Basic Course in Ornithology
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Lecture -9
Life History

Hello, welcome to basic Ornithology. In today's lecture, I will be talking about life history in the context of birds. Before I begin, I would like to step you through some key definitions of terms that I will be using throughout the lecture.

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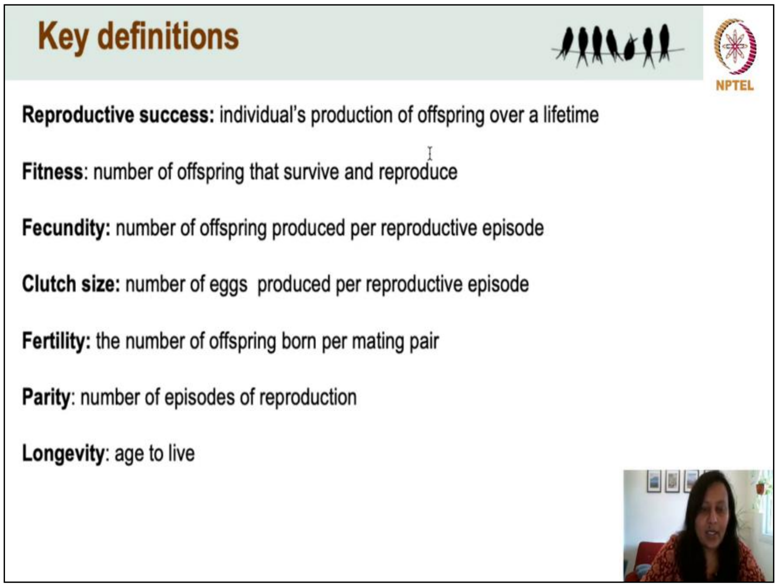

The first term is reproductive success which refers to an individual's production of offspring over a lifetime. The second is fitness which refers to the number of offspring that survive and go on to reproduce. The next term is Fecundity which refers to the number of offspring produced per reproductive episode which in the context of birds is the same as clutch size which is the number of eggs produced per reproductive episode.

Fertility refers to the number of offspring born per mating pair and parity refers to the number of episodes of reproduction. And finally, longevity refers to the age that an organism lives for.

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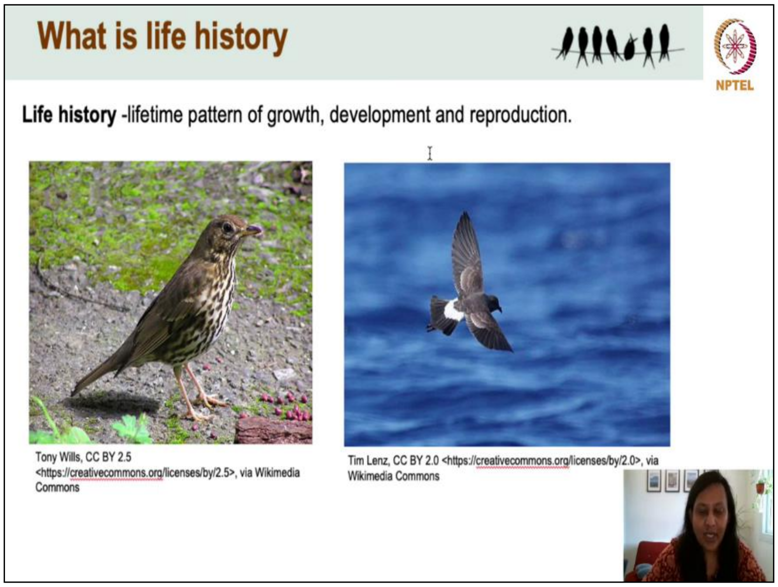

So, let us first try to define life history. Life history is a complex phenomenon involving multiple stages involved with both survival and reproduction across generations in a natural population. However, a finite amount of resources are available to individuals to devote to these processes and the end goal essentially is to maximize reproductive success and different species adopt varied strategies and trade-offs to achieve this.

These variations are essentially an outcome of the influence of both biotic and abiotic factors such as food supply, the physical condition of the bird, the presence of predators and abiotic factors such as environmental conditions. And this results in very different life histories in otherwise similar species. For example, thrushes typically start to reproduce at the age of one produce several broods of three to four chicks each year and rarely live longer than three or four years.

In contrast Petrels, which are very similar size birds start to reproduce when they are four to five years old have one chick each year but live for 30 or 40 years. Now, we will look at the important stages of life history.

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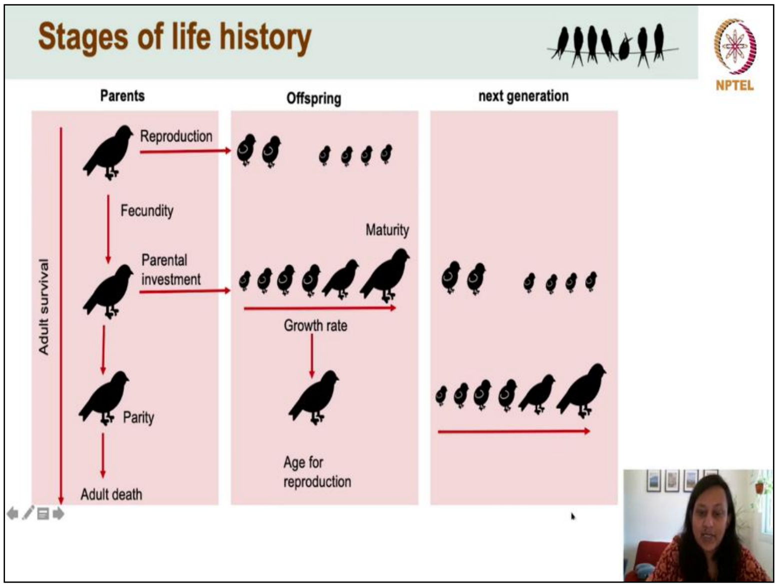

Since the end goal of every individual is to maximize its reproductive fitness which goes just beyond producing offspring, the stages of life history typically span generations. And at every stage there are some decisions that have to be made since there are limited amount of time energy and nutrients which need to be judiciously allocated to increase an individual's overall fitness. For the parent or matured adult, the decision being made is between investing more time and energy into reproduction versus allocating resources to prolonging its own life.

