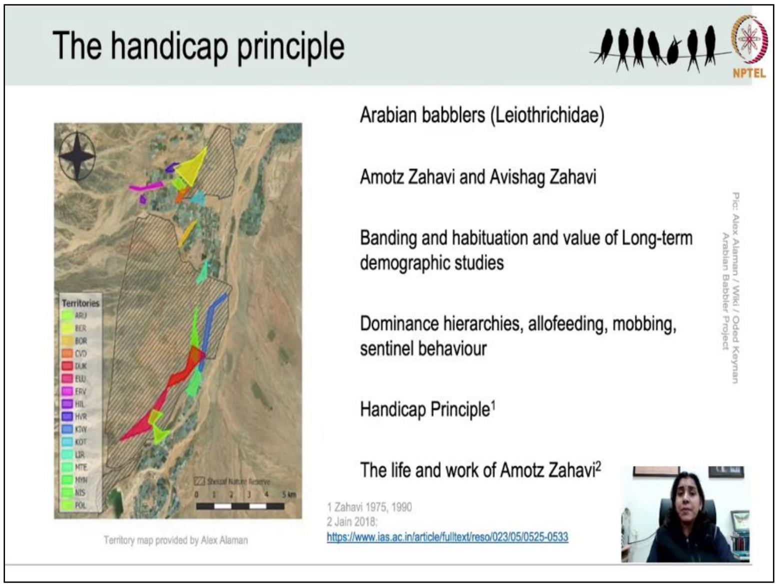

Zahavi and researchers in the project followed the babbler groups, painstakingly marking and mapping the territories of individual groups. Seen here is a recently mapped territory map of some groups of Arabian babbler provided by Alex Alaman and his colleagues.

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Researchers in the group have consistently year after year banded individual babblers and have even habituated them to the presence of humans and this has allowed them to observe these birds at very close quarters facilitating long-term demographic studies on these cooperatively breeding birds and the project remains unparalleled in the wealth of historical records of individual life histories and behaviour of any bird species.

Arabian babbler groups have a clear age and sex-dependent hierarchy, which for members of the same brood is established by aggression and fights within the first few weeks of leaving the nest and then it is maintained for life. This can occasionally be challenged but that would mean that one of the two will have to leave the group, if not get killed but other than that within-group fights are rare.

Babblers also exhibit many interesting behaviour such as allofeeding in which members of the group feed individual group members (offsprings of the breeding pair) and even each other. So eager are the higher-ranking individuals to feed subordinates that they sometimes may even try to feed individuals who are not even hungry. Sometimes these individuals who are trying to be fed even refuse and try to move away.

Altruism is not reciprocal in Arabian babblers and the lower ranking individuals never seem to attempt to try and feed the higher-ranking individuals who are so eager to feed them. Altruism is puzzling enough but it is not clear as to why higher-ranking individuals give up their hard-earned food items more often than the lower ranking ones, in fact one would have expected the opposite. Further group members exhibit other costly behaviours such as mobbing predators which can be extremely risky and even fatal.

As you can see in the picture below there is a snake which is being mobbed by group members of an Arabian babbler group.

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More interestingly Arabian babblers indulge in cooperative vigilance in which one individual takes up duty as a guard on an elevated platform and watches out for predators while other group members forage. It even appears that the Arabian babblers actively seek to go on duty and higher-ranking individuals even vacate subordinates from these sentinel posts. They found that in about 30% of their observations of sentinels, the sentinel was replaced within one minute of it taking up duty.

The replacing guard oftentimes would not even stay on guard for a very long time and would leave shortly after replacing the original guard making it likely that the replacing individuals merely wanted to vacate the original guard from duty. Now, why give up opportunity to eat and instead serve as a watchman for others? That is a puzzling question and this has been addressed using the Arabian babblers through the extensive studies on them.

The answers found by Zahavi were so path-breaking that they have completely changed the way we look at animal behaviour especially cooperation and communication. Most animals establish dominance by threat and aggression but in Arabian babblers it seems that the dominant individuals establishes its dominance over others by acts of altruism. The act of sacrifice, Zahavi proposed, was a costly signal indicating the superior quality of the altruistic individual who can bear the cost of this altruistic act and yet survive.

