

Chapter 5 Populations

Overview

Population ecology is the study of factors that affect and change the size and composition of populations of organisms and how they interact with the environment.

Knowing how many individuals of a species are in a particular area, and how populations are changing over time are among some of the most basic yet crucial questions that wildlife and conservation managers need in order to protect species.

In this chapter we will cover the basic theoretical concepts in population ecology and population genetics, and explore some common methods used to measure and monitor wildlife populations.

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Population Structure

Populations

A population is a group of interbreeding organisms of the same species, found in the same place at the same time.

There are a number of characteristics of populations that are important to ecologists:

- population size (abundance)
- density
- distribution
- age structure (the proportion of young : old)
- sex ratio (the number of males: females)
- geographic range

The statistical study of populations and how they change over time is called **demography.**

Population Size (N) and density

Often the term 'population' is used in many different ways, but populations at different spatial scales can be defined as follows:

Species population: all individuals of a species.

Metapopulation: a set of spatially distinct populations, among which there is some immigration.

Population: a group of conspecific individuals that is demographically, genetically, or spatially distinct from other groups of individuals.

Aggregation: a spatially clustered group of individuals.

Deme: a group of individuals more genetically similar to each other than to other individuals, usually with some degree of spatial isolation as well.

Local population: a group of individuals within an investigator-delimited area smaller than the geographic range of the species and often within a population (as defined above). A local population could be a distinct population as well.

Subpopulation: an arbitrary spatially-delimited subset of individuals from within a population (as defined above).

Population Size (N) and density

Population size is simply the total number of individuals of the same species occupying any given area, and is usually denoted by *N*. The term abundance is often used.

Population density refers to the number of individuals in a given unit of space. For instance, density may be measured as the number of trees per hectare or the number of wolves per square kilometre.



Fluctuations in population abundance of an island population of song sparrows, Canada, 1975- 1998 (Arcese et al., 1992. Ecology, 73: 805-822.



Population Size (N) and density

Population size and density are among the most basic, yet important biological parameters that wildlife managers require, to inform conservation management actions. However, they can be remarkably challenging parameters to measure.

In most cases, it is not possible to obtain a direct value for population size. Many species are distributed over large geographic areas, are too numerous to count, or are too rare or elusive and difficult to observe and find. Therefore, population size and density is often estimated by taking sets of samples and extrapolating to the population as a whole.

Four general approaches to estimate population size are used: total counts, incomplete counts, indirect counts, and mark-recapture methods. These are discussed in more detail in Section 5.4.





Distribution

Distribution patterns refer to the spatial arrangement of a species or population.

The geographic **range** of a species is the area within which that species can be found, limited by the biophysical limits that the species can tolerate, and/or by the presence of humans or other species. Within that range, the **distribution** of a population can provide insights into the general structure of the species population, how large home ranges are and what the relationships are between individuals.

For example, if individuals are spread evenly across an area it is often due to negative relationships that cause each individual to be as far away as possible from others. In contrast, individuals may be attracted to each other and live in groups causing a very uneven distribution of the population across the landscape.



Distribution

On small scales, individuals in a population may be distributed evenly, randomly or clustered in groups. Distribution patterns can differ at different spatial scales, and are often affected by season, resource availability, or time of day.



Uniform distribution occurs when the distance between individuals is maximised. Examples include plants that use toxins to inhibit growth of nearby plants (e.g. *Salvia leucophylla*—sage) and territorial birds such as the Emperor penguin.



Random distribution occurs when individual positioning is independent of others. It is the least commonly found type of distribution. Examples include plants with wind-dispersed seeds (e.g. Dandelion).



Clumped distribution is most commonly found in nature and occurs when the distance between neighbouring individuals is minimized. It is seen in groupliving animals (e.g. chimpanzees, buffalo) who gather together for social reasons, to access resources, to migrate or to avoid predators.

Age structure

The age structure of a population can be helpful in determining the future growth rate of a population. Individuals can be categorized into three groups: pre-reproductive, reproductive and post-reproductive. Populations with large pre-reproductive and reproductive groups are likely to experience growth in the near future.

If large proportions of populations are post-reproductive it means recruitment of new individuals is proportionally low for the population. This is likely to lead to either zero growth or a decrease in the population's size.

