M.Sc. Final Year

Zoology, Paper III

POPULATION ECOLOGY AND ANIMAL BEHAVIOUR



मध्यप्रदेश भोज (मुक्त) विश्वविद्यालय — भोपाल MADHYA PRADESH BHOJ (OPEN) UNIVERSITY - BHOPAL

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SYLLABI-BOOK MAPPING TABLE

Population Ecology and Animal Behaviour

Syllabi	Mapping in Book		
 UNIT-I 1. Demography : (a) Life Tables. (c) Net Reproduction. (b) Generation Time. (d) Reproductive Value. 2. Population Growth : (a) Growth of organisms with non-overlapping generations. (b) Stochastic and time Lag models of population growth. (c) Stable age distribution 3. Life History Strategies : (a) Evolution of life history traits. (b) Longevity and theories of ageing. (c) Energy apportionment between Somatic Growth and Reproduction. (d) Parental Investment and offspring. (e) Reproductive Strategies - Ecology and Evolution of Sex and mating system, Optimal Body Size, r - and k - selection. 	Unit-1: Demography, Population Growth and Life History Strategies (Pages 3-40)		
 UNIT-II Predation : (a) Models of prey-predatory dynamics. (b) Optimal foraging theory (Patch Choice, Diet Choice, Prey selectivity, Foraging time). (c) Role of Predation in nature. Competition and niche-theory : (a) Intraspecific and Interspecific competition. (b) History of niche concepts. (c) Theory of limiting Similarity. Mutualism : (a) Evolution of Mutualism, (b) Plant - Pollinator and Animal - Animal Interactions. (c) Basic Models. Population regulation - Extrinsic and intrinsic mechanism. Case studies in population dynamics - Fisheries, Wild Life and Biological Control of Agriculture pests. 	Unit-2: Predation and Mutualism (Pages 41-68)		
 UNIT-III Innate Behaviour. Perception of the environment (a) Mechanical. (b) Electrical. (c) Chemical. (d) Olfactory. (e) Auditory. (f) Visual. Neural and hormonal control of behaviour. Genetic and environmental components in the development of behaviour. Communication (a) Chemical (b) Visual (c) Light (d) Audio (e) Species specificity of songs (f) Evolution of language. 	Unit-3: Introduction to Animal Behaviour (Pages 69-90)		
 UNIT-IV Ecological Aspects of Behaviour : (a) Habitat selection, Food selection. Anti-Predator defenses. (b) Aggression, homing, territoriality, dispersal. (c) Host - Parasite Relations, Social Behaviour : (a) Aggregations - Schooling in fishes. Flocking in birds, herding in mammals. (b) Group selection, Kin selection, reciprocal altruism, inclusive fitness. (c) Social organization in insects and primates, Reproductive behaviour : (a) Reproductive Strategies. (b) Mating Systems. (c) Courtship. (d) Sexual Selection. (e) Sperm Competition. (f) Parental care. Biological Rhythms : (a) Circadian and Circannual Rhythms. (b) Orientation and navigatin. (c) Migration of fish and birds. Learning and memory : (1) Conditioning. (2) Habituation. (3) Insight learning. (4) Association Learning. (5) Reasoning (6) Cognitive skills 	Unit-4: Various Aspects of Animal Behaviour (Pages 91-140)		

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INTRODUCTION

The study of the factors that influence the distribution and abundance of animal and plant populations is known as population ecology. A population is a subgroup of individuals from a single species that inhabits a specific geographic area and interbreeds in sexually reproducing species. For some species, defining the geographic boundaries of a population is simple, while for others, it is more complicated. Plants and animals that live on islands, for example, have a geographic range bounded by the island's perimeter. Some species, on the other hand, are distributed across wide swaths of land, making determining the borders of small populations more challenging. There is a continuum between closed populations that are physically isolated from other populations of the same species and lack interchange, and open populations that show variable degrees of connection. Each local population of sexually reproducing organisms carries a unique set of genes. As a result, a species is a group of populations that differ genetically to varying degrees from one another. These genetic differences show up in appearance, physiology, behaviour, and life histories among groups; in other words, genetic features (genotype) influence expressed, or observable, qualities (phenotype).

Animal behaviour is the study of how animals move around in their environment, engage socially, learn about their surroundings, and develop cognitive awareness of their surroundings. Niko Tinbergen, a Nobel Laureate, devised four guiding questions for studying human behaviour. He claimed that conduct should be studied in terms of its origins, mechanisms, adaptive value, and evolution. Animals were most likely monitored for practical reasons at first, as early human existence depended on understanding animal behaviour. Success needed deep understanding of an animal's habits, whether hunting wild game, managing domesticated animals, or evading an attacking predator. Information regarding animal behaviour is still extremely valuable today.