This he used as the example, for this he used the example of the long train of the peacock and the principle that he proposed is known as the handicap principle.

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Now the long train of the peacock serves as a handicap, potentially reducing the fitness of the peacock because it is a heavy load to carry around and it also makes the peacock a poor flyer thereby reducing its ability to escape from predators. However, Zahavi argued that only high quality individuals can bear the cost of this handicap which is the long train of the Peacock and thus costly traits such as the long train of Peacock and altruistic behaviour such as going on sentinel duty and allo-feeding are evidence of better quality individuals who can afford to bear the cost of sacrifice or afford to bear the handicap.

So, radical was this idea of handicap principle that for a long time it was not accepted by biologists and yet to date it remains one of the most significant breakthrough in the field of animal behaviour. So, basically Zahavi proposed that Arabian babbler group member are using helping instead of aggression to gain higher social status in the group. Helping is a handicap and not all group members would be able to contribute equally thereby demonstrating a helper's superior quality.

The one who helps more gains more prestige and thus helping can even be seen as a means of showing off your higher status in the group argued Amotz Zahavi. Amotz Zahavi was also a staunch conservationist and worked hard towards the conservation of birds and an entire ecosystem in Israel. You can read more about his life and work in an article I wrote in resonance the link is provided here and the article is freely available. Amotz passed away in 2018 and his wife and lifelong collaborator Avishag passed away recently in October 2021.

However, their legacy continues with the Arabian babbler project and through their many contributions to our understanding of social behaviour of birds.

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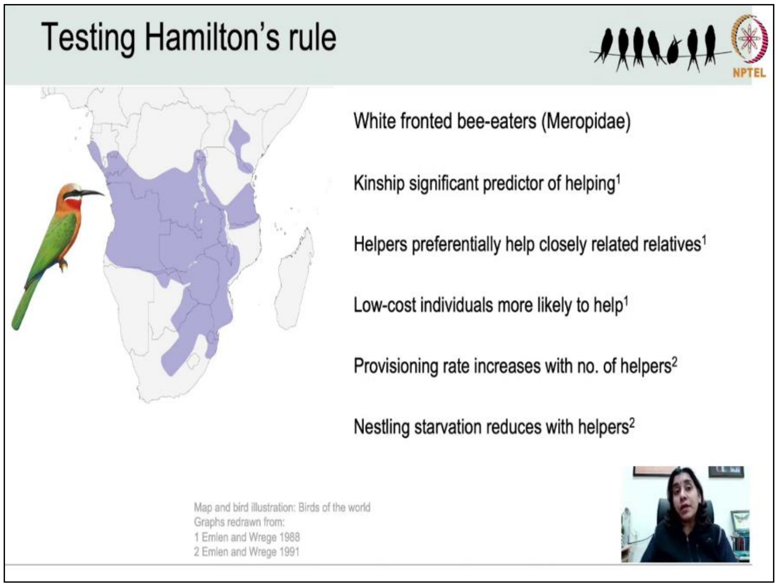

Bee-eaters have highly variable breeding and social systems ranging from species that exist as solitary paired nesting birds in nuclear families to large colony nesters. Some solitary nesters in the Bee-eater group exhibit cooperative breeding whereas some others do not. The same is true for colony nesting Bee-eater species wherein some show cooperative breeding and some other species do not show cooperative breeding even though they are colony nester species.

Thus, this family offers a good model system for comparative studies of social organization in birds. One species in particular has been studied extensively and that is the White fronted bee-eater found in central and south eastern parts of Africa. Long-term studies conducted by Stephen Emlen and his colleagues on the African White-fronted bee-eater provides one of the best documented evidence of genetic and ecological factors that influence the expression of altruistic behaviour.