Then again, it has to decide whether to produce many small or few large offspring at each reproductive episode. It also has to decide how many times to reproduce in its lifetime or its parity. Another decision being made by the parent is how much energy to invest in parental care which in turn decides how fast the chicks fledge. The young one then has to grow and decide when to start reproducing itself which is often at the expense of self maintenance.

Again, this process of weighing costs and benefits and making decisions is repeated over multiple generations. Please remember it is not the individual which is consciously making these decisions but these strategies have evolved over many generations through natural selection to determine what works best to increase an individual's fitness. So, essentially a life history is governed by trade-offs influencing survival and reproduction in a species and we see such a diverse range of strategies amongst birds.

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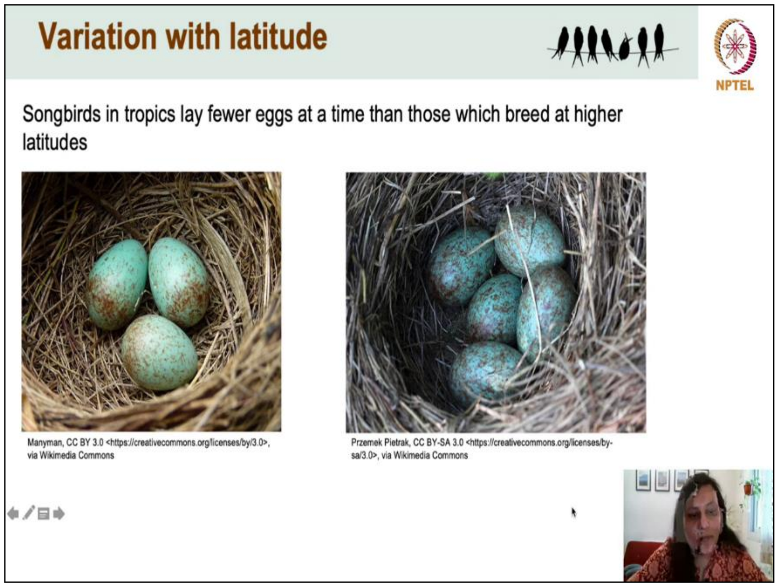

We will start with one such large scale variation wherein song birds in tropics lay fewer eggs than those that breed at higher latitudes. How do we explain this?

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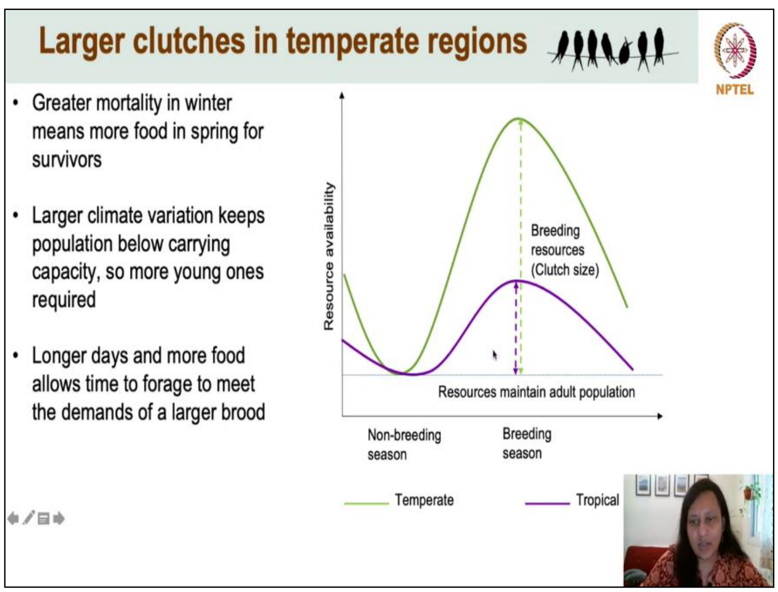

It has been observed that in temperate regions. There is considerable seasonality in the availability of resources. Winters are harsh with low food availability and high mortality of adults and it is this lowest point in the annual resource availability that determines the adult population a particular temperate habitat can support. But this leads to accumulation of food in spring and this big difference between the minimum that we see in the non-breeding season and the breeding season carrying capacity is what allows for more young ones to be added in in the breeding season and therefore a larger clutch size as well.

It is also hypothesized that longer days during the summer in temperate regions allows more time to feed these larger broods. In contrast, there is very less or much less seasonal variation and resource availability in tropical habitats and therefore there is a less pronounced difference in the food availability between the non-breeding season and the breeding season and therefore we see lower clutch sizes in tropical habitats.

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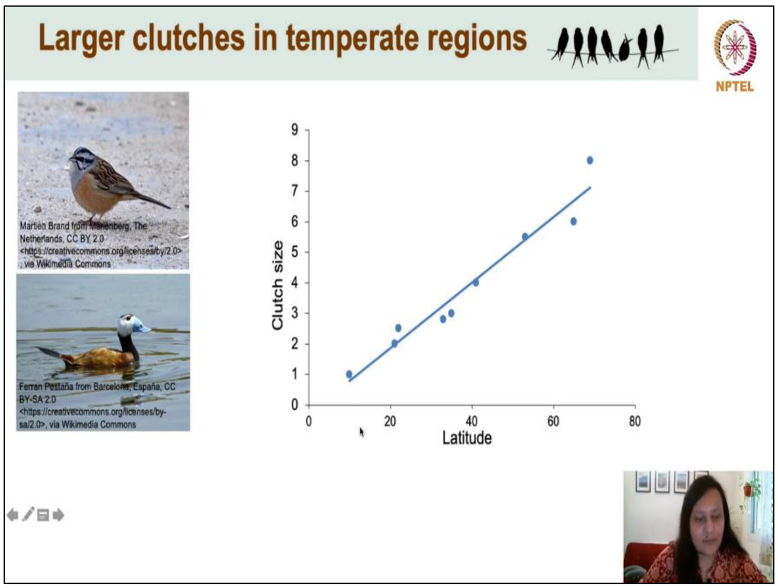

This is seen across diverse groups of species such as Emberiza buntings and Oxyura ducks and in all these cases, we see that clutch size indeed increases as we move from lower latitudes to higher latitudes.