This book, *Population Ecology and Animal Behaviour*, contains four units and is written with the distance learning student in mind. It is presented in a user-friendly format using a clear, lucid language. Each unit contains an Introduction and a list of Objectives to prepare the student for what to expect in the text. At the end of each unit are a Summary and a list of Key Terms, to aid in recollection of concepts learnt. All units contain Self-Assessment Questions and Exercises, and strategically placed Check Your Progress questions so the student can keep track of what has been discussed. Introduction

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UNIT 1 DEMOGRAPHY, POPULATION GROWTH AND LIFE HISTORY STRATEGIES

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1.0 INTRODUCTION

A population is a group of individuals of the same species living in the same region and interbreed. Members of a population frequently rely on the same resources, face comparable environmental restrictions, and rely on the availability of other members to survive in the long run. Scientists examine how individuals in a population interact with one another and how the population as a whole interacts with its environment while studying a population. Population ecologists use a set of statistical metrics known as demographic parameters to define populations as a tool for objectively researching them. The field of science interested in collecting and analyzing these numbers is termed as population demographics, also known as demography.

Demography, in its broadest sense, is the study of population characteristics. It gives a mathematical representation of how certain traits develop over time. Demographics can encompass any statistical characteristics that influence population

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growth or decline, although population size, density, age structure, fecundity (birth rates), mortality (death rates), and sex ratio are all essential.

Population ecology is the study of how and why populations fluctuate through time, as well as the variables that influence them. The study of population growth, regulation, and dynamics, or demography, has the deepest historical origins and the richest evolution in population ecology. Human population expansion is one of the most critical environmental challenges of the twenty-first century, and it serves as a model for population ecologists. Basic and applied population biology has studied everything from disease organisms to wild-caught fish stocks and forest trees to species in a successional sequence to laboratory fruit files and paramecia.

The life history of an organism is a record of significant events in its growth, development, reproduction, and survival. From one species to the next, life cycles differ dramatically. Why is there so much variety? Why do some species, such as salmon and bamboos, many insects, and all grain crops, die immediately after reproducing, whereas others, such as plants and vertebrates, survive on to reproduce repeatedly?

Understanding, interpreting, and predicting species distributions are all part of population ecology research. Why do certain species prefer certain habitats, and how are they kept from expanding beyond their range limits? In response to concerns about climate change, such range questions have grown increasingly popular in the last decade or two.

In this unit, you will learn about demography and how it affects a variety of issues. Population growth and the models that go along with it. Aside from that, numerous life history strategies among animals will be investigated.

1.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the concept of demography including life tables, net reproduction, generation time and reproduction value
- Discuss the phenomena of population growth and the models associated with it
- Examine how animals evolve the life strategies

1.2 DEMOGRAPHY

Demography is the science of describing and forecasting population growth and age/size distribution patterns. Demography calculates vital data for a population, such as survival probability, mortality, and fecundity. The origins of demographic considerations can be traced back to Malthus in the year 1826, when the human population began to expand exponentially. He observed that although human populations were growing exponentially, food supply was only growing linearly. Resources would eventually limit the human population, as predicted. Malthus was influenced by Darwin at the time, which led him to coin the phrase 'struggle

for existence,' implying that natural selection (i.e., polymorphisms in a population that improve their ability to gather scarce resources) will lead to differential survival and 'select' for such traits.

Demography is used as the foundation for population research in ecology (especially population and evolutionary ecology). As a result, it is the statistical study of populations that examines any type of dynamic living population, that is, one that evolves through time. As a result, it includes the study of these population's size, structure, and distribution, as well as spatial and/or temporal changes in response to birth, migration, ageing, and death.

Theories of Demography

The four theories of demography are:

- (i) Malthusian Theory
 - Thomas Malthus (1766–1834) was an English priest who predicted that the population of the planet will outstrip its ability to support it. According to Malthusian theory, three causes, such as war, starvation, and illness, would regulate human population that surpassed the earth's carrying capacity, or how many people can survive in a given region given the amount of available resources.
 - He called them 'positive checks' since they raise mortality rates, which keeps the population under control. They are opposed by 'preventive checks,' which limit the population by lowering fertility rates. Examples of preventive checks are birth control and celibacy.
 - He said that people could only produce a certain amount of food in a given year, despite the fact that the population was growing at an exponential rate. He predicted that humans will eventually run out of food and starve. They'd go to fight for ever-dwindling resources, reducing the population to a sustainable level, and then the cycle would start all over again.

Of course, this has not exactly happened. The human population has continued to grow well beyond Malthus's predictions. So what happened? Why didn't we die off?

- There are three reasons sociologists believe we are continuing to expand the population of our planet:
 - o Increase in food production has increased both the amount and quality of calories we can produce per person.
 - o Human ingenuity has developed new medicine to curtail death from disease.
 - o The development and widespread use of contraception and other forms of family planning have decreased the speed at which our population increases.

But what about the future? Some still believe Malthus was correct and that ample resources to support the earth's population will soon run out.