The study on the species by Emlen also provides data on when specific individuals are likely to help and whom are they likely to provide help. They found that kinship was a significant predictor of helping behaviour

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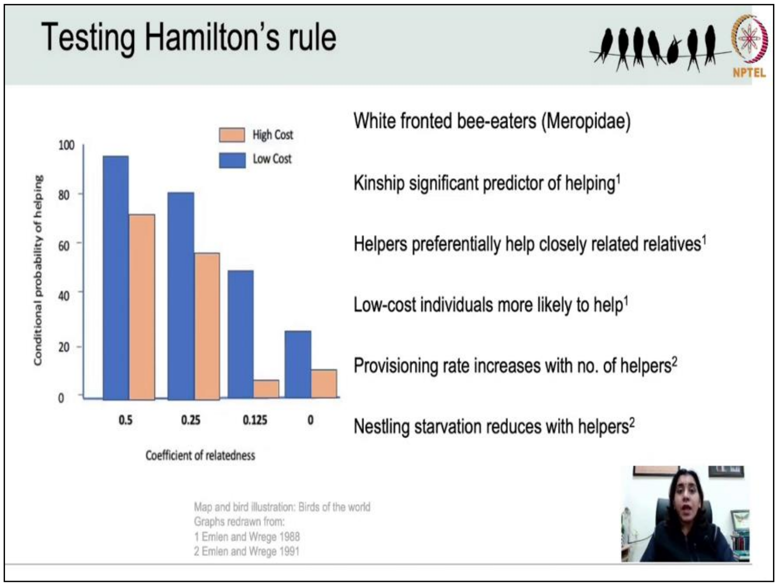

wherein both non-breeders and failed breeders can provide help at the nest. Natal members refer to birds that are born within the clan and in-laws refer to unrelated mates that joined the clan at the time of pairing. Their study showed that natal birds were more likely to help than unrelated ones, further they showed that the helpers preferentially helped kin that were closely related to them than those that were unrelated to them and the average relatedness of the helper with the nestling receiving help was 0.33.

They also accounted for the cost of providing help wherein the effort put in towards providing aid and delaying the personal reproduction was taken into account as a cost of helping. Potential helpers were grouped in two categories. Those that come under low effort category included all potential helpers that had not participated in any previous nesting event that season whereas the high effort category included all potential helpers that had been involved in the first nesting attempt that had reached the point of feeding young ones.

Now, when the nest reaches this stage a lot of effort has to go in because feeding young one requires a lot of effort and energy. The results of Emlen and his colleagues was that the potential helpers that had engaged in high effort activities in the few weeks prior to when helping opportunities showed up showed decreased likelihood to become helpers. And those that had not put in so much effort in the weeks prior to the breeding were more likely to become helpers.

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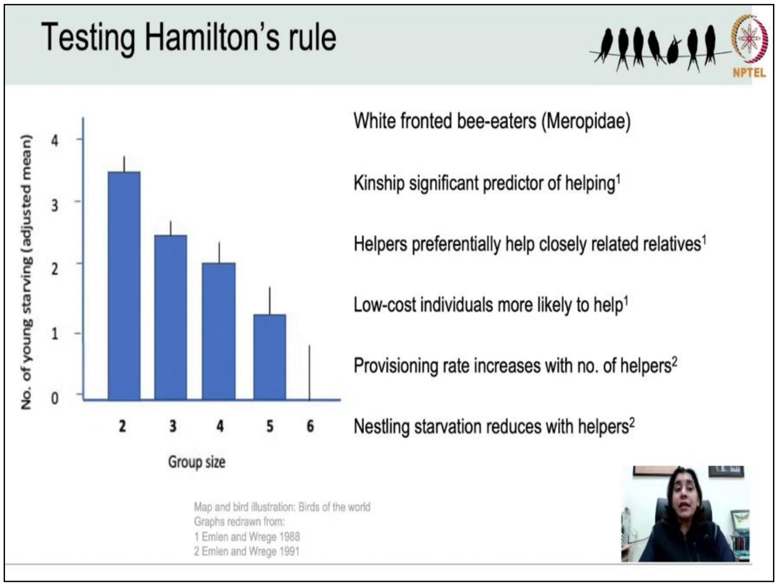

In a follow-up publication, Emlen and Wrege demonstrated the benefit of helping to the recipient White fronted bee-eater helpers significantly increase the provisioning rate for the nestling thereby increasing fledgling success through their feeding contributions and this significantly decreased the probability of nestling starvation. Further, they found that the presence of one helper effectively doubled the fledgling success as compared to the fledgling success of a pair that had no help at hand.

