

Basic Course in Ornithology
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Lecture -20
Bird Populations Concepts

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What is a population

• A population is the sum of individuals belonging to the same species that live in the same region at the same time.

sum of individuals	Interbreed, same region	same time
Number of individuals	Geographic closure	Temporal closure

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Video feed of Dr. Mousumi Ghosh

Hello! Welcome to the lecture on bird populations as part of the Basic Course in Ornithology. In today's lecture, we will be looking at concepts related to bird populations, their growth and regulation. Let's begin with a definition of population. A population is basically individuals belonging to the same species that occupy a certain space at a certain time. The important terms to consider in this definition are the fact that there are many individuals they belong to this same species that can interbreed and add individuals to the same.




And co-occur in space that is there is geographic closure. It also refers to a certain point in time suggesting temporal closure.

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What processes govern a population

• Populations change over time

$$N_1 \longrightarrow N_2$$

$$N_t \longrightarrow N_{t+1}$$







With time of course, population also changes and the changes in population happen due to four different processes.

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What processes govern a population

• The change $\Delta N = (N_{t+1} - N_t)$ is a result of 4 processes


+	Birth (B)	Immigration (I)
	Population change	
-	Death (D)	Emigration (E)
	Internal change	Migration


There are births and immigration that is the movement of individuals from outside the geographic region under consideration then there are deaths and emigration which is movement of individuals from the population to outside areas. Births and immigration add to the population while deaths and emigration remove from the population. Births and deaths represent internal changes to the population while the other are forms of migration.

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What processes govern a population



- The change $\Delta N = (N_{t+1} - N_t)$ is a result of 4 processes
 - BIDE - Births (B), Immigrations (I), Deaths (D) and Emigration (D)
 - So,
 - $N_{t+1} = N_t + ((B+I)-(D+E))$




So, essentially changes in population size from time t to time $t + 1$ are caused by these four different processes or BIDE – births (B), immigration (I), deaths (D) and emigration ϵ . And population size or N at time $t + 1$ is basically population size at N at time t + sum of births and immigration minus the sums of deaths and emigration.


$$N_{t+1} = N_t + ((B+I)-(D+E))$$

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Discrete population change



- $N_{t+1} = N_t + ((B+I)-(D+E))$
- $N_{t+1} = N_t + B - D$ ignoring migration
 - If we express Births per capita (b) as $b = B/N_t$ &
 - Deaths per capita (d) as $d = D/N_t$
- $N_{t+1} = N_t + N_t(b-d)$
- $N_{t+1}/N_t = 1+b-d$ dividing by N_t
- $N_{t+1}/N_t = 1+b-d = \lambda$ finite population growth rate



Often, we are interested in rates of change of population size. Let's consider a geographically close population with no migration. So, those changes are caused by just births and deaths. We then express births per capita (b)

$$b = B/N_t$$

Similarly, we can also calculate deaths per capita (d)

$$d = D/N_t$$

So, we can say that

$$N_{t+1} = N_t + N_t(b-d)$$


Dividing the whole equation by N_t , we get the rate of change parameter which is equal to $1 +$ per capita birth minus per capita death which is denoted by lambda.

$$N_{t+1}/N_t = 1 + b - d = \lambda$$

Lambda represents a finite or discrete population growth rate when we move from one discrete point in time to the other.

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Continuous population change



- $N_{t+1} = N_t + bN_t - dN_t$
- $\Delta N = N_t(b-d)$
- $dN/dt = N(b-d)$


Subtracting N_t

Measure change in population (dN) over a very small time interval (dt)

- $dN/Ndt = b - d = r$
- $dN/Ndt = r$

Divide by N

Intrinsic rate of change



To measure the continuous rate of population change first we calculate the change in population size or delta N as N_t multiplied by the difference between births and deaths per capita.

