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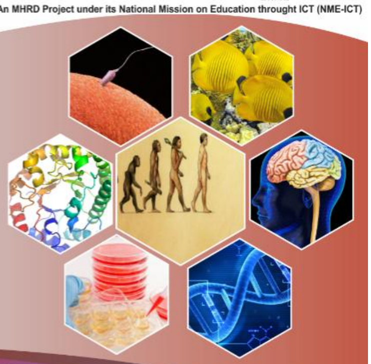

Production of Courseware

e-Content for Post Graduate Courses

Paper : 12 Principles of Ecology
Module : 7b Life History Strategies (Part 2)

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Description of Module	
Subject Name	ZOOLOGY
Paper Name	Principles of Ecology: Zool 012
Module Name/Title	Life History Strategies (Part 2): ***r*- and *K*- strategists**
Module Id	M7b; Life History Strategies (Part 2)
Keywords	*r*- species, *K* –species, "opportunist- equilibrium" continuum

Contents

1. Learning Outcomes

- Students will be able to understand concept of *r* and *K* selected species/strategists.
- Will be able to appreciate the opportunist- equilibrium continuum as different organizations and strategies to match the environment organisms live in and resources at their disposal to achieve the common goal- fitness.
- Will get familiar with contrasting attributes of *r* and *K* selected species/strategists, reflecting trade-offs.
- Will be able to distinguish "*r* and *K*- selection" from "*r* and *K* selected species" (i.e concept of selection from concept of strategists).
- Will understand how *r* and *K*- selection works (working of natural selection under the different combinations of physical environment and biotic factors) .
- At the end will be able to appreciate the world just cannot be divided into *r* and *K* species as life exists as a continuum reflecting range of possible strategies with *r* and *K* strategists at opposite ends and all organisms fall somewhere on this spectrum.

2. Introduction

On a hot summer afternoon, a gravid fruit fly lands on an inviting over ripe banana thick with other flies. After probing the surface with her mouth parts for a while she decides to lay eggs. By next afternoon those tiny eggs have already hatched into larvae. For next five days the larvae feed digging deeper into the flesh, grow and shed their skin (moulting) twice, inside the slowly liquifying banana. More females visit the fruit and lay eggs but the first laid larvae go on feeding and growing till its fifth day. On fifth day, larvae move up out of the flesh and hide among the skin folds as they get ready to pupate. The encapsulated pupae stay inside their tough brown cylinders for almost six days. Its morning on seventh day and a few plump, white bodied adults are spotted. They emerged last night from their pupal skin and now are busy stretching their crumpled wings. By afternoon their soft and white body hardens and darkens and they are ready to make their life's first flight. Meanwhile their twenty –two days old mother had laid more than 400 eggs into various fruit. She is busy again laying few more eggs on a rotting apple but accidently slips in fruit sap. As she struggles for life her wings got mired in fruit sap and she drowns. An hour later her daughter visits the same apple settles down and probes the skin with her mouth-parts as she gets ready to deposit her first batch of eggs.

Fig 1: Fruit- flies on banana
Source: http://www.diptera.info/forum/viewthread.php?thread_id=63602&pid=270202#

The fruit fly is not alone in the league of animals leading such a fast-paced life. There are many others who believe in this live- fast die young philosophy.

In another part of the world a different story is going on!

In a flimsy nest from twigs on Chirstmas Island, a red footed booby's chick is hungry again. It is three months old with an ever increasing appetite and completely dependent on its parents. As usual the food is in short supply making rapid feeding of the chick impossible. The father gets ready to make another long trip to sea. Flapping wings it leaves the nest, rising on high winds of Indian Ocean, to fetch food for the chick. Passing the colonies of other relatives and feeding grounds of smaller birds it carefully scans the water for flying fish, a favourite. Fortunately it spots a few, plunge dives and swallows. In the evening it returns to a patient chick quite used to waiting for a meal. It opens the bill and regurgitates the swallowed fish to the chick.