And this therefore provides evidence of the effect of providing help to the breeding pair and this effect was shown in terms of increasing numbers of nestlings that finally fledged. So, the increase in number of helpers for a particular breeding group was found to be linear across all commonly observed group sizes. In this way Emlen and Wrege tested Hamilton's rule in a comprehensive way examining each variable of Hamilton’s equation not only looking at the benefit of helping by virtue of reduced nestling starvation but also how cost and the coefficient of relatedness are likely to influence the probability of helping.

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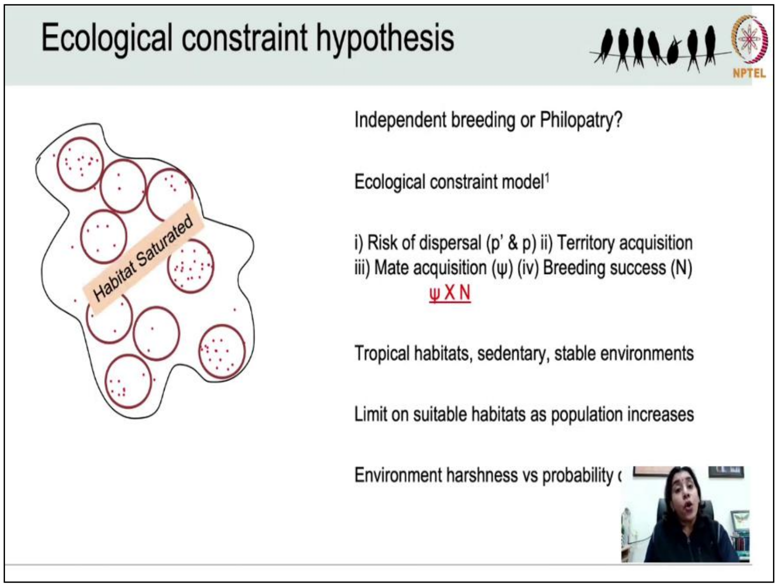

So, should helpers breed independently or show Philopatry? Philopatry means staying back at home territories. This question can be viewed from an ecological point of view as well. Under what conditions should an offspring remain at home? Emlen proposed the ecological constraint model in 1981 and stated that this can be examined from the offspring's point of view in terms of the relative costs and benefits of two opposing options.

Option one was to disperse and attempt to breed independently, option two was to exhibit philopatry by postponing dispersal and remaining as a non-breeder with the parental group. He proposed that four factors will go into making this decision. First would be the cost of dispersal itself measured as a difference in survival probabilities of early disperses p dash versus late disperses p. So, these survival probabilities would be different and this needs to be accounted for.

This itself will be affected by availability of food, shelter and predation pressure in that habitat. The second factor is the probability of successful establishment in a suitable territory following dispersal and the third is the probability of obtaining a mate. Emlen combined the second and the third factor into a parameters called psi and he proposed that this will be dependent on competition for vacant territories and competition for suitable mates.

This will depend further on population density, vacant territory turnovers and the population sex ratio. Last but not the least, the fourth factor he proposed would be the likelihood of success after an individual has dispersed, found itself a territory, found itself a mate and what is the chance that it will be able to raise successfully young ones for that breeding season. So, this would be a measure of the number of young ones successfully raised by the individual that has dispersed and this can be depicted by n.

The ecological constraint model suggests that the fitness of an individual attempting to breed independently in the first year would be a product of psi and n. The model proposes that when dispersal risks are low, mates and territories are plentiful and initial breeding success is high then the likelihood of initial dispersal increases. On the other hand, when dispersal risk is high and the chance of acquisition of territories or mates is poor then the initial and reproductive success is low then the offspring will be selected to postpone their dispersal and exhibit Philopatry.

It has been observed that most cooperative breeders reside in warm temperate subtropical or tropical areas. Many species who breed cooperatively are sedentary and inhabit stable predictable environments. Furthermore, many have specific ecological requirements such as availability of a suitable habitat suitable habitat which is often limited. In the figure, I have depicted a habitat of a cooperatively breeding species.