$$\Delta N = N_t(b-d)$$

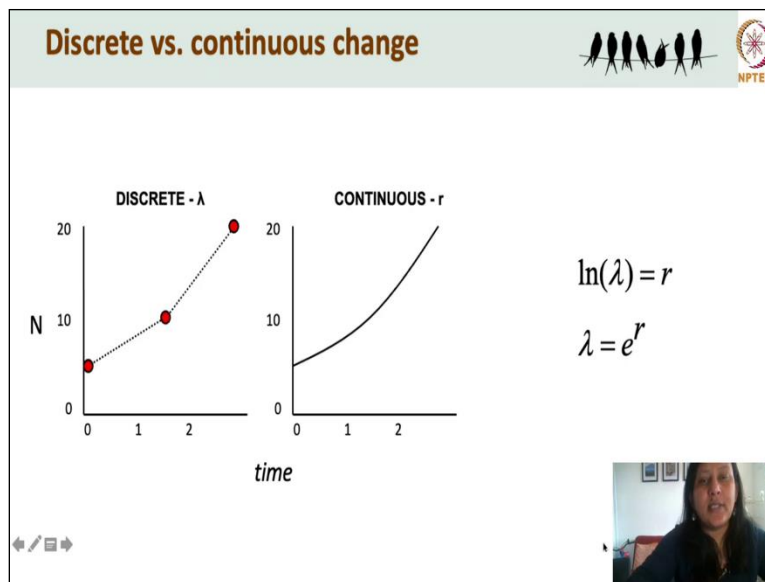
To measure the change in N over very small time intervals or almost continuously, we use differentials. We then divide this equation by N.

$$\frac{dN}{Ndt} = b - d = r$$

So, that dN by dt per capita is equal to births per capita minus death per capita and this is represented by r or the intrinsic rate of change.

$$\frac{dN}{Ndt} = r$$

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Here is a representation of how these two parameters change with time where λ is discrete off or r we get a smooth line since r is simply an integration of lambda.

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Management implications



$$N_{t+1}/N_t = 1+b-d = \lambda$$

$$dN/Ndt = b - d = r$$

- Population increasing
 - $r > 0, \lambda > 1$
- Population stable
 - $r = 0, \lambda = 1$
- Population decreasing
 - $r < 0, \lambda < 1$



Let's see how these two parameters help us in managing populations of birds in the wild. These two rates, while difficult to measure for most species give us a very good idea about how their populations are performing. Often, this is measured to see if a certain management practice which could be habitat improvement or protection is benefiting the target species or not. If a population is increasing, we find that

$$r > 0, \lambda > 1$$

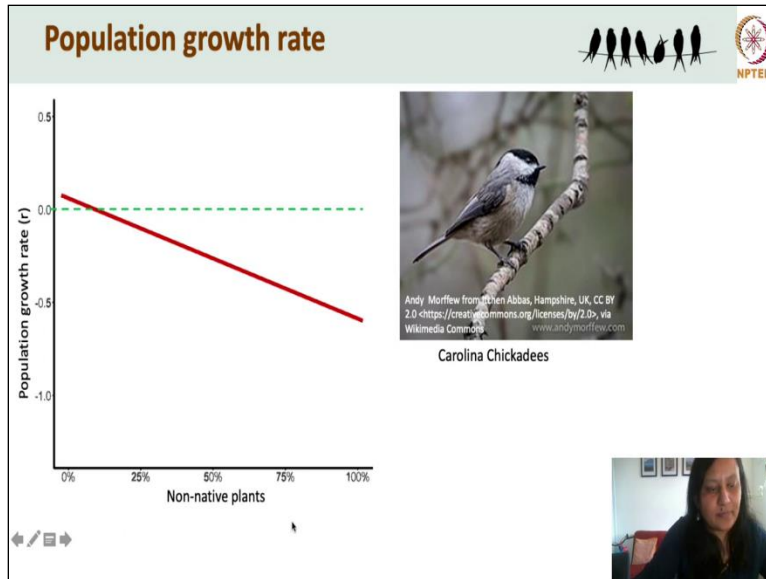
For a stable population, we find that

$$r = 0, \lambda = 1$$

For decline population

$$r < 0, \lambda < 1$$

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Here is an example, where the response to an invasive speed plant species is evidenced through the intrinsic population growth rate or r of Carolina Chickadees declining below zero as the frequency of the non-native plants increases in their habitat.