Demography, Population Growth and Life History Strategies

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(ii) Zero Population Growth

- Paul Ehrlich, a neo-Malthusian researcher, pushed Malthus' predictions into the Twentieth century. However, according to Ehrlich, the environment, not the food supply, will play a critical role in the planet's population's continuing health.
- According to Ehrlich's theories, the human population is rapidly approaching environmental collapse as affluent individuals deplete or contaminate a variety of natural resources such as water and air.
- He pushed for a goal of **zero population growth (ZPG)**, in which the number of individuals who enter a population via birth or immigration equals the number of persons who leave through death or emigration.
- While support for this concept is mixed, it is still considered a possible solution to global overpopulation.

(iii) Cornucopian Theory

- Cornucopian thought dismisses the idea of humanity annihilating themselves, claiming that human creativity will address any environmental or societal problems that arise.
- It uses the issue of food supply as an example. If we need more food, agricultural scientists, according to the argument, will figure out how to grow it, just as they have for generations.

(iv) Demographic Transition Theory

- According to demographic transition theory, future population growth will follow a predictable four-stage (occasionally five-stage) pattern.
- In Stage 1, the rates of birth, death, and infant mortality are all high, with a short life expectancy. The United States in the 1800s is an example of this period. As countries begin to industrialize, they enter a new phase of development.
- Stage 2, with higher birthrates and lower infant mortality and death rates. In addition, life expectancy rises. This is where Afghanistan is right now.
- Stage 3 occurs after a culture has become fully industrialized; birthrates fall but life expectancy rises and death rates continue to fall. Mexico's population has reached this point.
- In the final phase, Stage 4, we witness a civilization in the postindustrial era. People are healthier and live longer, and society is entering a period of population stability. The population as a whole may possibly be declining.
- Sweden, for example, is classified as being in Stage 4. Stage 5 has been introduced by some researchers, implying that fertility will either remain below replacement levels or begin to steadily grow again.



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Fig: 1.1 Impact of changes in birth and death rate on total population at demographic transition stages

1.2.1 Life Tables

A **life table** (also called a **mortality table** or **actuarial table**) is a table which shows, for each age, what the probability is that a person of that age will die before their next birthday ('probability of death').

A life table is a summary of age-specific mortality rates in a group of people from a specific community. The creation of life tables is a simple approach for tracking the rate of births, deaths, and reproduction in a community.

A life table is a mathematical sample that depicts death in a country and serves as the foundation for calculating a society's average life expectancy. It describes the likelihood of a person dying at a specific age or living to a specific age. For example: The microorganisms are the most abundant and diverse group of organisms on the planet earth. Their metabolic repertoire and capacity for rapid reproduction across environmental conditions help them in catalyzing and regulating the biogeochemical processes that are responsible for sustainment of life on Earth. Yet, these micro-organisms are often challenged by energy supplies that barely meet their basal metabolic demands. As a result, many microorganisms in nature rest on the cusp of life and death. For example, more than half of the microbial cells in the global ocean reside in deep sediments or underneath continental plates where exploitable energy is vanishingly small. Even in the mammalian gut, which is commonly known as the resource-rich environment, microorganisms must tolerate feast-or-famine conditions if they are to survive passage and colonize new hosts. Despite being recognized as a universal constraint, the mechanisms by which energy limitation affects microbial populations has the potential to reshape the understanding of microorganisms in environmental and host-associated ecosystems.

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Types of Life Tables

Life tables are of two types:

- The **Cohort or Generation Life Table** 'summarizes the age-specific mortality experience of a given birth cohort (a group of people born at the same time) over the course of their lives, which might span many calendar years.'
- The '**Period Life Table**,' on the other hand, summarizes the age-specific mortality conditions for a specified or other brief time period.

Construction of Life Tables

Age specific mortality rates are applied to a notional population, typically of 100,000. Starting at birth, the probability of dying in each period is applied to the number of people surviving to the beginning of the period, so that the initial figure slowly reduces to zero. The different elements required for a life table include (using standard notations):

Ix	Number of survivors at age x
nqx	Probability of dying between age x and x+n
nDx	Number of deaths between age x and x+n
nLx	Number of person years lived between age x and x+n
Tx	Total number of person years lived after age x
ex	Life expectancy at age x

Table 1.1 Elements using Standard Notations for a life table

Period life tables are the most commonly used type of life table since they are based on current age-specific death rates for each age or age band used. Actual life expectancy of a given birth cohort, on the other hand, can only be estimated after everyone in that cohort has died. This method employs a cohort life table and necessitates the collection of data over a long period of time in order to create a single full cohort life table.

Methods of Constructing Life Table

A single cross-sectional temporal data for a generation is used to create life tables. A longitudinal life table technique uses an actual cohort of people who begin their lives at a fixed age interval and follow them throughout their lives until they die.

Furthermore, a complete life table can be built using only single years of age. An abridged life table can be created by grouping ages into 5 or 10 year intervals, with the first year being 0-1.