The red dots depict resources and in such a habitat the breeding pairs will begin to occupy suitable territories and start their nests. As the population increases, the suitable habitat starts to get saturated quickly and consequently the competition for space increases. Fewer and fewer individuals will have access to quality territories and therefore the option of breeding independently becomes increasingly limited.

This has been suggested by many researchers including Brown in 1974 and by Gaston in 1978 and other researchers working on cooperatively breeding birds as an important determinant of Philopatry.

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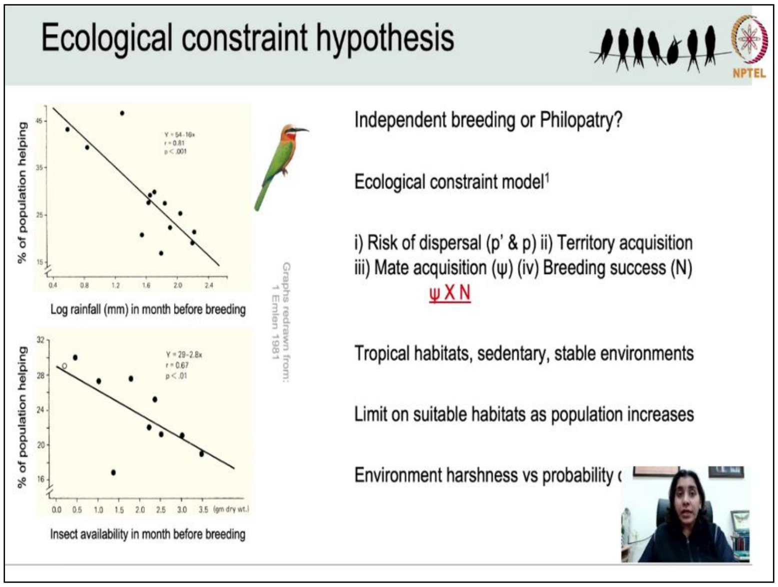

Using White fronted bee-eaters, Emlen modeled helping incidents as a percentage of the population initially helping in any one breeding colony. Harshness of the environment was measured in that study as rainfall in the month preceding the date of egg laying and also the mean daily biomass of insects sampled during the month preceding egg laying. So, it represents environmental harshness as well as food availability.

Now figure 1 depicts the percentage of helpers in each colony against the log of the amount of rainfall received in a month prior to egg laying. As you can see a significant negative regression emerges with the largest nesting group sizes occurring under drought conditions. Figure 2 depicts the regression of percentage of helpers against food availability. Here again the significant negative regression emerges indicating highest incidence of helping during times when food was in short supply.

Thus Emlen, in his landmark study, provided empirical evidence for his theoretical model of ecological constraint and the data collected in White fronted bee-eaters was carried out over five years and these were consistent with the predictions of the ecological constraint model.

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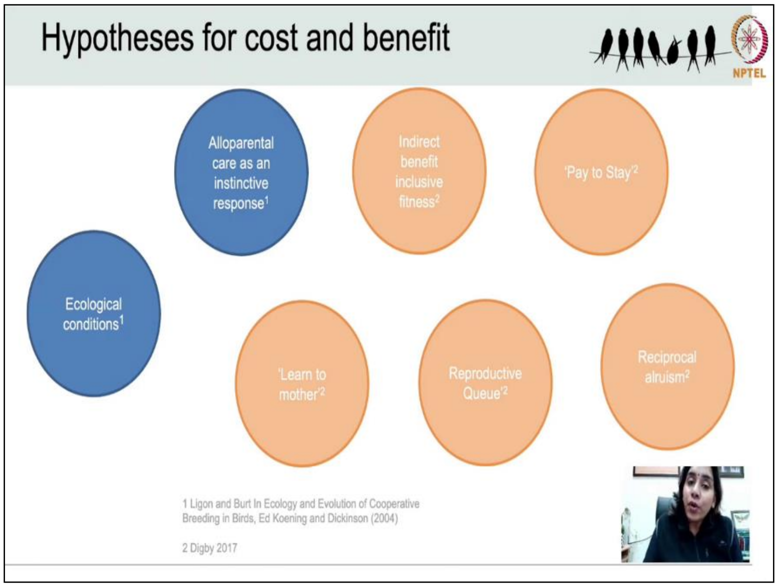

So, to summarize, why help instead of dispersing to breed on your own? The factors that promote the origin of cooperative breeding in the ancestors of today's cooperative breeders could be ecological, environmental, it could be other kinds of factors driving the evolution of cooperative breeding in birds. Scientists have grappled with this question of the evolution of alloparental care for a very long time and concrete answers are still lacking.