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Population parameters

Annual survival

Proportion of individuals surviving from time t to $t+1$

$$\phi = \{N_{t+1} - (B+I)\} / N_t$$

Recruitment

Number of individuals added from time t to $t+1$

$$f = N_{t+1} / N_t - \phi$$

We can also calculate annual survival using this expression where $\phi(\Phi)$ is equal to per capita difference between population at time $t + 1$ and additions due to births and immigration.



$$\Phi = \{N_{t+1} - (B+I)\} / N_t$$

Similarly, we can calculate the per capita additions (f) or recruitment into the population as

$$f = N_{t+1} / N_t - \Phi$$

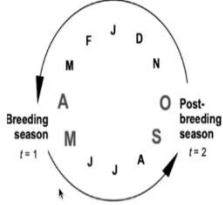
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Population survival




ϕ_{t-1} - probability of surviving and not emigrating
 f_{t-1} - addition of individuals from immigration

Δt_{t-1} : post-breeding to breeding interval




ϕ_{t-2} - probability of surviving
 f_{t-2} - addition of individuals from reproduction

Δt_{t-2} : breeding to post-breeding interval



Srinivasan, U., Hines, J. E., & Quader, S. (2015). Demographic superiority with increased logging in tropical understorey insectivorous birds. *Journal of Applied Ecology*, 52(5), 1300.




Let's look at this example to understand this better. This study looked at how six forest dependent understory insectivores perform in selectively logged tropical forests. For this they considered both ϕ and f or survival and recruitment and defined them for two different transitions, breeding season to post breeding season and again from the post breeding season to the breeding season interval.

Following their biology for the post breeding to breeding season interval, ϕ or survival is defined as the probability of surviving but not emigrating or moving out of the area. Recruitment for this period is defined as the addition of individuals from immigration and not births since they are not breeding now. For the breeding to post breeding interval ϕ is defined as the probability of surviving whereas recruitment f is defined as the individuals added due to reproduction.

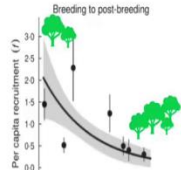
So, you see how you really need to inform your definitions of these population parameters through your knowledge of species ecology.

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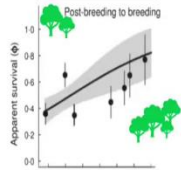
Population survival




Breeding to post-breeding




Post-breeding to breeding





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Srinivasan, U., Hines, J. E., & Quader, S. (2015). Demographic superiority with increased logging in tropical understorey insectivorous birds. *Journal of Applied Ecology*, 52(5), 1374-1380.

This study had some unexpected findings. They found that recruitment through reproduction was higher in selectively logged forest when compared to more intact forests with greater tree densities but there are higher natal dispersal into intact forest from the logged forests as indicated by the apparent survival of these individuals. These results show how important logged forests could be for maintaining the demographic processes of even forest dependent species.

This is important to take into consideration for management since such forests are routinely regarded as being unimportant for biodiversity conservation and recommended to conversion to other uses such as exotic and commercial plantations.

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Population density




Number of individuals per unit area

Expressed as number per sq. km or hectare

Used to understand populations and their responses

Methods used to estimate:


(a) Distance sampling: point counts and line transects




Another population parameter often estimated in ecological studies and monitoring is population density and that is the number of individuals of a species occurring per unit area and for birds it is often expressed in terms of numbers per square kilometer or per hectare. Density is measured to monitor for changes in population size and also to assess how species respond to changes in their environment. One of the most popular methods to estimate density of birds is distance sampling using point counts or line transect methods. You will be learning more about it in a later lecture.

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Population parameters



<ul style="list-style-type: none"> • N • D • P • b & d • ϕ • f • λ • r 	<ul style="list-style-type: none"> - population size - population density (N/area) - Proportion of patches occupied by the population - births and death per capita - survival - $N_{t+1} = N_t \phi + (B+I)$ - recruitment rate - $N_{t+1}/N_t = \phi + f$ - finite population growth rate - intrinsic rate of change
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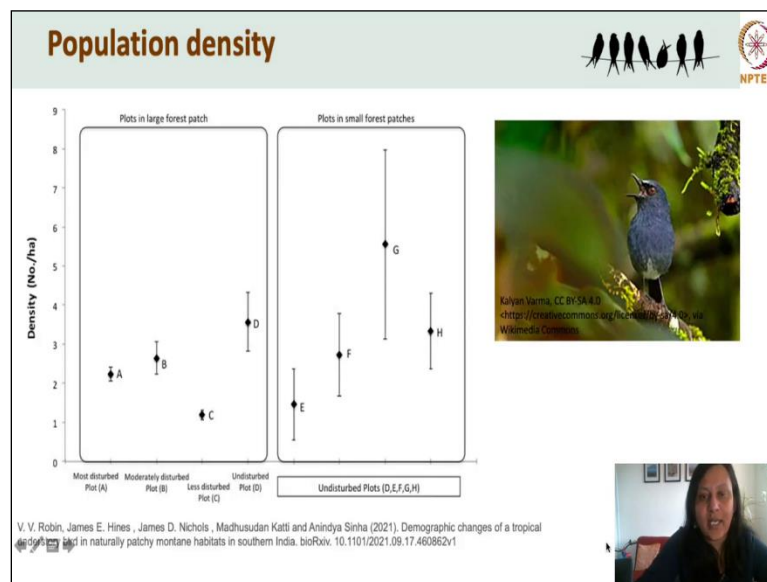