Age structure is very important in the management of fisheries and wildlife populations. In management schemes it is important to maintain significant levels of reproductive individuals and in harvested stocks knowledge of the populations age structure can be used to influence which individuals are important to keep in the population.



Age structure

The percentage of males and females in different age categories can be represented as a bar graph. On the left, the graph shows the bulk of the population is young, meaning that the population size may soon increase as the large number of young tortoises reach reproductive age. On the right, the graph indicates a stable population with all age levels roughly comprising the same percentage of the whole population. The population is probably not growing or decreasing in size.







Sex Ratio

The sex ratio of a population is simply the number of males relative to females. Sex ratio is often influenced with time and the life stage of individuals. In most sexually reproducing species, the sex ratio is around 1:1. This ratio is explained by **Fisher's principle**, which states that the sex ratio always reverts back close to 1 as a result of the nature of evolutionary biology. If there are more females than males, a single male and his male-producing genes will be spread to more females, as a result of the short supply of males in the population. More male offspring are produced and the sex ratio becomes more balanced. If there are more males in the population, than more females with their female-producing genes are going to reproduce and as a result, more females are born and the sex ratio shifts back closer to 1.



Sex Ratio

Monitoring sex ratios can provide important information concerning the health of a population in response to environmental pressures. Some crustaceans, annelids and reptiles have environmental-dependent sex determination, where factors such as incubation temperature, length of daylight (photoperiod) or nutrient availability determines the sex of offspring. Such species are particularly vulnerable to global climatic changes as highly skewed sex ratios can result.

Sex ratios can also indicate the extent of hunting pressures, where one sex is targeted more than the other, such as elephants, where poachers target the largest individuals (usually males) for their greater tusk sizes.





Population Growth

Population growth

Population growth is affected by natality (births), mortality (deaths), immigration and emigration. Populations gain individuals through births and immigration, and they lose individuals through deaths and emigration.

Population growth rate is how fast a population changes in size over time. It is expressed as *r*: a positive value means the population is increasing in size, and a negative value means it is decreasing.

Population ecologists use a variety of mathematical methods to model **population dynamics** (i.e. how populations change in size and composition over time).

Some of these models represent growth without environmental constraints, while others include "ceilings" determined by limited resources.

The two main factors affecting population growth are the birth rate (b) and death rate (d).



Exponential growth

The most basic approach to population growth is to assume that every individual produces two offspring in its lifetime and then dies, therefore doubling the population size each generation.

This kind of growth can be illustrated by growing a colony of bacteria in a lab. Bacteria reproduce by splitting into two, so with a division time of 1 hour, an initial colony of 1000 bacteria would produce a population size of 16 billion after 24 hours.

This is known as exponential growth and produces a **J-shaped curve**.

Exponential growth can only occur if resources are unlimited. Because birth and death rates do not change over time, the per capita **growth rate** of the population is constant.



Exponential growth

Mathematically, this is expressed by the exponential growth equation:

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

Here, dN/dt is the growth rate of the population at a given time, N is the population size, t is time and *r* is a constant known as **the intrinsic rate of natural increase** (or *per capita* rate of increase), which is calculated as the birth rate *b* minus the death rate *d* of the population.

This differential equation helps us understand the growth pattern over time. It simply means that the rate change of the population is proportional to the size of the population, or in other words: the rate of change of the population over time equals the growth rate (r) multiplied by the population size (N).

When the per capita growth rate (r) stays the same no matter what the population size is, an exponential growth pattern is seen.



Logistic growth and Carrying Capacity

When a species is introduced into a new habitat where resources are plentiful, it may show exponential growth for a while. However, extended exponential growth is only possible if infinite natural resources are available, which is usually not the case in the real world.

Eventually, a population will start to exhaust its resources and the growth rate will slow down, eventually levelling off. The population size at which it levels off is the maximum population size that a particular environment can sustain, and is called the **carrying capacity** (K).

A graph of logistic growth yields the S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, the growth rate levels off at the carrying capacity of the environment, with little change in population number over time.

Logistic growth is a more realistic model of population growth than exponential growth.