Table 1.2 Hypothetical Complete Life Table for India

Demography, Population Growth and Life History Strategies

Age x to	dx	$\int fx fx - dx$	qx dx/fx	рх 1 – ах	Lx (fx0 + fx1)/2	Tx Trl =	es Tr/F
x+n		(3-2)	(2/3)	(1-4)	(#1610 #110 fr	Txx0 - Lxx0	
1	2	3	4	5	6	7	8
0.	13000	100000	0.13000	0.87000	93500	4930250	49.3
1.	1300	87000	0.01494	0.98506	86350	4836750	55.6
2.	1200	85700	0.01400	0.98600	85100	4750400	55.4
3.	100	84500	0.00118	0.99882	84450	4665300	55.2
4,	800	84400	0.00948	0.99052	84000	4580850	54.3
5.	500	83600	0.00598	0.99402	83350	4496850	53.8
6.	300	83100	0.00361	0.99639	82950	4413500	53.1
7.	200	82800	0.00242	0.99758	82700	4330550	52.3
8.	100	82600	0.00121	0.99879	82550	4247850	51.4
9.	70	82500	0.00085	0.99915	82465	4165300	50.5
10.	65	82430	0.00079	0.99921	82398	4082835	49.5
11.	60	82365	0.00073	0.99927	82335	4000438	48.6
12	80	82305	0.00097	0.99903	82265	3918103	47.6
13.	100	82225	0.00122	0.99878	82175	3835838	46.7
14.	200	82125	0.00244	0.99756	82025	3753663	45.7
15.	210	81925	0.00256	0.99744	81820	3671638	44.8
16.	215	81715	0.00263	0.99737	81608	3589818	43.9
17.	220	81500	0.00270	0.99730	81390	3508210	43.0
18.	225	81280	0.00277	0.99723	81168	3426820	42.2
19.	230	81055	0.00284	0.99716	80940	3345653	41.3
20,	225	80825	0.00278	0.99722	80713	3264713	40.4
21.	230	80600	0.00285	0.99715	80485	3184000	39.5
22.	235	80370	0.00292	0.99708	80253	3103515	38.6
23.	240	80135	0.00299	0.99701	80015	3023263	37.7
24.	245	79895	0.00307	0.99693	79773	2943248	36.8
25.	260	79650	0.00326	0.99674	79520	2863475	36.0
26.	275	79390	0.00346	0.99654	79253	2783955	35.1
27.	285	79115	0.00360	0.99640	78973	2704703	34.2
28.	295	78830	0.00374	0.99626	78683	2625730	33.3
29.	320	78535	0.00407	0.99593	78375	2547048	32.4
30.	350	78215	0.00447	0.99553	78040	2468673	31.6
31.	400	77865	0.00514	0.99486	77665	2390633	30.7

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Demography, Population	32.	450	77465	0.00581	0.99419	77240	2312968	29.9
Growth and Life History	33.	550	77015	0.00714	0.99286	76740	2235728	29.0
NOTES	34.	600	76465	0.00785	0.99215	76165	2158988	28.2
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	37.	900	74365	0.01210	0,98790	73915	1932543	26.0
	38.	1000	73465	0.01361	0.98639	72965	1858628	25.3
	39.	1050	72465	0.01449	0.98551	71940	1785663	24.6
	40.	1150	71415	0.01610	0.98390	70840	1713723	24.0
	41.	1200	70265	0.01708	0.98292	69665	1642883	23.4
	42.	1300	69065	0.01882	0.98118	68415	1573218	22.8
	43.	1325	67765	0.01955	0.98045	67103	1504803	22.2
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	50.	1550	57715	0.02686	0.97314	56940	1064698	18.4
	51.	1600	56165	0.02849	0.97151	55365	1007758	17.9
	52.	1625	54565	0.02978	0.97022	53753	952393	17.5
	53.	1650	52940	0.03117	0.96883	52115	898640	17.0
	54.	1675	51290	0.03266	0.96734	50453	846525	16.5
	55.	1700	49615	0.03426	0.96574	48765	796073	16.0
	56.	1725	47915	0.03600	0.96400	47053	747308	15.6
	57.	1750	46190	0.03789	0.96211	45315	700255	15.2
	58.	1755	44440	0.03949	0.96051	43563	654940	14.7
	59.	1760	42685	0.04123	0.95877	41805	611378	14.3
	60,	1765	40925	0.04313	0.95687	40043	569573	13.9
	61.	1760	39160	0.04494	0.95506	38280	529530	13.5
	62.	1750	37400	0.04679	0.95321	36525	491250	13.1
	63.	1725	35650	0.04839	0.95161	34788	454725	12.8
	64,	1700	33925	0.05011	0.94989	33075	419938	12.4
	65,	1675	32225	0.05198	0.94802	31388	386863	12.0
	66.	1650	30550	0.05401	0.94599	29725	355475	11.6
	67,	1600	28900	0.05536	0.94464	28100	325750	11.3
	68,	1575	27300	0.05769	0.94231	26513	297650	10.9
	69.	1550	25725	0.06025	0.93975	24950	271138	10.5
	70,	1500	24175	0.06205	0.93795	23425	246188	10.2
	71.	1475	22675	0.06505	0.93495	21938	222763	9.8
	72.	1425	21200	0.06722	0.93278	20488	200825	9.5

The above life table provides the column wise information which is generally provided and followed by all life tables.