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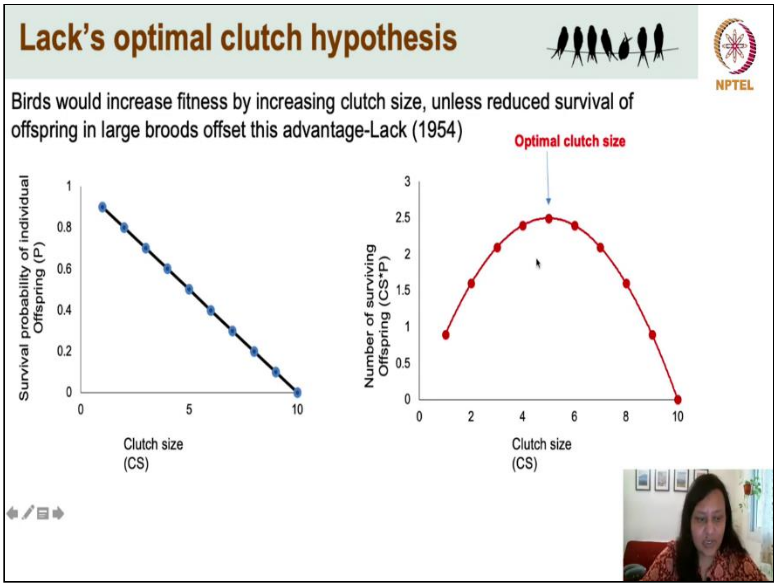

This brings us to Lack's optimal clutch hypothesis which was proposed by David Lack in 1954. Let us see what it says: Assume the more eggs a bird lays the lower are the odds of survival for individual fledglings or offspring. So, if we multiply the clutch size or the number of eggs that are laid by the probability of survival for these or individual offsprings, we can arrive at the optimal clutch size and this is basically what the Lack's optimal clutch hypothesis says.

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This has been tested experimentally in the case of European Magpies. It has been seen that the average clutch size is seven which is the maximum a pair can handle, that is this is the number a pair is able to fledge successfully in usual cases. And these researchers experimentally manipulated the clutch sizes by both removing eggs from a nest and adding more eggs to the nest and in both these cases of deviations we saw that the number of chicks that were fledged reduced or which basically reduced the individual's overall fitness. So, there indeed seems to be an optimal clutch size that works best for a species.

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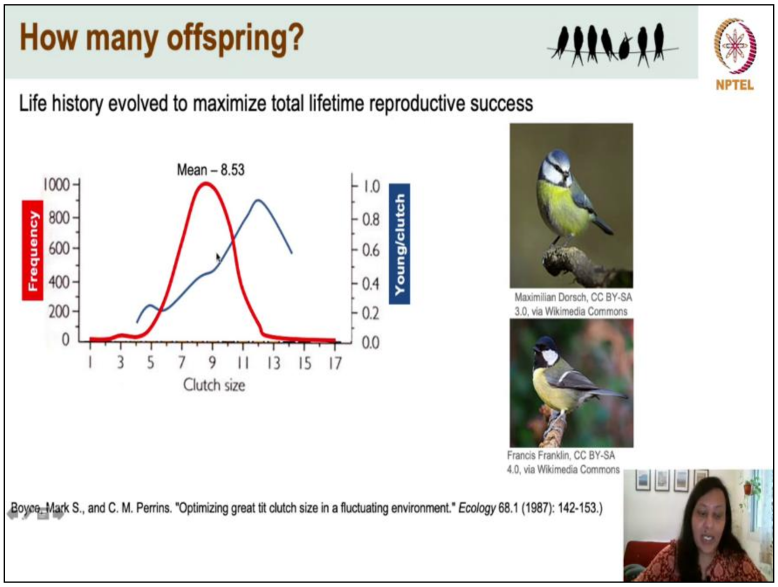

But we also must remember that the end goal is to maximize reproductive success over a lifetime and not just a single reproductive event. This is demonstrated clearly in this study which monitored both Great tits and Blue tits in the Wytham woods near Oxford between 1962 to 1982. These results are based on data from 4489 clutches. Firstly, they found that the optimal clutch size was 12, that is, this was the maximum number of eggs that could be laid by these tits for which the most number of chicks were fledged successfully repeatedly.

However, based on the mean that was observed across the data for all these clutches that were studied it was found that the mean was not 12 but it was 8.53. Why does this happen and it is basically seen that this happens because the pair which laid 12 eggs spent so, much time feeding the egg or in parental care that often such pairs could not reproduce in the subsequent years leading to reduction in their lifetime reproductive success.

Birds that instead laid between eight and nine eggs which was closer to the mean that was observed instead saved more energy for future reproduction and had higher fitness over their lifetime.