Logistic growth

Logistic growth is expressed by the following mathematical equation:

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

Here, at any given point in time during a population's growth, the expression K - N tells us how many more individuals can be added to the population before it reaches carrying capacity. (K - N) /K is the proportion of the carrying capacity that still remains for growth.

We get logistic growth when the per capita growth rate (r) gets smaller as the population approaches its maximum size.

In real populations, a growing population often overshoots its carrying capacity, causing an increase in mortality and the population size to decline back to the carrying capacity or below it. Most populations usually fluctuate around the carrying capacity in an undulating fashion rather than existing right at it. These patterns are explained in more detail in Chapter 6.





However both these models assume a closed system where no emigration or immigration is occurring.

While the two main factors affecting population growth are the birth rate (*b*) and death rate (*d*), population growth may also be affected by individuals coming into the population from somewhere else (**immigration**, *i*) or leaving the population for another area (**emigration**, *e*).

The formula for population growth takes all these factors into account.

Population change = (Births+Immigration) - (Death+Emigration)

r = (b + i) - (d + e)

Where:

- r = population growth rate
- b = birth rate
- *i* = immigration rate
- d = death rate
- *e* = emigration rate

Dispersal

Dispersal is the spreading of individuals away from others, often close relatives such as parents and siblings, which are left behind in the original area. This may be done to prevent offspring from competing with relatives for resources (kin competition), to reduce the risk of inbreeding (inbreeding avoidance) or to maximise spatiotemporal variation in habitat suitability or resources. Dispersal results in gene flow: through moving from one area to another, the dispersal of an individual has consequences not only for individual fitness, but also for population dynamics, population genetics and species distribution.

Dispersal in animal populations is often sex-biased, that is, one sex disperses more frequently or further than the other. For example, in many bird species it is females that disperse whereas in mammals male-dispersal is more common. Sex-biased dispersal is often explained in terms of mating systems, and is therefore a much-discussed concept in Behavioural ecology (see Chapter 6).

Dispersal in plants can be done through abiotic means (e.g. wind, water), by animals (zoochory), or plants can disperse their own seeds (authochory, e.g. ballistic seed dispersal).



Migration

Migration is another type of movement that affects population size and dynamics, however it differs to dispersal because it refers to the large scale movement of members of a species from one place to another, usually leaving none behind.

Animal migration is usually long-distance and is either annual or seasonal. It is found in all major groups, including birds, mammals, fish, reptiles, amphibians, crustaceans and insects.

The purpose of migration is to take advantage of more favourable conditions for food availability, safety from predators, mating and reproduction, or other environmental factors.

Environmental cues such as photoperiod or local climate may trigger migration.



r/K selection

An important concept in population ecology is the r/K selection theory. As we know, r is the intrinsic rate of natural increase in population size and K is the carrying capacity of the population.

The theory states that *r*-selected species are those that have high reproductive rates, low levels of parental investment in young, and high rates of mortality before individuals reach maturity. Evolution favours productivity in *r*-selected species. Examples of r-selected species include many kinds of insects, such as aphids, or molluscs, such as clams.

In contrast, *K*-selected species are those that have low reproductive rates, high levels of parental investment in young, and low rates of mortality as individuals mature. Evolution in *K*-selected species favours efficiency in the conversion of more resources into fewer offspring. Examples of K-selected species include humans, apes and elephants. K-selected species fluctuate at or near carrying capacity, possess relatively stable populations and tend to produce relatively low numbers of offspring.





Regulation of Population Growth

In nature, population size and growth are limited by many factors. Some are density-dependent, while others are density-independent.

Density-Dependent limiting factors cause a population's per capita growth rate to decrease as population density increases. The more individuals are crammed into a finite space with finite resources, the more severe are the density-dependent Limiting Factors. One example of this is competition for limited food among members of a population.

Density-Independent limiting factors affect *per capita* growth rate independent of population density. They are more or less random in that they don't act as a function of population density. However, these limiting factors can have extreme effects upon population growth. Such factors include: floods, drought, lighting, fires, volcanic eruptions.







Population Genetics

Population genetics

Population genetics is the study of the genetic basis of naturally occurring variation within and between populations.