0.93047

0.92663

19088

17725

9.1

8.8

180338

161250

Col. 1. x = Specific Age

19775 0.06953

18400 0.07337

1375

1350

73. 74.

If the age at birth is x then the age at one year is x + 1. Similarly the age at 15 years is x + 15.

Col. 2. dx = Number of deaths, at any particular age. i.e., at the age x, 13000 deaths occur out of 1,00,000 births, then at age x + 1 : 87,000 persons will be alive. In this age, if 1300 deaths occur then at age x + 2 : 85700 persons will be alive.

Col. 3. fx = The number of persons surviving at age x to x + n i.e. , at the age x + 1 = 1,00,000-13,000 = 87,000

Col. 4. qx = Probability of death per person in the specific age i.e., total deaths occurred. (Out of 1,00,000 = 13,000)

Probability = $13,000 \div 1,00,000 = 0.13$

Similarly, at the age x + 1, 1300 persons died out of 87,000 live population then,

Probability = $1300 \div 87,000 = 0.01494$.

Col. 5. Px = 1 - Probability of surviving per individual person or 1 - qx,

i.e.;

At age x, 1 - .13000 = .87000 and at age x + 1, 1- . 01494 = .98506.

Col. 6. Lx = Number of years lived by the cohort in the age x to x + n or fx of any two age groups $\div 2$

Suppose,

fx-15 = 81925 [col.: 3, row 15]

fx-16=81715 [col.:3, row 16]

 $Lx = 163640 \div 2 = 81820$

Col. 7. Tx - Total number of years lived by the cohort after exact age x.

This can be found out from the reverse side of life table, i.e.,

At the age of 94 Lx = 525 and

at age 93 Lx = 925 then at age x + 93,

total number of years lived by

Cohort = 525 + 925 = 1450 and at age x + 92,

it will be 525 + 925 + 1400 = 2850.

Col. 8. $Ex = T.v \div Fx$. This gives average life expectancy.

In a nutshell, the life table is based on a population's age of death period. We can determine the likelihood of mortality for any person of any age group by looking at this table. It should be noted that not everyone in a given age group dies according to the life table's predictions. The life table merely depicts a pattern.

Life Tables and their Demographic Applications

One of the most crucial parameters that determines population shifts is mortality. There are a variety of questions, such as whether mortality is higher in young organisms. Is it true that an older person has a higher death rate than a younger person? We can design a life table to address these kind of problems. Human demographers who worked for life insurance firms and were interested in estimating people's life expectancy created the life table. Plant and animal populations can Demography, Population Growth and Life History Strategies

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have a variety of people, which a demographer might group together or retain separate in any given analysis.

A life table is an age-specific summary of mortality rates applied to a group of people. A cohort might be made up of the total population or just the males and females born during a specific time period. The life table is most commonly used by life insurance firms to determine the probability of human population survivorship in order to determine the premium, whereas ecologists use it to examine natural populations.

The building of a life table is a very basic approach for keeping track of the birth rate, death rate, and reproductive events in a population. In general, constructing life tables of non-human species living in the wild is quite challenging. Animal life tables fall into two groups. The following types of data can be used to construct the ecological life table.

Laboratory Animals: The life tables of these known-age animals (flies, mice) can be created by personally monitoring the individuals who are dying at regular intervals and continuing the observation until the entire population has died. It is quite possible to count a captive population of potentially mobile animals, such as flies or mice, daily, and to deduce their laws of mortality under these conditions, when they are certainly protected from predators and may be so from disease.

Natural Conditions: This is most easily done for animals which stay put for most of their lives. Thus, a researcher cleared some areas of rock, so that the swimming larvae of barnacles could settle on them in July, and then made monthly counts of the population of barnacles which had fixed itself on these areas. Another researcher followed up several species of insects living in galls which could be collected in any month of the year. Since they mostly passed a year in the gall, but only lived for a week or so in the winged state, his life table, based on population counts in over 50,000 galls, is fairly complete and more accurate than most human tables.

Survivorship Directly Observed: A big cohort's survival can be investigated by tracking them at regular intervals until they die. The mortality of the barnacle Chthamalusstellatus, which flourished on the rocks in Scotland throughout the fall season, was investigated. The mortality of these barnacles was monitored on a regular basis, and the data was utilized to create a life table. The scientist conducted several studies in which he removed one competitive barnacle, *Balanus balanoides*, from certain rocks and measured the number of Chthamalus that survived for a month.

1.2.2 Net Reproduction

In population ecology and demography, the Net Reproduction Rate, NRR, is the average number of offspring (typically daughters) that a female would have if she lived her entire life according to the age-specific fertility and mortality rates of that year. This rate is identical to the gross reproduction rate, but it accounts for the fact that some females will die before they reach childbearing age. With a NRR of one, each generation of mothers produces exactly enough daughters to replace themselves in the population.