Fig 2: *Sula sula* (red footed booby) with its chick
Source:http://checklists.datazone.darwinfoundation.org/static/photos/species/display/dscn9552.jpg

The chick grows and fledges after few weeks. For another six months the parents care for it. After six months it makes its first, extensive flight. Three years passes as it learns the hunting skills (of catching a flying fish or squids, the main food) and those elaborate mating rituals. Post-acquiring the skills it makes the first attempt to mate. It mates once after every fifteen months or so lays a single egg after a successful mating. It mates and raises the first chick with the partner, successfully. Next year it returns to the same nest and mates with same male. This year feeding the growing chick is becoming a progressively difficult task as food supply is scarce. Assessing the food supply one morning it goes back to sea along with its partner, to ensure their own survival. The unfortunate chick waits for parents to return with food. The chick starves and dies. After fifteen months the female is back on the same nest trying its luck again. This time it successfully raises a chick. During its long life it mates every fifteen month and tries to raise a single chick each time. In its 21^{st} year it dies in a fishing accident. Only 2 of the 7 chicks it has raised leave offspring that survive to reproduce themselves.

3. *r*-Species and *K*-Species

The diversity of organisms on earth is astonishing. The vivid life forms exhibit broad differences among their body- size, life- span and reproductive patterns. Irrespective of the life history pattern they show all organisms are adapted to gain fitness. Some are small, start reproducing at a young age, produce enormous number of offspring and are short lived (like the fruit fly). Others are large, postpone reproduction to a later age, produce few offspring and long lived (like the red footed booby). The populations of former species grow rapidly within a short time span owing to their high reproductive rates and progeny also start reproduction at an early age. On the other hand, populations of later species grow slowly, raising few juveniles each time. Owing to their long life span they can afford reproducing more than once in their life time. The population reaches and is maintained at a more or less stable size. Based on these features, former species are referred as ***r* species** and later as ***K* species**. The idea of *r* and *K* species is borrowed from the logistic equation of population growth (where the two terms, *r* and *K* were used).

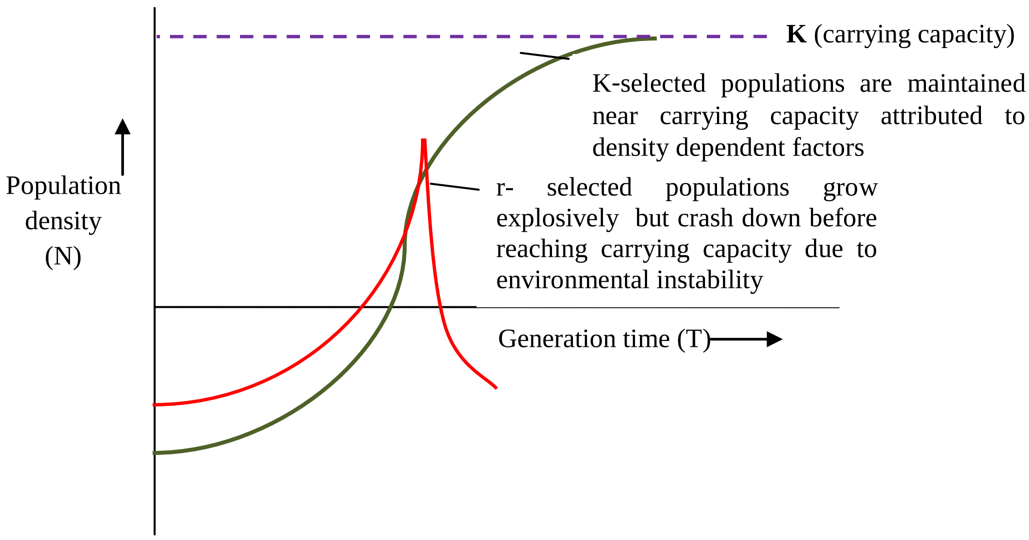

Fig 3: *r* and *K* – selected species population size (graphical representation)
Source: Author's contribution