So, now we are familiar with a whole bunch of population parameters of interest which are used in ecological studies. Of these the top three that is population size or density and proportion of area

occupied or occupancy are known as state variables. A state variable is basically a figure or amount that tells us about the state of the population and this can change over time. The rest are known as vital rates. Vital rates describe processes such as births deaths migration and such that can either raise or lower the value of these state variables.

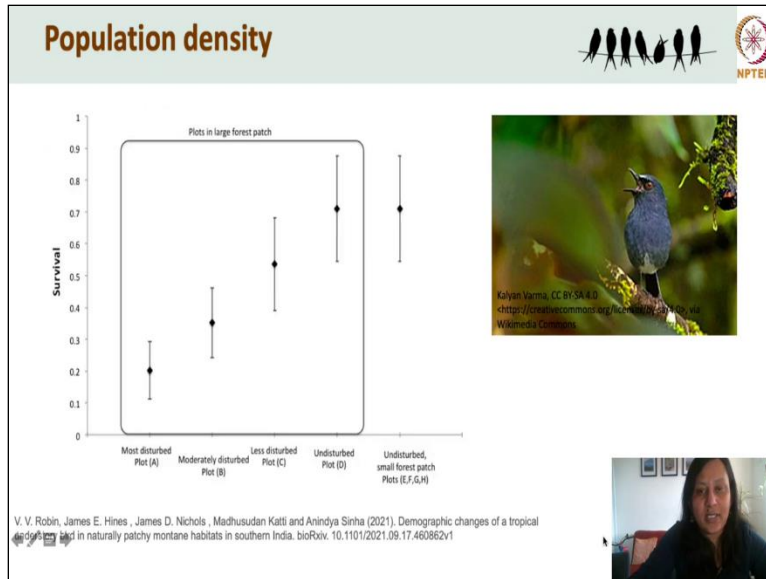
Vital rates, though requiring more time and effort to estimate in the field, are more informative than state variables for monitoring the health of bird populations or any ecological populations.

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Here is an example to illustrate this point. This study by Robin Vijayan and colleagues shows how population density and survival vary across a disturbance gradient for the white bellied short wing. They find that while density does not differ significantly across a disturbance gradient in different forest patches.

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Survival is highest in the undisturbed forest patches. This is seen across many taxa since state variables often do not capture any of the processes that affect a population such as disturbance or habitat change very accurately. Hence, we need to be very cautious while making any inference about changes in habitat or any form of disturbance affecting any population based solely on abundance or density data.

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Population growth



Idealized models describe two kinds of population growth:

1. **Exponential Growth**
2. **Logistic Growth**

Let's now look at how populations grow and the way they are regulated. Two idealized models that are often used to describe population growths are exponential and logistic growth forms.


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Exponential growth



- Population grows exponentially, and after attaining the peak value, the population may abruptly crash
- This increase in population is continued till large amount of food materials exist in the habitat



Photo: U.S. Department of Agriculture, Public dom



Populations growing exponentially grow rapidly till resources are readily available in the habitat such populations may eventually crash abruptly when the resources are exhausted.