However, two possibilities have been discussed. First is related to delaying dispersal from a natal group due to ecological constraints and condition as we just discussed. The second route proposed for the evolution of cooperative breeding considers the hardwired response to begging calls of con-specific young ones. Let us have a look at both. Ecological conditions: for that let us consider an altricial offspring, altricial species are those that where the young ones are dependent on adult for care.

So, let us consider an altricial offspring with prolonged chick development time. Now these neonates will need adult protection and will need the help of adults for feeding in such species if the ecological conditions are unfavorable for instance unavailability of suitable territories, then group members may delay dispersal. Alternatively, or in addition, there might be benefit of natal Philopatry or staying back in your natal group for instance one may be more familiar with natal territories than two territories that you are new to.

Thus, those who stay back in the group help raise the offsprings of the breeders, which may affect their chances of being allowed to stay back in the group. Alloparental care can also be looked at as an instinctive response and in this case the helpers are considered to be failed breeders. Given that parental care is an instinctive behaviour such failed breeders may simply be stimulated by the begging sounds of chicks and provide food to the begging chicks as a hard-wired feeding response.

Thus, alloparental care has also been argued to have evolved due to the adaptive value of parental care and the instinctive response to begging behaviour. There have been various hypotheses, as we have discussed, that explain the evolution of helping behaviour and cooperative breeding and to understand what mitigates the costs of delayed reproduction by helpers. The first of course is the indirect benefits through inclusive fitness as we have discussed as proposed by Hamilton.

Then there is a direct fitness benefit of staying back in the group and not dispersing which is referred to as pay to stay hypothesis where helping behaviour has been proposed as a type of payment in exchange of staying back in the group and enjoying the benefits of group living. Another direct benefit of staying back in the group could be that non-breeding individuals may gain experience in infant care.

Further, there is a possibility for helpers who stay back to inherit the breeding territories of their parents once the breeders disappear or die and the young ones that they have cared for may return the favour or show reciprocal altruism by caring for the young ones of the helpers who have now turned breeders.

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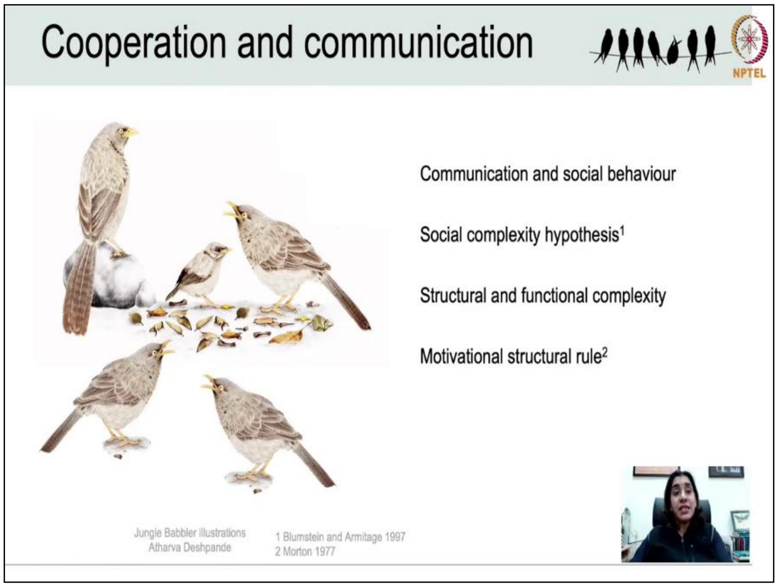

An important aspect that needs to be mentioned in relation to social behaviour in animals is communication. Animals must carry out various life functions that involve social behaviour including mate attraction, territory defense, collective movement, group coordination and avoiding predators. In all of this communication plays a central role. Animals can pass and gather information through a variety of signals including visual acoustic and olfactory signals.