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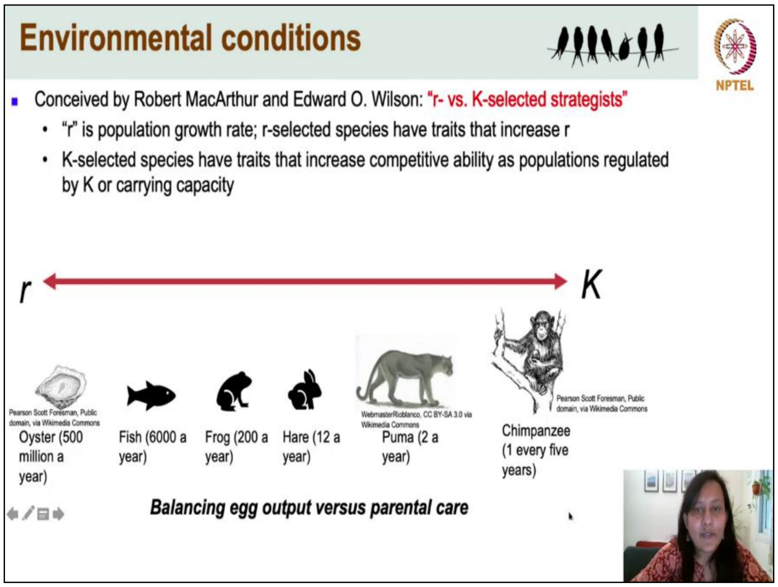

Life history of species is also a product of evolution and should reflect adaptation to environmental conditions where natural selection occurred. If this is the case, do species inhabiting similar environments exhibit similar life history characteristics? Broadly, if we consider two types of habitats, one which is stable over time and the other which is more variable and short-lived. We come up with two different strategies that species have adopted to occupy these contrasting conditions.

This concept was developed by Robert MacArthur and E.O. Wilson. The r-selected species have traits that increase r or growth rate and the K-selected species have traits that increase their competitive ability. Since these populations are often regulated by K or their carrying capacity of the environment. Species lie along a spectrum between these two contrasting strategies. For example, short-lived, small bodied oysters produced nearly 500 million eggs a year.

But larger mammals such as Puma produce just two eggs a year or in the case of Chimpanzees, it is a single egg produced every five years.

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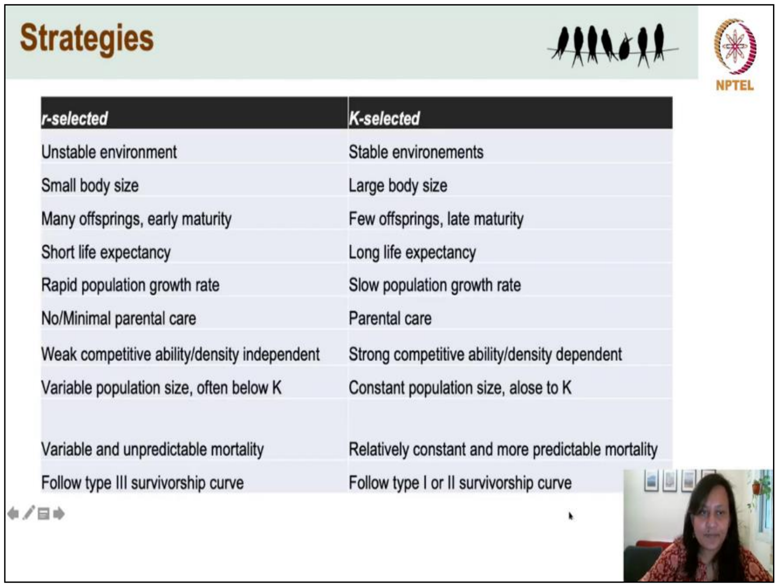

r selected and K selected species show some fundamental differences in their life history strategies as tabulated here. r selected species are found in unstable environment typically have small body size produce many offsprings and start reproducing really early. They have shorter life expectancy rapid population growth almost no or minimal parental care. They have weak competitive ability and do not show any density dependence.

They have variable population size which is often maintained below the carrying capacity of the environment the populations remain variable and the mortality is often unpredictable and they typically follow type 3 survivorship curve, which I will explain a little later. K selected species on the other hand, are found mostly in stable environments, larger body sizes produce few offsprings and they start reproducing little late, they have longer life expectancies lower population growth rate they typically show popular parental care of young.

They show strong competitive ability and density dependence. They usually maintain a constant population size which is close to the habitat carrying capacity. They show relatively constant and more predictable mortality rates and follow type 1 or type 2 survivorship curve. Let us see how these survivorship curves look like.

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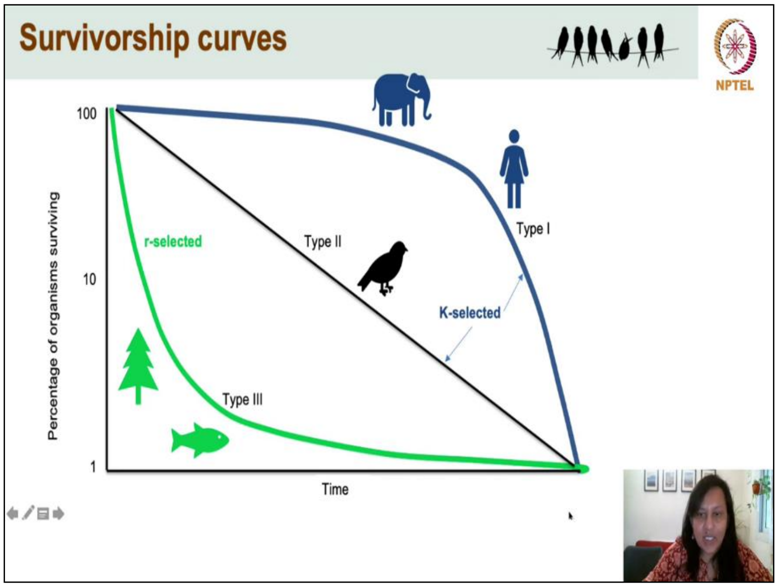

In case of r selected species, we see the type 3 survivorship curve where there is high mortality in the early years followed by relatively stable numbers later on. This is seen in species like across plants and species of fish. k selected species follow two types of survivorship curves, type II where the mortality remains constant through the lifetime of the organism. This is the curve we see in case of most birds.