If the NRR is less than one, the reproductive performance of the population is below replacement level. The NRR is particularly relevant where sex ratios at birth are significantly affected by the use of reproductive technologies, or where life expectancy is low. The average number of daughters that a hypothetical cohort of females starting life together would bear if they experienced a given set of age – specific mortality and fertility rates.

NRR =
$$\frac{\sum}{x} \left[\left(nF^{f}x \right) \frac{\left(n^{L}x \right)}{l_{0}} \right]$$

 $nF^{f}x$ = Each five – year age – specific fertility rate including only female live births $n^{L}x$ = The number of person – years lived between exact ages x and x + n l_{0} = Radix of the life table (100,000 people)

1.2.3 Generation Time

'The period required for the average breeder in the population to be replaced by her average breeder-offspring' is defined as a generation. The average period between an individual's birth and the birth of its children is known as generation time. If breeding females produce offspring when they are young, the offspring will become breeders quickly, and generation-time will be short; if breeders produce offspring breed late, generation-time will be longer; thus, we must use the distribution of values of survivorship and breeding across the cohort (age-class by age-class). For example, under ideal conditions, a bacterium like *E. coli* can generate in as little as 20 minutes, despite the fact that many bacteria in nature have development rates of several hours. For example, one *E. coli* cell with a 20-minute generation period will multiply to 512 cells in three hours, 4096 cells in four hours, 32768 cells in five hours, and so on.

To determine the mean generation time of a population, the age of the individuals (x) is multiplied by the proportion of females surviving to that age (lx) and the average number of offspring left by females at that age (mx). This calculation is performed for each age group, and the values are added together and divided by the net reproductive rate (R0) to yield the result

$$T = \frac{\sum x l_x m_x}{R_o}$$

1.2.4 Reproductive Value

The discounted number of future female children born to a female of a certain age is referred to as reproductive value in demography and population genetics. In the book 'The Genetical Theory of Natural Selection,' Ronald Fisher advocated that future children be discounted at the population's rate of growth; this implies that sexually reproductive value gauges the contribution of a person of a particular age to the population's future growth. Thus, Fisher defined the reproductive value of individuals of a given age as their expected contribution to future population growth, determined by the age-specific vital rates. This has the property that in a constant environment the total reproductive value in a population always increases at a constant rate. Demography, Population Growth and Life History Strategies

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OR

Reproductive value is a concept in demography and population genetics that represents the discounted number of future female children that will be born to a female of a specific age.

Consider a species with a life history table with survival and reproductive parameters given by l_x and m_y , where,

1 = probability of surviving from age 0 to age x

 m_{y} = average number of offspring produced by an individual of age x

In a population with a discrete set of age classes, Fisher's reproductive value is calculated as

$$v_x = \sum_{y=x}^\infty \lambda^{-(y-x+1)} rac{\ell_y}{\ell_x} m_y$$

where λ is the long-term population growth rate given by the dominant eigenvalue of the Leslie matrix. When age classes are continuous,

$$v(x)=\int_x^\infty e^{-r(y-x)}rac{\ell(y)}{\ell(x)}m(y)dy$$

where r is the intrinsic rate of increase or Malthusian growth rate.

1.3 POPULATION GROWTH

Population growth is the increase in the number of people in a population. In biology or human geography, population growth is increase in the number of individuals in a population.

Fertility, mortality, and migration are the only factors that influence population growth (positive or negative). The effect of migration on the population growth of countries and other national populations is usually not as significant as the effects of fertility and death, which are usually considered to be the key variables directly affecting national population growth. When the number of people entering a population (immigration) equals the number of people leaving (emigration), population growth occurs as a result of more births than deaths. This relationship is summarized by a formula known as the balancing equation. It is expressed as:

$$P2 = P1 + (B - D) + (I + E)$$

Where:-

P2 = Size of population for the year under consideration

- P1 = Size of population in the preceding year
- B = Number of births between the two dates
- D = Number of deaths between the two date
- I = Number of immigrants in the time under consideration (between P2 and P1)
- E = Number of emigrants in the time under consideration (between P2 and P1)

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The Natural Increase (or Decrease) of a population is the difference between births and deaths in a population. The rate of Natural Population Increase is the percentage of the base population that a population grows (or shrinks) in a given year due to an excess (or deficit) of births over deaths.

RNI= Births-Deaths / Total Population \times 100

OR

Birth rate- Death rate/10

Two types of population growth patterns may occur depending on specific environmental conditions:

- An exponential growth pattern (J curve) occurs in an ideal, unlimited environment
- A logistic growth pattern (S curve) occurs when environmental pressures slow the rate of growth

Exponential Growth

Exponential population growth will occur in an ideal environment where resources are unlimited. In such an environment there will be no competition to place limits on a geometric rate of growth. Initially, population growth will be slow as there is a shortage of reproducing individuals that may be widely dispersed. As population numbers increase the rate of growth similarly increases, resulting in an exponential (J-shaped) curve. This maximal growth rate for a given population is known as its biotic potential. Exponential growth can be seen in populations that are very small or in regions that are newly colonized by a species.