The social complexity hypothesis posits that communication complexity is likely to increase with social complexity. Thus, social animals are likely to possess a complex communication system. This is because they may require higher sophistication in communication to coordinate complex group level behaviours and sustain repeated interactions with individuals within the social groups. Birds in particular use sound as a mode of signaling and acoustic communication mediating social behaviour has been examined in many species of bird with particular relation to mating behaviour and territory defense.

However, cooperative breeders that live in stable social groups offer to provide a good model system to examine this further. Calls produced by birds can be functionally complex by which we mean that the behavioural context in which the calls are produced can be diverse. And this has been studied in many species of group living birds for several decades. More recently with advance in signal processing techniques and lowered costs of equipment to record bird vocalizations some studies have examined structural complexity in some social bird species as well.

In such studies, researchers examine the acoustic features of calls produced in different behavioural contexts to examine which features are similar or different depending upon the different behavioural contexts. In 1977, Eugene Morton proposed a framework of motivational structural rules wherein calls produced in similar behavioural context (which are functionally similar) should also be structurally similar.

So, they should have similar acoustic features. So, there should be structural convergence in calls that are produced in affiliative context and structural convergence in calls that are produced in agonistic context. Further, he proposed that affiliative context would be a calls produced in affiliative context would be tonal with higher frequency components and those that are produced in agonistic context would be harsher containing lower frequency components.

These have been tested in mammals but less so in birds and a study conducted by my group on Jungle babblers has examined these questions.

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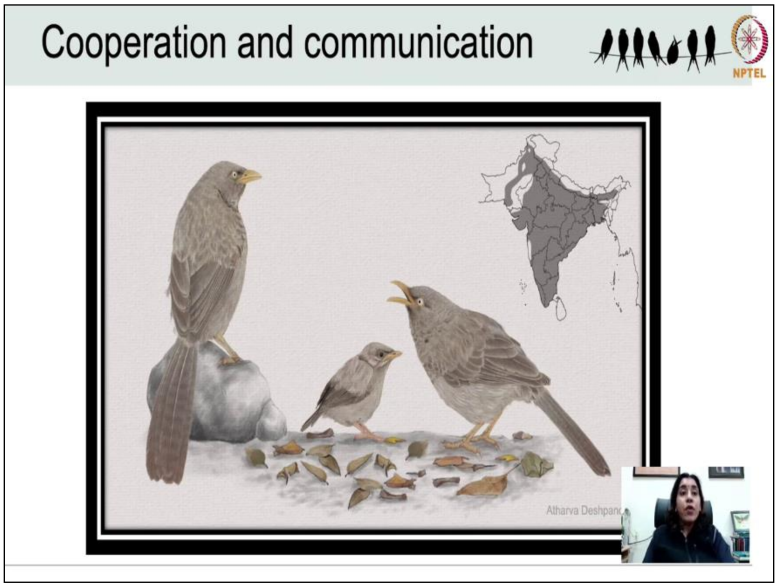

Jungle babbler is a cooperatively breeding passerine found across lowland India. My lab has been examining their social and vocal behaviour for many years now and we have found that babblers produce context-specific calls thus exhibiting functional complexity in their communication. We have also found that the calls that are produced in different behavioural contexts are structurally different wherein different features of the calls may be different depending upon what context the call is being produced in.

So, these calls could be multi-syllabic or monosyllabic, that is, they can contain a single note as shown in the contact call of the Jungle babbler or they can contain multiple notes as shown in the other calls where there are multiple notes that combine together to form one call.