Large bodied mammals such as elephants and humans have low mortality among young ones but it increases rapidly after a certain age and this is called a type 1 survivorship curve.

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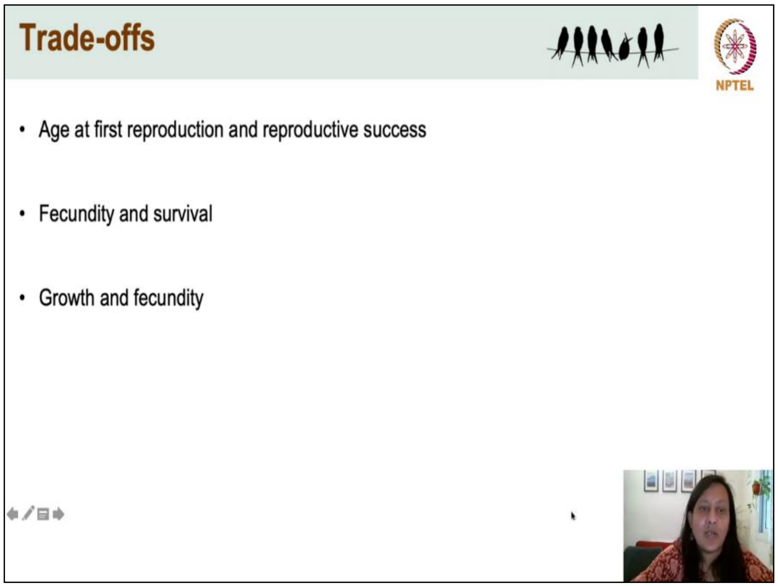

An optimal life history represents the best resolution of conflicting demands of survival and reproduction to increase an individual's fitness. For example, watching more carefully for predators takes time away from feeding young and so while this tactic might increase an individual survival the watchful individual may produce fewer young. Each of these responses affect other aspects of an individual's life.

Because breeding takes time and resources from other activities and entails risks, investment and offspring generally diminishes the survival of parents. In many cases, rearing offspring drains parents resources to such an extent that it produces fewer or no offsprings later. We see many such trade-offs among birds and we look at these three that is trade-offs between age at first reproduction and reproductive success, fecundity and survival, growth and fecundity in the following slides.

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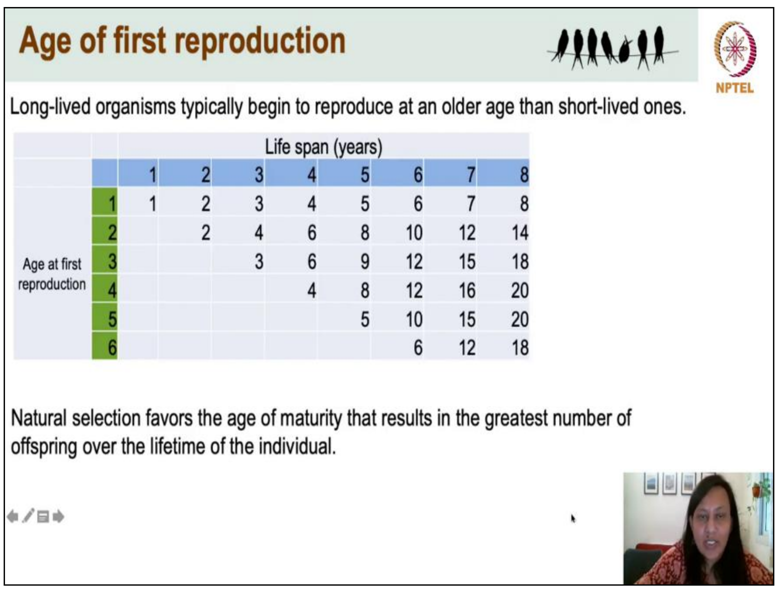

Let us first look at how age of reproduction affects reproductive success. In this hypothetical example, a bird's longevity is 8 years. If it starts reproducing at 1 years of age, each year it keeps on producing one egg. If it starts reproducing at three every year it produces three eggs and if it starts reproducing at six every year it goes on to produce six eggs each time. This table shows the number of eggs it produces by a certain year.

For instance, an individual which starts reproducing at the age of three has produced nine eggs by the time it is five years old. As you can see for each span of life, there is a certain optimal age of first reproduction that yields the maximum reproductive success. For this bird, which lives for eight years it seems most it seems optimal to start reproducing at four or five years of age. So, that the lifetime reproduction reaches a maximum of 20 eggs.

But if it lived for just five years, it seems better to start reproducing at 3 years of age to make sure that it produces the maximum number of eggs for that lifespan.

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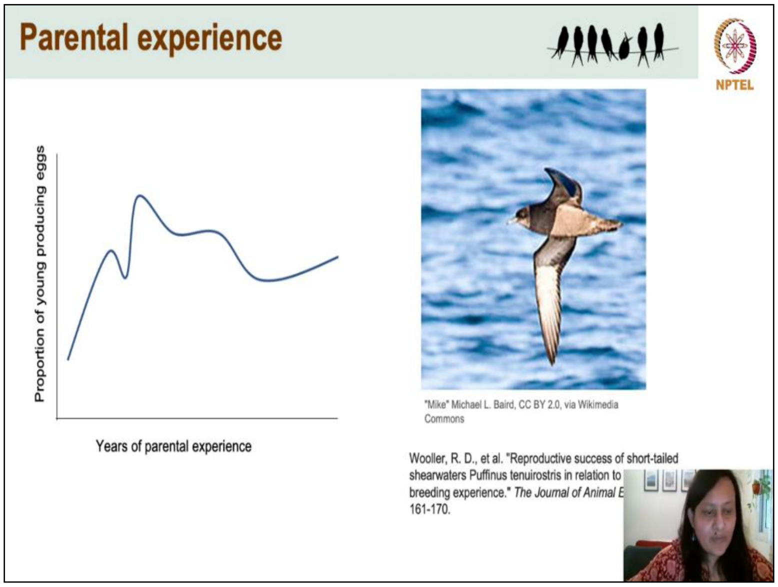

Similarly, parental experience has also been shown to have a positive influence on how many of the offspring go on to reproduce themselves. But it tapers off after a certain age, when most likely older parents are nearing the end of their reproductive age.