The *r* species mostly represent the species inhabiting marginal habitats with hostile or unpredictable environments or resource rich ephemeral habitats. The acceptance of high chances of death under such fluctuating environmental conditions is rewarded in terms of resources. These species almost never face any competition for resources as very few species inhabit such hostile habitats. When resources are in plenty an exponential population growth is possible and that is exactly what these species practice when it comes to reproduction. They are called *r* species as they spend most of their lives in the either exponential or near exponential, *r*- dominated phase of population growth and never reaching the upper limit or carrying capacity. As the chances of future survival are lean, investment in growth or saving for future reproduction would be a futile effort. The organisms tend to channel most of the resources into reproductive effort, producing as many offspring as possible. The probability of juvenile survival under hostile conditions is very low. Investing heavily per offspring would not be a sound approach. Instead a large crop of small sized offspring ensures survival of at least a few. The short-lived resource rich environments with favourable conditions lack competition thus, offspring size can be compromised. In both the scenarios, small investment per offspring works well.

The *K* species invariably depict animals of settled existence with favourable or stable environmental conditions. Such living conditions invite intense competition for limited resources. The theory of natural selection predicts survival of fittest under such crowding conditions. Fitness is measured as reproductive success. Only those individuals are successful in leaving descendents that have captured the larger share of resources. They win the battle of existence because they have grown faster and thus better competitors. The growth comes at the expense of reproduction, which is delayed here. The natural selection favours packaging of resources into few but large offspring. The size of offspring is important as individuals live under crowded conditions facing intense competition for limited resources. Large offspring would be favoured by natural selection. With that fixed budget of energy only few large offspring can be produced. They are called *K*-species as their populations spend most of their lives in the *K*-dominated phase of population growth (near carrying capacity).

4. "Opportunist – equilibrium" continuum

The *r* and *K* species represent life at two opposite ends. However, that does not necessarily means that *r* and *K* strategists cannot be found within same species. In Trinidad the guppies (*Poecilia eticulate*) present in different streams are preyed upon by different predators and thus exposed to different predator selection pressures. The streams dominated by cichlid fish *Crenicichla alta*, which preys heavily on large (mature) guppies harboured small- sized guppies that matured faster, reproduced earlier and produced more and small sized offspring than guppies from streams where cichlid predator was absent and guppies faced lower predation. Further, guppies were experimentally moved from a site where they were preyed upon by *Crenicichla* , to sites where both guppies and the predator *Crencichla* were absent. After several generations guppies were collected from both, the place of origin and introduction, and offspring were reared under common laboratory conditions. Guppies relieved of *Crencichla* predation exhibited delayed maturation and reproduction, large adult size, fewer and larger offspring. (Reznick et al., 1990; Reznick and Travis, 2002). Clearly, the selection pressure resulting from the impact of predation (biotic factor) is shaping the pattern of life style (*r* or *K*) among the populations of Trinidad guppies.

Fig 4: The fish at the top-*Crenicichla alta*.One of the key predators in high-predation localities. The middle fish-*Rivulus hartii, the* only predator co-occurring with guppies in low-predation sites. The fish on the bottom left-an adult male guppy, on the bottom right- adult female guppy. Source: http://newsroom.ucr.edu/1209

Under natural conditions two or more populations or species exposed to different selection pressures due to effect of physical environments and various biotic interactions exhibit an adaptive combination of life history traits. Obviously the two demand different organizations and strategies to achieve the common goal- fitness. Their extremely opposed life history patterns or strategies are simply alternative ways to achieve fitness.

It is also important to remember that life forms do not always exist at extremes. It is therefore logical to conclude that a range of compromise strategies is possible between the two extremes. There are many species which show traits between the extremes of *r* and *K*. Therefore, a classification into *r* and *K* species or strategists is oversimplification of a more complex real world. In nature exists, a continuous and variable spectrum or continuum of strategies between two extremes. This continuum of strategy is called the **“opportunist-equilibrium”**. The continuum describes a range of strategies (from *r* to *K*) observed among different species. All living organisms are supposed to fall somewhere on this continuum between the two extremes (*r* and *K*). On the spectrum as one moves from *r* towards *K*, population show a mix of *r* and *K* – selected traits progressively becoming more *K*- selected. Similarly, species populations relying more on *r*- selected traits are met as one move from *K* towards *r*.