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Exponential growth




Change in population size is represented as

$$\frac{dN}{dt} = rN$$

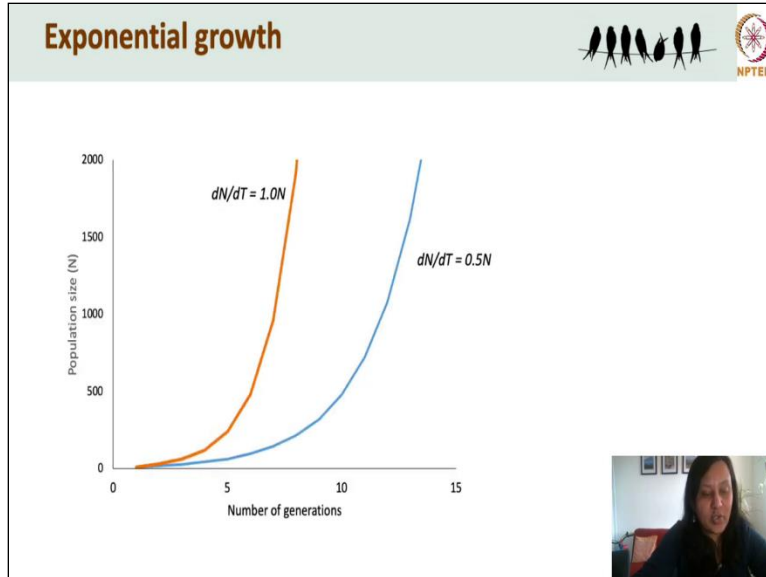
Here, dN/dt represents rate of change in population size,
 r is the intrinsic population growth rate,
 N stands for population size

Photo: U.S. Department of Agriculture, Public dom



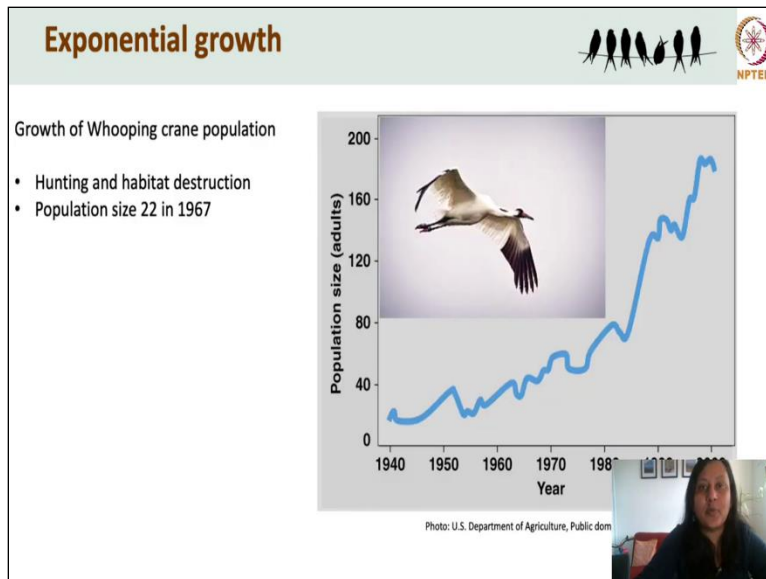
This is the mathematical expression denoting exponential growth rate where the rate of growth is simply a product of the population size and the intrinsic growth rate (r) of particular population.

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When we plot such growth, it looks something like this with a rate of 0.5 growing at a slower rate than a rate of 1.



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The most well-known example of exponential growth among birds is the case study of Whooping crane recovery in North America. This species was endangered due to excess hunting and habitat destruction and was reduced to just 22 individuals in 1967. Subsequent conservation measures have led to a rapid population recovery due to the habitat and resources being more than enough for this relatively meager population for the time being.


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Logistic growth

- No population can grow exponentially indefinitely
- Finite amount of resources
- Limits the number of individuals that can occupy a habitat
- Carrying capacity (K) is the maximum population size a habitat can support



K is not fixed, it can vary across time and space



However, in reality hardly any population can grow exponentially forever. That is because populations persist on a finite amount of resources which imposes a limit on the number of individuals that could occupy a certain habitat. We use the term carrying capacity denoted by K to refer to the maximum population size that a particular habitat can support. We must note that K or carrying capacity is not fixed but can vary across space and time as conditions change in that particular habitat.