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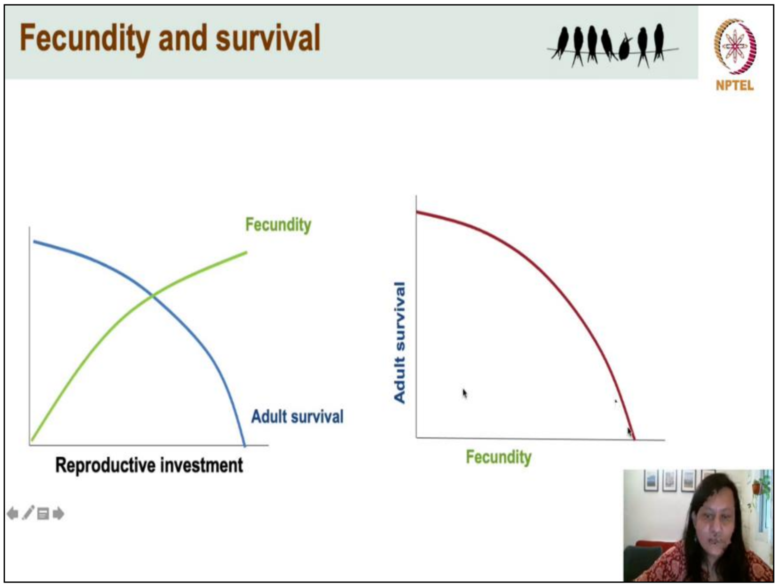

There is also a trade-off between fecundity that is number of eggs produced per episode of reproduction and survival of adults. Usually, the greater the investment in reproduction, the higher will be the fecundity but it tapers off due to diminishing returns on investment. Adult survival on the other hand declines since reproduction is taking away resources which could be otherwise used for self-maintenance of the adult. This results in an inverse relationship between fecundity and survival.

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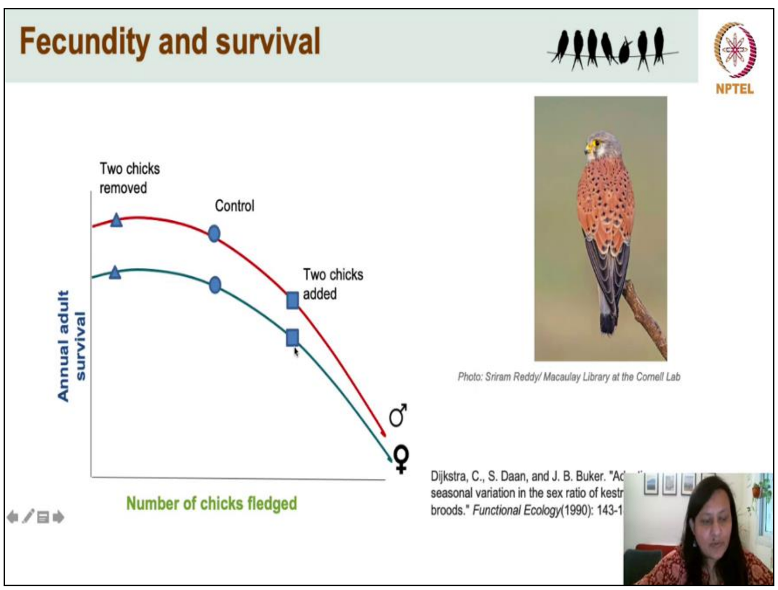

This experimental study demonstrates this. We can see that adult survival for both males and females improves when eggs were removed from the nest in this case and declines when two eggs were added to the kestrel nets nests that were studied here. These eggs refer to the fecundity. At the same time addition of chicks led to more competition between the siblings and fewer survive to reach adulthood.

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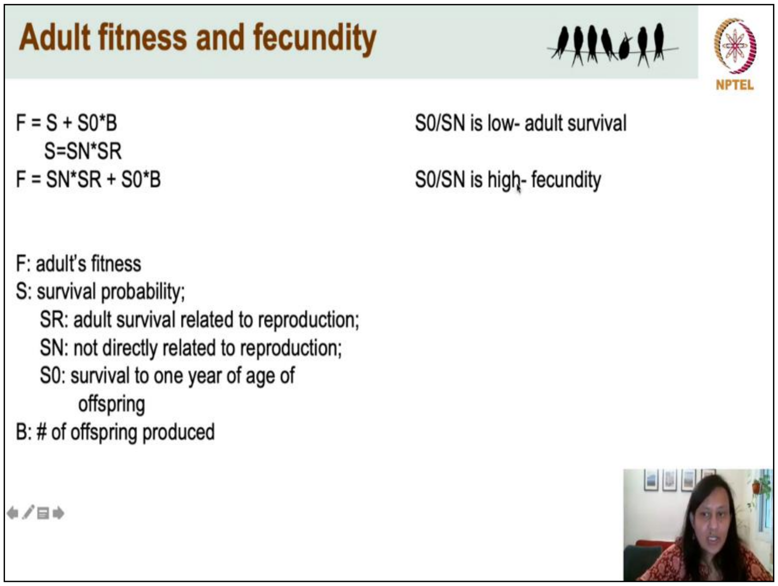

The relationship between adult fitness and fecundity is shown in these equations.