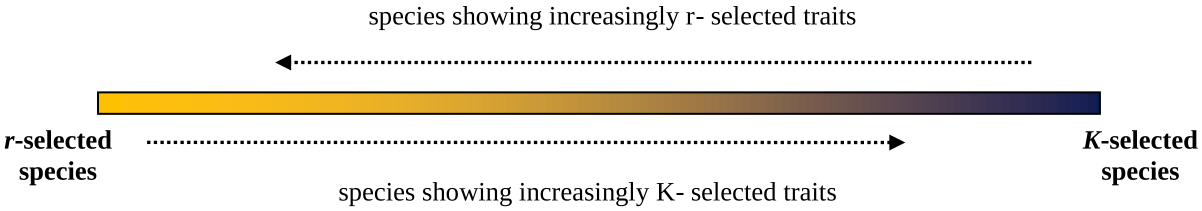

Fig 5: *r – K* or “opportunist – equilibrium” continuum
Source: Author’s contribution

Thus, various species can be differentiated or grouped together based on their relative reliance on one strategy over the other. Even within species *r* and *K* strategists can be found among different populations (e.g. guppies in Trinidad).

4.1. *r*- strategist: a colonist/opportunist/generalist species

The marginal habitats are often inhabited by organisms which are bestowed with high reproductive rates (*r* species). Their potential to multiply rapidly proves advantageous in environments that are short-lived. The organisms are skilled at making the best use of short but favourable periods achieving enormous population size which allows them to colonize new habitats quickly and exploit new resources. The other adaptations of such organisms help them to survive hostile periods which follow the ephemeral favourable times. Thus, there is little or no time to invest resources into growth and all the energy is focussed on reproduction. These organisms are able to disperse rapidly. The ability to disperse helps in invading disturbed habitats after a catastrophe or colonize newly opened habitats like temporary puddles or forest clearings or other remote habitats. These are the first ones to colonize any new unoccupied habitat, or arriving after the last disaster and therefore referred as **colonists**. As the environmental uncertainty poses a limit species cannot afford to be picky in their choices of food. Under such conditions it is favourable to be a **generalist** (not specializing on one particular food) for selection purpose. Fitness here is achieved via producing large number of widely scattered progeny, as the chances of death are high during unfavourable seasons. These species are also known as **opportunists** as they take advantage of scarce and fleeting habitat. The harsh unfavourable environments where other species cannot exist or ephemeral yet favourable habits, both present an opportunity to establish populations. They have the life cycle properties favoured by natural selection to excel under such conditions. This kind of life style is called opportunistic. Most of the short-lived animals of highly seasonal environments exhibit such life histories.

4.1.1 *r*- strategist: as a fugitive species

There exists another possible explanation for residents of marginal habitats. Perhaps the dwellers are not actual lovers of these harsh or ephemeral habitats but are fleeting away from other inhabitants of their original a much desirable or permanent environment. What if the so called opportunist species are not actually looking for chance good times to exploit but avoiding competition? The opportunists can be looked upon as **fugitives,** (Hutchinson, 1951) running away from competition existing at their actual (desirable) habitats and making the best of whatever is left for them.

The term fugitive species was introduced by Hutchinson (1951) to describe **species which disperse quickly to colonize new habitats away from close competitors**. The Gause's competitive exclusion principal helps to understand the fugitives in a better way. The species having identical or highly similar resource requirements cannot coexist. Sooner or later the stronger species will exclude the weaker species from the niche. The species which have been residing for long in a habitat are adapted and therefore better competitors than a recent introduction. The fugitives colonize new places without close competitors and disperse quickly to new habitats as the competition arrives. The fugitive is also an opportunist as it live in places where others cannot reach easily. The beautiful example of such fugitive species comes in the form of copepod *Eurytemora lacinulata*. In 1927, it was noticed that only one species of copepod (*Eurytemora lacinulata*) was present in Oxford municipal sewage works. However, in the local water bodies other copepods were also present. The commonest copepods were of the genus *Diaptomus*. The sewage works ponds were regularly drained and cleaned as they were part of filter system (disturbance in habitat). The copepod *E. lucinulata* was also the lone species in the brackish waters of a river estuary near Liverpool. The same copepod was also present in other fresh water bodies where *Diaptomus* was absent. Perhaps some other animal prevented *E. lucinualta* from invading fresh waters of the river. The *E. lucinualta* existed by efficient dispersal to habitats where others (competitors) could not reach (Elton, 1927). It multiplied and survived as lone species till the competitors arrived and then it quickly moved to another habitat leading a fugitive life. It is an opportunist too as it dispersed with ease quite efficiently, multiplied and survived as generalist at places where others could not.