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Logistic growth

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right)$$


Where, dN/dt is the rate of change in population size,

r is intrinsic growth rate

N is population size at time t ,

K is carrying capacity,

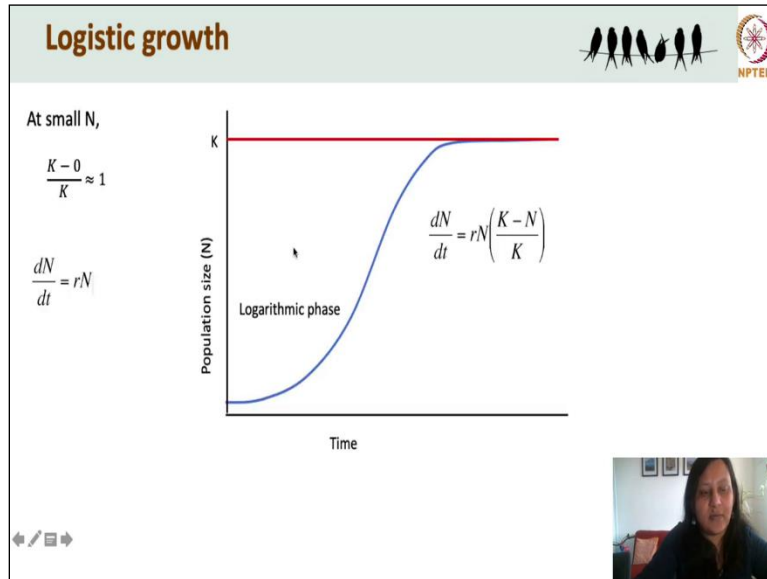
$K - N/K$ or $1 - (N/K)$ is for environmental resistance



Logistic growth rate is expressed using this mathematical equation where we multiply the exponential growth rate or r into N by this term which is the difference between the carrying

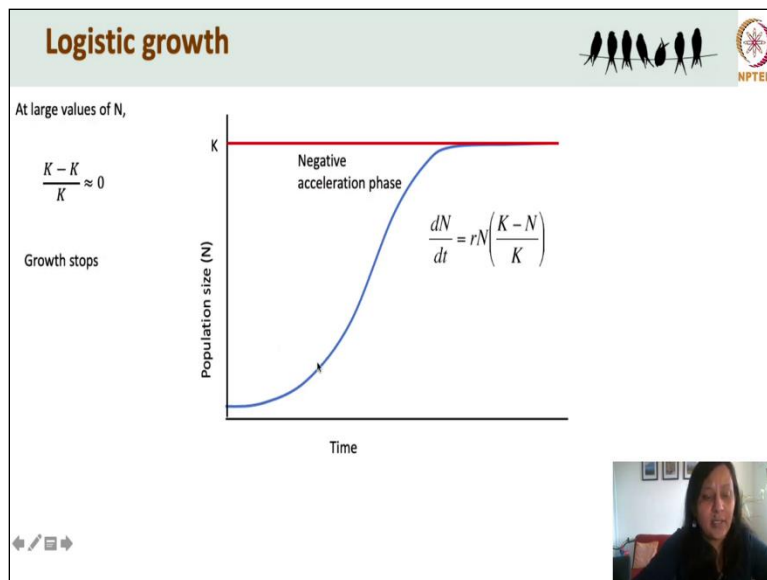
capacity and the population size divided by the carrying capacity for that habitat. This term basically describes the environmental resistance faced by the growing population that tries to keep it within habitat specific carrying capacity. The higher the N the higher the resistance.

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There are two distinct phases that we can see during a logistic population growth. When N is small and closer to zero, the environmental resistance is close to one and so that the population grows at almost an exponential rate. This is referred to as the logarithmic phase.

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Later, when the population size gets closer to K the resistant terms becomes almost zero and the growth stops or slows down. This is referred to as the negative acceleration phase.

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Regulation of population growth

$$\left(\frac{K - N}{K} \right)$$
 Environmental resistance

Density-dependent factors

- Depends on density (N/K)
- Disease, competition for resources, predation, parasites, stress

Density-independent factors

- Unrelated to density
- Natural calamity (hurricanes, fire, flood)

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Based on this concept of environmental resistance we can identify two different ways in which population growth is regulated. First are the density dependent factors which are dependent on the population density or the ratio between N to K which describes how close to the carrying capacity is the population size. The closer it is the more intense are the effect of these factors which are mostly biotic in nature.

Examples include – diseases, competition for resources, predation, parasite infestation and stress. The second group of factors have no relationship with density and impact the population with equal intensity whether we have 10 individuals or a thousand. Most natural calamities fall into this category and include hurricanes, flood, fires and extremes of temperature.


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Regulation of population growth



Density-dependent factors


- Birth-rate and death-rate vary as a function of density
- Intraspecific competition-between individuals of the same species for the same resources
- Intensifies with increase in population size
- Growth declines in proportion to intensity of competition



The density dependent factors typically impact either or both birth rates and death rates. It is also caused due to competition for resources between members of the same species. The effects intensify with increase in population size and accordingly growth rate declines.