F=S+S0*B

S=SN*SR

F=SN*SR+S0*B

The adult fitness (F) is equal to the survival probability (S) of the adult and added to the product of survival to one year of age of the offspring (S0) and the number of offspring produced (B). Survival probability (S) itself is explained as the product of adult survival related to reproduction (SN) and adult survival not directly related to reproduction (SR). Overall, when adult life span is long and few offspring survive that is S0/SN is low the best strategy is to choose adult survival over fecundity. In contrast when adult lifespan is short and many offspring survive that is S0 by SN is high, the best strategy is to choose adult fecundity over adult survival.

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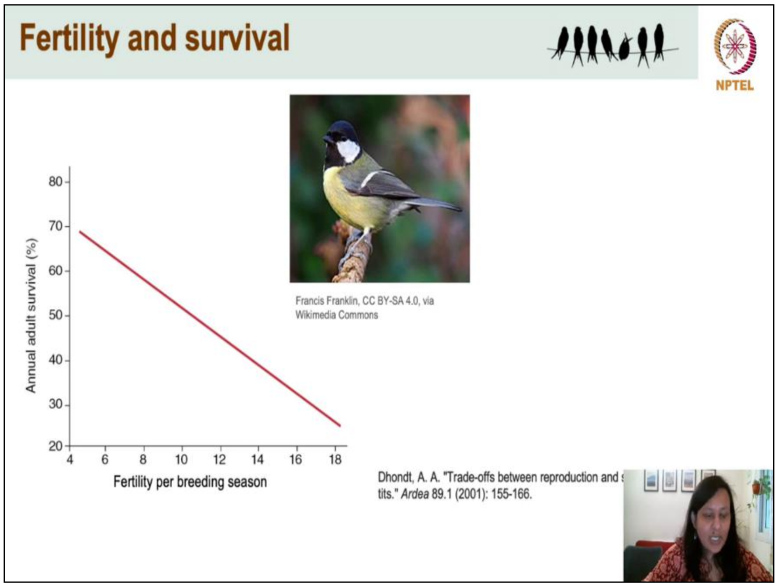

Again, the relationship between fertility, which refers to number of offspring per mating pair produced during a reproductive episode and annual adult survival is understandably negative given the investment in producing the eggs and parental care.

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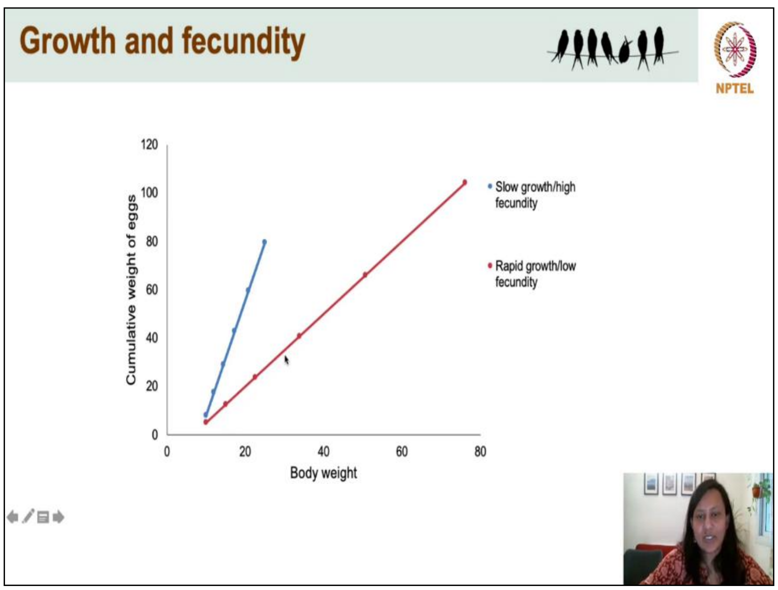

Now, growth and fecundity are again negatively related as can be seen here, the species which produce a lot of eggs or show high frequency grow very slowly as indicated by this blue line in contrast to those which show low fecundity and they seem to be able to grow at much faster rate.

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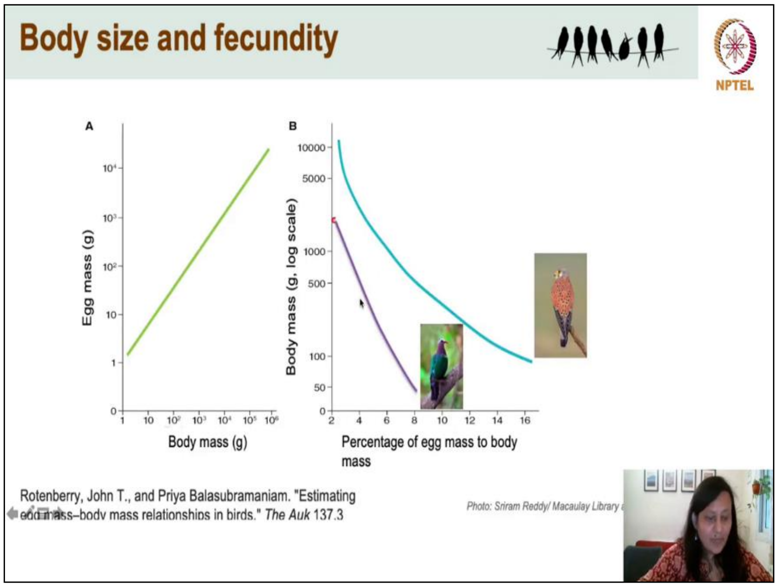

Further, typically larger bodied birds produce more egg during their lifetime but it has been seen that they relatively invest lesser into producing eggs as the body size increases. As and this has been seen amongst both raptors and doves and pigeons.