4.2. *K*-strategist: equilibrium/competitor/specialist species

Life doesn't always exist in harsh environments. Life does flourish at extremely fertile patches under stable permanent environments. Obviously, these are the more desired habitats and several species compete to secure a place for themselves. This leads to crowding. Species cannot afford explosive populations and maintain stable populations. The perquisite for life under stable populations is adaptations which help persistence. The populations of such species tend to be in equilibrium and thus also known as **equilibrium species**. The focus is on maintaining populations at or near K, the carrying capacity of the environment. Individuals face intense competition both within and among species populations. A large body proves advantageous in crowded habitat rather than dispersal and high fecundity. Thus, these species are good **competitors** for shared limited resources. Large size competitors have easy access to resources and acquire the greater share of it. Therefore, channelling energy (resources) into growth and maintenance is advisable rather than spending it on reproduction. As most of the species are good competitors, to co-exist the species occupy different niche and exhibit **resource partitioning** (following Gause's principle: **Complete Competitors cannot Co-exist**). Resource partitioning or **differential resource utilization** refers to the difference in manner a resource is utilised by different species. The species that co-exist either eat different sizes and kinds of food or feed at different times or different areas. This often leads to the specialization on particular food type, making them **specialist species** (specializing on one or few food resources). Under such severe competition conditions ensuring survival of young is more important than producing enormous number of offspring. Competitor pays the toll in terms of reproduction. Competitors are conservative breeders and their fitness results from a longer life span in which they produce few young with high survival probability. Parental care is another attribute of these species. The parental care is a good tactic under these conditions of intense intra-specific and inter-specific competition as it is likely to yield high return in surviving offspring.

Attributes of r- and K-strategist		
Character	***r*- strategist**	***K*-strategist**
Population size	variable (usually below the maximum the environment can support)	constant(at equilibrium or near the maximum the environment can support)
Population growth curve	J- shaped/ exponential	S-shaped/sigmoidal
Mortality	often highly variable (not density- dependent)	often regular (density-dependent)
Competition	poor competitor	good competitor
Life- span	short	usually more than one year to very long
Environment /habitat	variable and unpredictable	constant or variable (seasonal) but predictable
Reproduction age	early	late
Number and size of offspring produced	many, small sized	few, large sized
Number of Reproductive efforts	once	more than once
Parental care	absent	present

Table 1: Some ecologically important attributes of *r*- and *K* –strategists
Source: Author's contribution

However, as life rarely exists at such extremes most of the organisms show a mix of *r* and *K* species traits. Organisms in a struggle to make the best of whatever is available to them make compromises or show adjustments in various characters. Therefore, one may come across opportunist species living under harsh environment and investing in parental care. Similarly, the fixed number of young produced (clutch or litter-size), another attribute of equilibrium species can be a solution to unpredictable environment in certain cases.

The Galapagos penguins (*Spheniscus mendiculus*) have a fixed clutch size of two eggs. The food supply (algae and fish) is highly unpredictable as it relies on ocean currents. Usually a breeding effort results in a failure to raise any chick.