Logistic Growth

Logistic population growth will occur when population numbers begin to approach a finite carrying capacity. The carrying capacity is the maximum number of a species that can be sustainably supported by the environment. As a population approaches the carrying capacity, environmental resistance occurs, slowing the rate of growth. This results in a sigmoidal (S-shaped) growth curve that plateaus at the carrying capacity (denoted by ê). Logistic growth will eventually be seen in any stable population occupying a fixed geographic space.

Types of Population Growth



Fig 1.2 Exponential vs Logistic Growth of population

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Limiting Factors

Limiting factors are environmental conditions that control the rate at which a process (e. g. population growth) can occur. Population growth can be determined by density-dependent or density-independent factors.

The relative size of a population has an impact on **density-dependent** environmental parameters. Predator numbers, food and other resource availability, and the spread of harmful diseases are all aspects to consider.

The proportional size of a population has no effect on **density-independent** environmental parameters. Weather and climate conditions, as well as the occurrence of natural disasters, are among these influences (e. g. earthquakes).

Net migration

Net Migration is the difference between the numbers of persons entering a geographic area (immigrants) and those leaving the area (emigrants). The phrase 'net migration' is commonly used in sociology to refer to population movements. The difference between how many individuals come from other regions to dwell in the region under discussion is the net migration rate for a certain period of time. These movements are referred to as immigration, and the number of people who leave the region to live elsewhere is referred to as emigration. A positive net migration rate indicates that more individuals are entering into a certain area than are leaving it. A negative net migration rate, on the other hand, indicates that more people are moving out of an area than are entering in. The net migration rate, like many other demographic data, is most commonly published per 1,000 residents over a one-year period and using mid-year population estimates.

The formula for net migration rate is:

N = 1000 x (I - E) / P

N = net migration rate

E = number of people emigrating out of the country

I = number of people immigrating into the country

P = the estimated mid-year population

Net Migration Rate Example

The population was 98 million people at the start of 2014. In the same year, 3 million people came to reside in the country, 1 million left, 6 million kids were born, and 4 million people died. His current objective is to figure out what his country's net migration rate was in 2014. The most difficult part is determining the mid-year population. Because 98 + 3 - 1 + 6 - 4 = 102, the population of 2014 starts at 98 million and concludes at 102 million. Because 100 is halfway between 98 and 102, the mid-year population estimate would be 100 million.

N = 1000 x (I - E) / P

Working in millions, this becomes:

N = 1000 x (3 - 1) / (100) = 2000 / 100 = 20

1.3.1 Growth of Organisms with Non-Overlapping Generations

Individuals are born or immigrate (come from outside the population) into an area, and others die or emigrate, causing population changes through time and place (depart from the population to another location). Some populations, such as mature forest trees, remain relatively stable throughout time, whereas others vary fast. The population growth can be

- Deterministic exactly predicting the outcome
- **Stochastic** giving a range of possible outcomes, with a probability of each occurring Geometric (discrete generations) and Exponential (overlapping generations) Population Growth

a) Geometric Population Growth

Discrete equations are used in **Non-overlapping generations** (univoltine insects, annual plants, and so on). In animals where the adult generation dies after one breeding season, non-overlapping generations are encountered. If a species, for example, can only survive the winter as a juvenile, the species will be made up of generations that do not overlap. Annual plants and some insect species are examples of species with non-overlapping generations.

The change in size over a generation is:

 $N_{t+1} = N_t R_0$

And the change over many generations is:

 $N_t = N_0 R_t^t$

 \mathbf{N}_{t} the population number after t generations, \mathbf{N}_{0} is the original population size

b) Exponential Population Growth

Populations with overlapping generations use continuous equations

- Overlapping generations means that births are continuous, so that dividing young into cohorts is purely arbitrary
 - o humans (and many great apes) have overlapping generations as do many small mammals (rodents) and many invertebrates in non-seasonal environments
 - Many mammals in seasonal environments do not have continuous generations, as all young are born within a few weeks of one another during a particular season
- Continuous equations describe events that occur continuously (like births in a population with overlapping generations)
 - o Calculus is best to describe continuous events
 - o Matrix algebra often better when generations are discrete

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• Predicting the future size of a population based on its current size and assuming exponential growth can be done with the following equation:

$$N_t = N_0 e^{rt}$$

- *r* is the **intrinsic rate of natural increase** and is an instantaneous rate, which the book points out is the difference between the instantaneous birth and death rates (r = b d), and is a *per capita* rate (an average rate taken over all individuals in the population)
 - we can approximate this as (approx. because gen. time is approx.)