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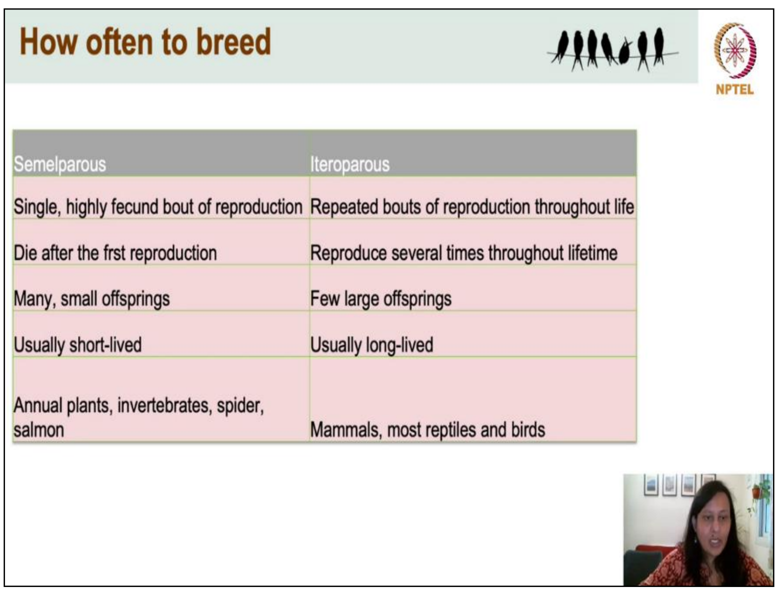

Another decision to be made is how often should an individual breed during its lifetime or what is referred to as its parity. We see these two contrasting strategies in nature -semelparous organisms such as annual plants, invertebrates, spiders, salmons. Typically have a single highly fecundity out of reproduction, they die after the first reproduction, produce many small offsprings and these organisms are usually short-lived.

In contrast iteroparous organisms have repeated bouts of reproduction throughout their lifetime they reproduce, several times produce larger offsprings. They are usually long-lived and larger bodied organisms such as mammals most reptiles and birds are all iteroparous in nature.

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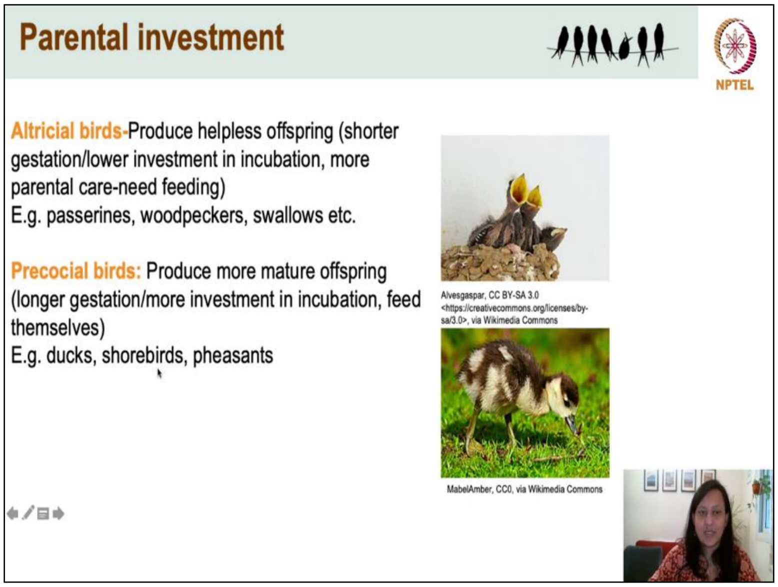

Finally, we come to parental care where the individual makes a decision regarding how much it invests towards caring of its young ones. We see two broad strategies that are seen amongst birds. There are altricial birds which produce very helpless offspring. These birds typically have a shorter gestation time. They invest very less in incubating their eggs and therefore the young ones that are produced rather helpless. They are naked, blind, they require a lot of parental care and feeding and such young ones are seen amongst passerines or songbirds, woodpeckers, swallows amongst many others.

The second strategy is that is seen is precocial. Being precocial, these birds produce more mature offspring. They in turn spend much more time in gestation and invest a lot more time in incubating their eggs and they instead produce young ones which are able to feed themselves as soon as they are born. We see such young ones amongst larger birds such as ducks, shorebirds and pheasants.

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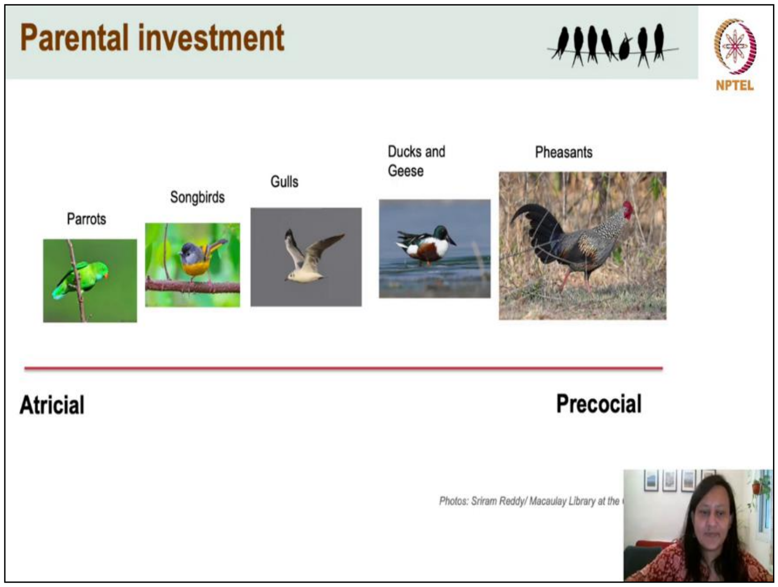

Among birds, we see a great range between these two extremes or that I just described in terms of parental care. This brings us to the end of this lecture on life history. You must have seen many studies that have been referred to in the slides through the lecture. And I hope you take up these studies and read them to learn about how researchers have studied these parameters of life history in nature for birds

Thank you.