It focusses on describing and understanding changes in the frequencies of genes and alleles in populations over space and time, and the evolutionary forces creating variation within and between species. Many of the genes found within a population will be **polymorphic** - that is, they will occur in a number of different forms (or alleles). Mathematical models are used to investigate and predict the occurrence of specific alleles or combinations of alleles in populations, based on Mendel's laws of inheritance and modern evolutionary theory. The focus is the population or the species - not the individual.

Genetic variation within and between populations is often analysed using highly polymorphic DNA nucleotide sequences: e.g. microsatellites or single nucleotide polymorphisms (SNPs). Genetic variation at the species boundary is often analysed using more conserved regions of mitochondrial DNA. Whole genome sequencing is becoming more commonplace as technology improves.

Gene pools and genetic diversity

The collection of all the alleles of all of the genes found within a freely interbreeding population is known as the **gene pool** of the population. Each member of the population receives its alleles from other members of the gene pool (its parents) and passes them on to other members of the gene pool (its offspring).

Genetic diversity within a gene pool is influenced by population size, mutation, genetic drift, natural selection, environmental diversity, migration and non-random mating patterns.

The **Hardy-Weinberg model** is a key concept in population genetics. It describes and predicts a balanced equilibrium in the frequencies of alleles and genotypes within a freely interbreeding population, under certain conditions.

When there are two alleles of a gene in a population, the frequencies are described as:

$$p + q = 1$$

Where p is the frequency of the dominant allele in the population and q is the frequency of the recessive allele. When Hardy-Weinberg equilibrium is met the following equation is true :

$$p^2 + 2pq + q^2 = 1$$

Where p^2 represents the frequency of the homozygous dominant genotype, q^2 represents the frequency of the recessive genotype and 2pq is the frequency of the heterozygous genotype (also, see Chapter 3.2: Punnet squares).

A population is said to be in Hardy - Weinberg equilibrium when 5 conditions are met:

- No mutations
- No gene flow (no immigration /emigration)
- Large population size (no genetic drift)
- No selective forces
- No non-random mating

Deviations from Hardy-Weinberg

Evolution is a change in allele frequencies in a population over time. When a population is in **Hardy-Weinberg equilibrium** for a gene, it is not evolving, and allele frequencies will stay the same across generations.

However, in reality populations are usually evolving, which means that deviations from Hardy-Weinberg may occur. Population geneticists often check to see if a population is in Hardy-Weinberg equilibrium *because* they suspect other forces may be at work.

If one of the 5 assumptions of Hardy-Wienberg equilibrium are not met (violated) for a gene, the population may evolve for that gene (the gene's allele frequencies may change). This could be due to mutation, non-random mating, gene flow, finite population size (genetic drift), and natural selection.

However, evolutionary forces may be acting on certain genes but not others, so while some genes may satisfy the Hardy-Weinberg equation, others do not.

Effective population size (N_e)

Another important parameter in population genetics is effective population size, denoted as N_e.

 N_e is defined as: "the number of breeding individuals in an idealised population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration".

It translates census sizes of a real population into the size of an idealized population showing the same rate of loss of genetic diversity as the real population under study.

 N_e is usually less than N (the absolute population size) and this has important applications for conservation genetics (see next slide).

 N_e is a primary factor responsible for the rate of loss of genetic diversity as well as the rate of increase of inbreeding and genetic drift in a biological population.

Because the N_e estimation helps to explore population demographic history, and allows for predictions of the behaviour of genetic diversity over time to be made, N_e is a key parameter for the genetic management of small and isolated populations.

Conservation genetics

Population genetics is a useful tool in conservation biology, and along with its sister discipline molecular ecology has developed into its own field: conservation genetics. Advances in molecular genetic techniques have changed the face of ecological research, and are now essential tools in the study of endangered mammals, wildlife forensics and conservation management.

For example, at the **population level**, the partitioning of genetic diversity within and among populations, estimates of gene flow and effective population size are important parameters for identifying populations that are most in need of new individuals, that require demographic and environmental considerations, or that require legal protection.

At the **species boundary**, genetics have an important role in helping to identify taxonomically distinct units for the allocation of resources and prioritization of conservation efforts. Species clarification is also useful in wildlife forensic applications, where the genetic identification of products from endangered species can be a great aid to law enforcement agencies.