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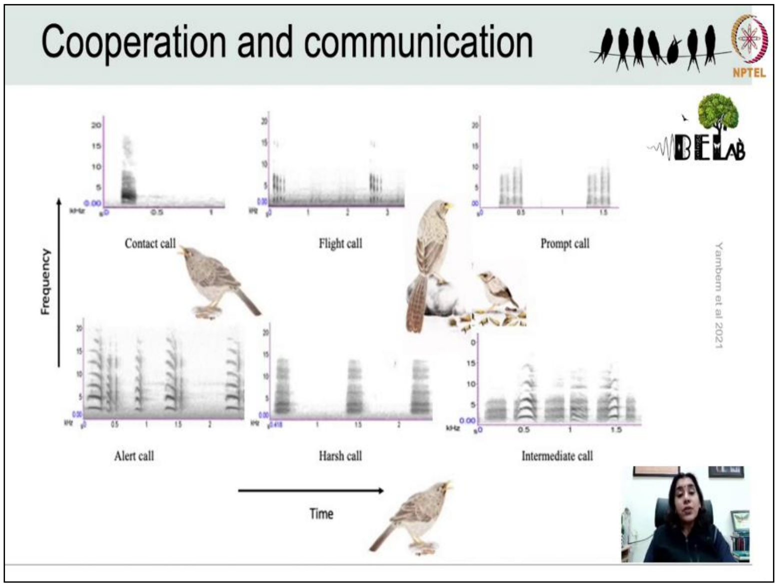

And these calls can have specific acoustic features thereby exhibiting structural complexity in their vocalizations. The first image is that of a contact call which the babblers produce to contact group members when they have been separated from each other. The second call is the flight call which is what the babblers produce when they are moving from one place to other. So, this is for group coordination. Then I have shown the prompt call which is what adult babblers produce when they are near nestlings.

And the behaviours that have been recorded for these babblers have been studied in great details in relation to the kinds of calls that are being produced. The three calls shown below the alert call the harsh call and the intermediate alert call are produced in agonistic context when the babblers are alarmed by the presence of a potential predator.

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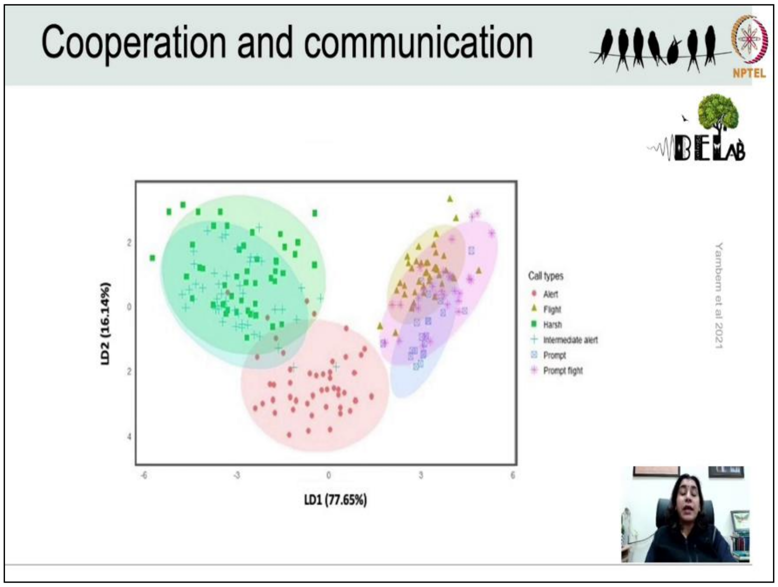

We also tested Morton's hypothesis in the species in which we asked whether affiliative calls are more similar to each other and if agonistic calls are more similar to each other. Affiliative calls as shown in this DFA plot are clearly grouped closer to each other and the agonistic calls were more similar to each other acoustically. However, in Jungle babblers most of the vocalizations produced in affiliative context lacked a tonal structure and were instead harsh and noisy.

And the agonistic calls like the alert call and the intermediate alert call, threat call, distress call they all showed the presence of notes with the harmonic structure. Thus, the vocalizations of Jungle babblers do not support Morton's second prediction. In summary, Jungle babblers were found to have a complex system of acoustic communication that lends support to the social complexity hypothesis wherein the calls of Jungle babblers are both functionally and structurally complex.

We also provide mixed support for Morton's motivational structural rules, it is apparent from the behavioural observations that this rich repertoire of vocalizations allow the babblers to coordinate their group activities and this underlines the importance of communication in mediating social behaviour. With this, I would like to end my lecture thank you very much I am Dr. Manjari Jain from the Behavioural Ecology Lab in the Department of Biology at IISER Mohali, I would love to hear from you and if you have any comments do consider writing to me, thank you.