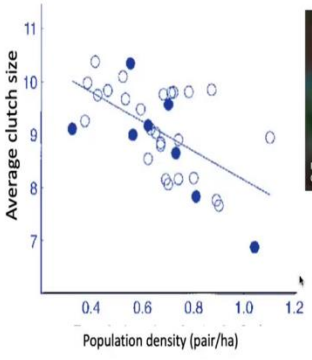
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Regulation of population growth



Density-dependent factors


Decreasing clutch size with increasing population density





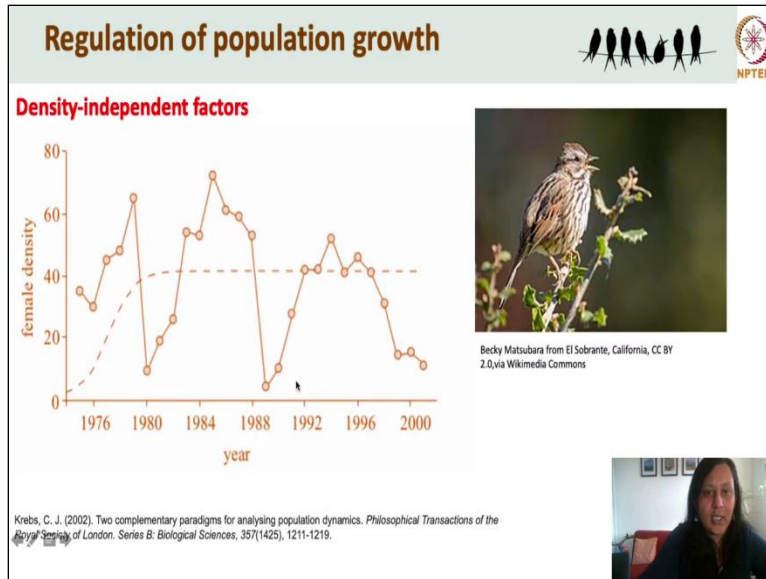
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Emlen, J. M., & Visser, M. E. (2000). Adaptive density dependence of avian clutch size. *Ecology*, 81(12), 3391-3403.



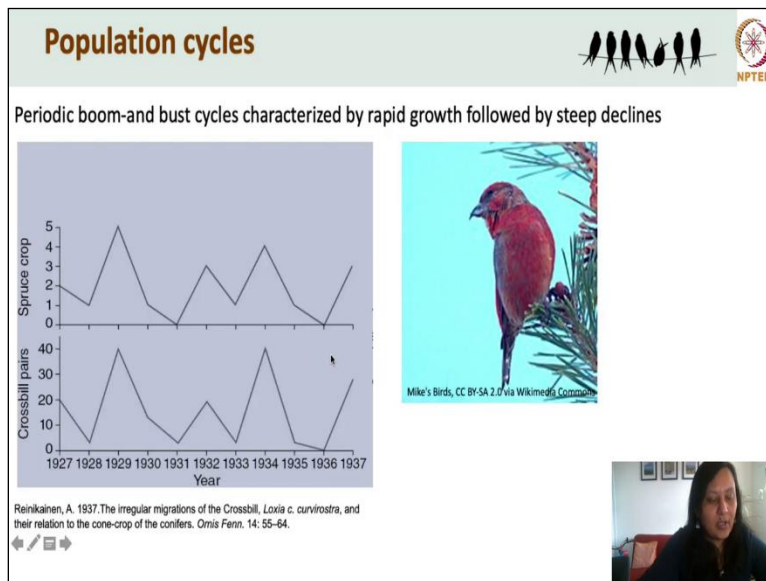
Here is an example of density dependent regulation of population growth. We can see that the average clutch size declines as the density of mating pairs of Great tits in an area goes up probably due to competition for resources that are required by the parents to lay the eggs as well as to feed the hatchlings.

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Here is an example of density independent factors regulating population size. These Song Sparrows nesting on Mandarte Island in British Columbia go through periodic declines in response to severe winters and it has nothing to do with their population size at that particular time.


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Another example of population growths not following a logistic or exponential growth structure are population cycles. Here you can see a population of Crossbills (Red Crossbills) which go through cycles in response to changes in cone crops of Norway spruce, a tree on which they feed on.