Conservation genetics methods are also used for monitoring and maximizing genetic diversity during captive breeding programs and re-introduction schemes.

Conservation genetics

Some examples of the application of population genetic techniques to conservation problems include:

- The genetic monitoring of translocated individuals to understand the viability of captive-released populations (e.g. chimpanzees);
- Genetic mark-recapture studies to monitor population trends of endangered species
- Genetic assignment of seized ivory to the elephant population of origin.
- Pedigree analysis of captive or translocated animals to evaluate breeding priority of particular individuals
- Genetic profiling of endangered/relic populations to evaluate and monitor translocation and breeding programmes to maximise genetic diversity and minimise the effects of inbreeding.



Measuring populations

There are four main approaches to estimate population size of flora and fauna. These are total counts, incomplete counts, indirect counts, and mark-recapture methods.

Total (or complete) **counts** means counting every individual in the population. This approach is rarely used by ecologists, as it is nearly always too expensive or practically unfeasible. However, it may be possible in restricted geographic areas for easily detectable species, e.g. a small island population of birds, or crabs in a tide-pool.

Incomplete counts involve counting a representative sample of a population and then extrapolating to the entire population. This is often done with methodological approaches such as quadrats, drive censuses, sweep censuses or line transect methods. It's a common approach for vegetation censuses.

Indirect counts are conducted when organisms cannot easily be located and detected directly. Instead, other –indirect- indices are used as a proxy for relative abundance to be estimated. For animals this is usually dung and nests. Indirect counts are commonly used for surveying mammals in tropical rainforests: e.g. dung counts are the standard method for censusing elephants in forests.

Mark-recapture methods are useful for surveying mobile animals that are hard to observe and monitor directly. It is used to estimate the size of a population where it is impractical to count every individual. The basic idea is that you **capture** a small number of individuals, put a harmless **mark** on them, and release them back into the population.



Biomonitoring is defined as the act of observing and assessing the state and ongoing changes in ecosystems, components of biodiversity and landscapes, including the types of natural habitats, populations and species. In ecology it is usually conducted as repeated surveys of populations of target taxa, using various survey methods. By tracking populations of different species over time, ecologists can monitor past changes, evaluate the status of current populations and make future predictions- all of which contribute to species protection plans and conservation strategies.

Biomonitoring also helps wildlife managers improve adaptive management practices - for example, by showing whether existing conservation efforts are helping an endangered species increase in numbers.

Biomonitoring is fundamental to many protected area and species management plans.

Because of the elusive nature of many animal species, combined with difficulties in sampling in certain kinds of habitats, as well as the areas needed to cover, it can be surprisingly hard to do!

Distance Sampling

Distance sampling is actually a group of methods widely used for estimate the abundance and density of animal populations, usually using indirect indices. Line transects or point transects are usually employed.

Line-transect sampling uses the perpendicular distance from the transect centre to detect and record animals. Point transects measure radial distances.

The method is based on the assumption that the probability of detecting an animal- or animal signdecreases as its distance from the observer increases.

The probability of seeing objects at different distances will depend on the density of the vegetation – in open areas you may be able to see an animal at 300m, whereas in dense rainforest large mammals may not be visible 10m away. Line-transect analyses calculate animal densities (or densities of sign) by using perpendicular distance measurements to estimate a function describing the probability of observing an animal at any given distance from the transect line.

These are known as *detection functions*, which model the probability of detecting an animal, given its distance from the transect.

Distance Sampling

A field observer detects an object and records distance r and angle θ to the transect line. This allows calculation of object distance to the transect (x).









One example of Distance Sampling in practice comes from a seminal study published by a large group of ecologists in 2013. This study was the largest survey dataset ever assembled for forest elephants, amounting to an incredible 91,600 person-days of fieldwork covering 13,000 km²! Data from about 80 line transect surveys conducted across Central Africa revealed that elephant population sizes decreased by more than 60% between 2002 and 2011: a catastrophic decline, mainly due to poaching. These important data are crucial for conservation managers and national authorities to increase anti-poaching efforts, and raise the alarm with the international community to intensify efforts to combat the global ivory trade.