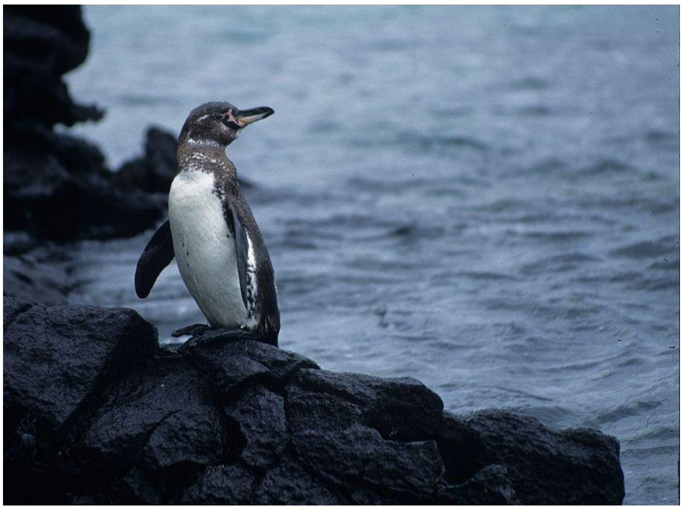

Fig 6: Galapagos Penguin (*Spheniscus mendiculus*), Galápagos Islands, Ecuador

Source:
http://commons.wikimedia.org/wiki/File:Gal%C3%A1pagos_Penguin_(Spheniscus_mendiculus),_Gal%C3%A1pagos_Islands,_Ecuador.jpg

The parents abandon both the chicks in times of food scarcity. A successful breeding effort results in rearing of one chick (Boersma, 1977). Penguins rarely raise the two chicks still invest in two eggs just to ensure survival of at least one in case of any accidental loss. Galapagos penguins are not the only exception as most of the sea birds have a fix clutch size and abandonment of chick is a usual phenomenon owing to fluctuating food supply.

The large size, life, long life span, delaying reproduction and breeding several times in the course of life are usually considered as attributes of K –strategists. The sea turtles including the olive green coloured Olive ridley (*Lepidochelys olivacea*) enjoy a long life span.

Fig 7: Olive ridley (*Lepidochelys olivacea*)

Source: http://animals.nationalgeographic.com/animals/reptiles/olive-ridley-sea-turtle/

The olive ridley lives for 50 years. It grows slowly to a size of 65- 70 cm. Its 13 years old (reaching sexual maturity) when it makes first attempt to mate (Zug et.al, 2006). The female after a successful mating lays around 100 eggs on the beach in a nest. After laying eggs it covers and leaves investing no time in raising the young. Only a handful of fortunate young make a successful trip to sea after hatching, as a gamut of hungry predators waits for them.

Fig 8: A hatchling making its first trip to sea

Source:
http://upload.wikimedia.org/wikipedia/commons/4/47/Olive_ridley_hatchling_in_Mexico_(8218893828).jpg

Once in the sea, the survival battle continues as there is no dearth of predators. As a result the juvenile survival is slim. The female may compensate for this huge loss by nesting up to three times in a year. Thus, in real world there are no hard and fast rules as organisms often employ a mix of *r* and *K* strategies to achieve the only goal, fitness.

5. *r*- Selection and *K*- Selection: not synonymous with opportunist and equilibrium species

The concept of opportunist (or *r* strategist) and equilibrium species (or *K* strategist) discussed so far refers to comparison made between species. There is another concept which may sound similar, the concept of *r* and *K* selection. The *r* and *K* selection describes processes acting within species populations. Thus, the two terms r- selection and K- selection are not synonymous with opportunist and equilibrium species. The terms *r*- and *K*- selection were used first by MacArthur and Wilson (1967) in their theory of island biogeography to distinguish between types of selection pressures on island colonists. Prior to that Wilson (1961) while studying Melanesian ants coined the term **'taxon cycle'** to describe **'the inferred cyclical evolution of species [of Melanesian ants], from the ability to live in marginal habitats and disperse widely, to preference for more central, species-rich habitats with an associated loss of dispersal ability, and back again'** (Wilson 1961). The phenomenon mirrors the *r* and *K* selection operating in a cyclic manner.

***r* and *K* selection**- The theory of Macarthur and Wilson (1967) explains how *r* and *K* selection operates. It describes the colonization of a newly raised volcanic island from the sea by different animal and plant species. The immigrants to reach this island are opportunist (or fugitive) gifted with excellent dispersal mechanisms. Once settled on the island the opportunists achieve rapid population growth attributed to their high fecundity (as they are descendents from populations that are *r*-selected). Consequently, in no time the island is crowded with their descendents. The species have to live in populations either at or near the saturation point, *K*. the populations struggle to establish equilibrium, facing competition for resources (once unlimited or nearly so). As the immigrant species are not adapted to crowded life style, natural selection tries to pick the most competitive variants from the island's opportunists. Being a competitor means diverting resources to traits which prove advantageous in the face of competition. This is the process of *K*- selection. The *K*- selection leads to attainment of sustained high density, a trait not practiced by populations showing *r*-selection.