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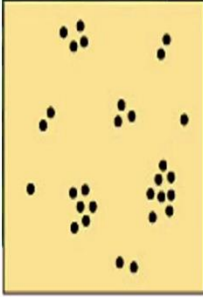

Population dispersion



Clumped distribution: Individuals aggregated in space, most commonly encountered pattern

Reasons:


- Some habitats more suitable
- Resources are heterogeneously distributed in patches
- Tendency of offspring to stay with parents
- Mating or social behaviour
- Protection from predators
- At large spatial scales all species appear to be clumped





Another important aspect to consider while studying populations is how they are distributed in space and this is called population dispersion. Clumped patterns are the most commonly encountered in nature and usually occur when some habitat patches are more suitable or resources are concentrated in smaller areas within a larger habitat or because of individuals forming social groups. At larger spatial scales most organisms appear to have clump distributions because their habitats are not uniformly distributed over large geographical areas.


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Population dispersion






Amur falcon in Nagaland





Mike Prince from Bangalore, India, CC BY 2.0 <<https://creativecommons.org/licenses/by/2.0/>>, via Wikimedia Commons




One example is the annual aggregation of Amur Falcons that we see in Nagaland every year. Such aggregations are often seen in migratory pathways of birds where they stop over to feed or rest.

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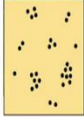
Population dispersion



Snow geese during their migration





USFWS Mountain-Prairie, Public domain, via Wikimedia Commons



This is another such aggregation scene for Snow Geese in North America.


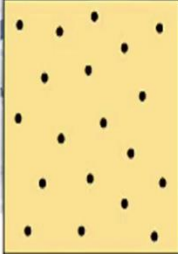
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Population dispersion



Uniform distribution: Individuals evenly spaced




- Seen among territorial species
- Maintained by antagonistic interactions
- Limited resources
- Helps individuals compete for limited resources and territory



Uniform distribution is seen where individuals are evenly spaced in nature. We see this among territorial species and this spacing is usually maintained by antagonistic interactions. This happens mostly when resources are limited and then individuals have to compete for such meager resources.



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Population dispersion

Nesting colony of gannets



Follash, Public domain, via Wikimedia Commons

Here is an example where Gannet nests are distributed uniformly across a suitable nesting beach which is rare to come across.

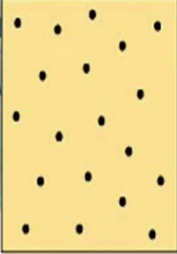

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Population dispersion

Random distribution: Individuals have equal probability of occurring anywhere in an area, rarely encountered


- Neutral interactions between individuals and between individuals and resources
- Resources randomly or uniformly distributed

We can see random distribution when individuals have an equal probability of occurring anywhere and this kind of distribution is rarely encountered. It is maintained by neutral or no interactions between individuals and between individuals and resources. Resources may be either uniformly or randomly distributed for organisms to reach random distribution.

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Population dispersion






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Dispersion of dandelions



An example of random dispersion comes from dandelions and other plants that have wind dispersed seeds. The seeds spread widely and sprout where they can happen to fall as long as the environment is favorable that is should have enough soil, water, nutrients and light.

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Population dispersion

Which pattern is it?

Variance-to-mean ratio (Krebs 1999)


$$\bar{X} = \frac{\sum X}{N} = 2.5$$

$$s^2 = \frac{\sum (X - \bar{X})^2}{n - 1} = 20$$

Variance/mean ratio = 20/2.5 = 8

If ratio > 1, clumped,
< 1, uniform,
= 1, random

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			●●●●●
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Let's see how we can find out or measure which pattern it is based on data gathered from field. Let's take this example where we sample across 16 quadrats, find 12 of them empty and find that four of them have 10 individuals each. Of course, it looks clumped, but how can we say it mathematically. For this, we can use a simple ratio called the variance to mean ratio suggested by Krebs in 1999.

Basically, we calculate the mean first which is 2.5 in this particular case. Then we calculate the variance using formula (in the slide) which comes up to be 20 for this particular case. The variance to mean ratio is equal to 8 in this case and using the rule that a ratio greater than 1 is clumped we can say that this population has clumped dispersion. If it was equal to 1 it would have been random and a value of less than 1 would mean that the population is showing uniform dispersion.

Since then, a number of more sophisticated and nuanced expressions have come up to measure the amount of dispersion that we see and I would urge you to explore these further. This brings us to the end of this lecture on bird populations. You will be learning more about how to measure these parameters in field in subsequent lectures. Thank you.