Quadrat method

The quadrat method is a classic tool in ecology, consisting of a series of squares or rectangles of a set size that are placed in a habitat of interest. The species within those quadrats are then identified and recorded. Abundance is calculated using the number found per quadrat and the size of the quadrat area. Quadrats are commonly used for sampling plants in relatively small areas (e.g. $1m^2$ quadrats), and can be used in terrestrial, coastal and even marine habitats.







Plot method

Plots are similar in approach to quadrats but generally used for sampling trees over larger areas (e.g. 1 ha plots). In addition to estimating the abundance and density of individual populations, they are also very useful for measuring species density, biodiversity (species richness), stem density, mortality, recruitment, basal area, growth rates, and carbon stocks. As such they are more than just a population abundance tool.





Mark-Recapture method

Mark-Recapture is a popular tool for measuring animal abundance; particularly for organisms that can be easily trapped, and when it is not practical to count all the individuals in the population.

Basically, a sub-set of animals from the population of interest are captured and marked. Marks take the form of physical tags, paint, tattoos etc. The individuals are released and given time to mix with the rest of the population. During a second sampling period, more animals are captured, and the ratio of marked : unmarked animals is used to estimate the total population size. An important distinction is made between closed populations and open populations. A closed population is one in which the total number of individuals is not changing through births, deaths, immigration or emigration. In practice, animal populations are not closed, of course, but in some cases, this assumption may be reasonable if the sampling interval is small enough.



Mark-Recapture method

Mark-Recapture methods have been an important tool to monitor and measure polar bear populations. Although a challenging species to study, by marking them with lip tatoos, much of what is known about polar bear population dynamics has come from long-term mark-recapture studies dating back to the 1970s.





Southern Beaufort Sea polar bear abundance over time

Mark-Recapture method with camera traps

As many animal species cannot be easily trapped and tagged, non-invasive methods are a more desirable way to study them. To counter this, mark-recapture methodology has been adapted to camera traps.

Here, sets of cameras are deployed to take photos of animals as they pass by. Unique markings are used to identify the same individuals that are photographed (or "captured") more than once. As you can imagine, this method works best for species that have distinctive markings that allow for individual identification. However, because of its ease of deployment and non-invasive nature, camera-trapping is a widespread method for conducting ecological surveys and monitoring population abundance . It has been widely used on carnivores, such as leopards, tigers, jaguars, bobcats, lynx and bear; ungulates (e.g. gorals, deer) and elephants.



Area	No. of individual		Estimated no. of leopards			Effective survey area	Density
	Captures	Recaptures	N	SE	95%CI	size (km ²)	(no./100 km ²)
Park	4	10	4	0.7	3-6	395	1.0
Farmland	10	15	13	3.6	11-29	364	3.6

Unique markings are used to 'capture' the same individuals in different camera traps and estimate population size

Genetic mark-recapture

For the most elusive species, e.g. those that are nocturnal, difficult to trap, and/or have no distinctive markings, most methods have proven extremely challenging, and as a result accurate population data for many species are still lacking.

Non-invasive genetic mark-recapture techniques have more recently been developed for the most elusive and cryptic species. This technique combines DNA analyses from non-invasively collected samples, such as shed hair of faeces with capture-mark-recapture (CMR) models to estimate population size and sex ratios.

This technique has now been successfully applied to many species and taxa, including the Eurasian otter, Yellowstone wolves, white sharks, southern bluefin tuna, Indiana bats, loggerhead turtles, Cabrera voles and capercaillie.



Resources

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Suggested Reading

- Cappucino, N. and Price, P (1995). Population dynamics- 1st Edition. Elsevier.
- Gillespie, J.H. (2004). Population Genetics- a concise guide. 2nd Edition. The John Hopkins University Press. <u>https://public.wsu.edu/~gomulki/mathgen/materials/gillespie_book.pdf</u>
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- Begon, M., Mortimer, M., and Thompson, D.J. (1996). Population Ecology, a Unified study of Animals and Plants, Third Edition. Wiley Online Library.

Online resources

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- R-selected species <u>https://www.britannica.com/science/r-selected-species</u>
- K-selected species https://www.britannica.com/science/K-selected-species