The concept of r and K selection was successfully demonstrated in *Drosophila* populations (Ayala, 1968). In the wild flies have high fecundity and they need to disperse to find food. The populations achieved equilibrium when reared on culture medium under standard laboratory conditions. Crowded conditions demanded competition for fixed food supply. The irradiated flies (to increase genetic diversity in population) were better skilled at coping life under crowded conditions than non-irradiated control flies.

5.1 How does it work?

Organisms acquire a limited amount of energy. They need to partition this energy between various life activities. They allocate energy mainly under three budget heads –maintenance (metabolic rate and survival), growth and reproduction. The prime importance is of course survival and maintenance followed by energy investment in to growth and reproduction. The organisms through natural selection try to find a favourable cost- benefit ratio as each of these activity bears some advantage and associated cost. The ration of energy allocated to maintenance and reproduction varies among species as well as among populations exposed to different living conditions. This ratio varies not only with the evolutionary history of a species and size of organism but also with carrying capacity and population density.

Thus, *r* and *K*- selection describes the working of natural selection under the different combinations of physical environment and biotic factors. The concept explains the selection operating **within species populations** i.e. how a population starting off as an opportunist leads to an adaptive evolution of a more stabilized equilibrium population. An opportunist population once settled in a marginal or recently disturbed achieves rapid population growth in no time. Once deserted habitat initially gleams and later overflows with life. The overwhelming number of individuals, the descendents from populations originally *r*- selected (opportunists) is not used to of life under crowded conditions. As the environment is not going to crash this humongous population down, natural selection picks the most competitive varieties from the existing opportunists. This is how *r*- and *K*- selection works within a population.

The terms *r* and *K* strategists refer to **strategies among species**. Thus, the two concepts (selection and strategy) are not equivalent and should be treated carefully.

6. Summary

The opportunist species are well adapted to make best use to opportunities, both in time and space. The traits such as early reproduction, high fecundity, great dispersal abilities, short life span etc. characterised their ready to take risk life-style. The fugitive species is also an opportunist but on a run from competitors. Owing to their high biotic potential (*r*) these species tend to flourish in uncertain or marginal habitats, subjected to periodic stress (natural catastrophes). Their ability to sit out when adversity hits and come out of refuge to re-colonize a recently disturbed habitat makes them resilient to perturbations.

The equilibrium species are tough competitors as they live under crowded conditions. Their populations are at equilibrium. They delay reproduction and invest more into growth and reproduction, produce few large young ready to face competition and enjoy a long life span. These species partition a larger fraction of energy in favour of maintenance, and competitive ability (attributed to their crowded conditions). As a result of this bias they perform better under stable environment and high density conditions (near saturation *K*). They are good at competition but less resilient to disturbances.

It is erroneous to think of world divided into either *r* or *K* strategists. Life exists as a range of possible strategies making few compromises or adjustments here or there. It would be better to imagine life as a continuum with *r* and *K* strategists at opposite ends. All organisms fall somewhere on this spectrum.

The *r* and *K* strategists represent species adopting different life styles attributed to their environment and a combination of various other biotic factors. The natural selection, an uncompromising master forces all organisms, irrespective of their habitat, to strive for fitness. The species occupying marginal habitat achieve it via high biotic potential. The natural selection under harsh or unpredictable environment favours individuals investing into reproduction without wasting much energy into growth or survival. They are called *r*-selected species as *r* is maximised. On the other side, desirable habitats invite more guests and hence intense competition. Natural selection favours organisms that compete better than others. Such species are called *K*-selected species.

The *r* and *K* selection another concept, works within a population. However, the natural selection process remains the same, selecting traits (but within the population) advantageous under present set of conditions.

In the end one must remember that the life whether as *r* or *K* strategists or falling anywhere on the "**opportunist equilibrium**" continuum, is nothing but a struggle for existence-survival and leaving behind as many reproductively successful offspring as possible.