- the rate of increase in the population (dN/dt) is dependent on two factors:
 - o the intrinsic rate of natural increase, which is one individual's contribution to population growth and so doesn't tell what the whole population is doing
 - o the population size (larger populations increase by more individuals)

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

• The instantaneous rate of increase of a population (dN/dt) is the result

The abundance of natural populations changes over time in response to:

- food and resource availability,
- weather conditions,
- competition,
- predation,
- disease

The simplest models describing changes in population size are exponential growth and logistic growth, which assume

- constant food and resource availability,
- a constant environment,
- no interactions with other species,
- no disease

The exponential model also assumes that there is no competition among members of a species for available resources (density independent), whereas the logistic model considers that there is competition for resources within a species (density dependent).

Both of these models can be described by equations in discrete time or continuous time.

• Discrete time models are appropriate for organisms with nonoverlapping generations such as an annual plant or an insect population with one generation per year. • Continuous time models work well for organisms that have overlapping generations in a non-seasonal context, such as microorganisms produced in culture. They're also good for species with overlapping generations that thrive in a seasonal habitat and are counted in the same season, as perennial plants counted in the spring.

Exponential Growth in Discrete Time

It describes the change in population size from generation to generation. In 1937, two cocks and six hen pheasants were introduced onto an island off the coast of Washington. Over the next five years the population experienced exponential growth:



Fig 1.3 Exponential Growth

The model of exponential growth in discrete time follows from the assumption that each individual will have the same number of offspring on average (R), regardless of the population size. If there are n[t] individuals in the population at time t, then in the next generation there will be:

n[t+1] = R n[t]

This is the recursion equation describing the change in population size from generation to generation. Starting at generation 0, there will be R n[0] individuals in the first generation, R2 n[0] individuals in the second generation, R3 n[0] individuals in the third generation, and so on.

$n[t] = R^t n[0]$

This is the general solution giving the population size over time.

Exponential Growth in Continuous Time

It can be defined as continuous population growth model if the individuals of a population show continuous breeding season. They never depend on parameters like season, food, climate for breeding. It is best described in terms of rate of population size change. The model of exponential growth in continuous time follows from the assumption that each individual reproduces at a constant rate (r), regardless of the population size. If there are n[t] individuals in the population at time t, then the rate of change of the whole population will be:

$$dn[t]/dt = r n[t]$$

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size.

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This is the differential equation describing the rate of change of the population

What is the solution to this differential equation?

 $n[t] = E^{rt}n[0]$

Notice that this general solution is the same as that in discrete time if we define $R=E^r$. Also notice that there can be exponential decline in population size if R<1 in the discrete model or r<0 in the continuous model. Exponential growth cannot, however, continue indefinitely.

Had the pheasants continued to grow exponentially, there would have been 7 million of them by the year 1950 and 10²⁸ by now — which at 2 kg per pheasant is 3000 times the mass of the earth! In fact, Lack observed that 'the figures suggest that the increase was slowing down and was about to cease, but at this point the island was occupied by the military and many of the birds shot.

1.3.2 Stochastic and Time Lag Models of Population Growth

Stochastic model of population growth deals with random influences on populations and on the vital events experienced by their members. It builds on the deterministic mathematical theory of renewal processes and stable populations.

There are two fundamental techniques to generate stochastic models. Starting with a deterministic model and recasting the model parameters as random variables derived from various probability distributions is one way. This option requires the specification of probability distributions for each model parameter, although it makes little or no difference to the core model structure. The expected or mean values of model outputs such as population size differ from the result of a deterministic model using mean parameter values in nonlinear models. The mistake of expecting that the outcomes of deterministic models utilizing point estimates will be directly equivalent to those of a correctly constructed stochastic model is illustrated by this finding, which arises from Jensen's inequality. Because deterministic relationships are still stressed, the deterministic model with random parameters is theoretically weak. In such models, stochasticity is merely noise that obscures a deterministic signal. Nature, on the other hand, is essentially stochastic rather than deterministic.

As a result, it seems reasonable to incorporate more fundamental stochasticity into models. This can be accomplished by concentrating on the model's state variables rather than its parameters. The likelihood or probability of all possible future states at time t + 1 are evaluated given the state of the system at time t. A probability distribution is the essential building component of a stochastic process model, and it defines the range of possible future states as well as their probabilities.

Time-lag Models

Because organisms rarely respond instantly to a change in the system, time–lag model's aim is to generate population growth forms that better match natural conditions. Depending on the length of the time delay, introducing a time lag into a model might destabilize the model and create dramatic variations in population size. A version of the birth and death rate model is the simplest time-lag model:

$$rac{\mathrm{d}N(t)}{\mathrm{d}t} = b(N(\mathrm{t}- au)) {-} d(N(t))$$

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Fig 1.4 Birth and Death Rate Time-lag Model

where b is the instantaneous birth rate, t is the current time, τ represents the time delay (the N(t – τ) term is the population size at time t – τ), and d is the instantaneous death rate. This model assumes that d is related to the current population size, but that b depends on the population size at time τ .

However, in many populations there are time lags (τ) in response to changes in population size,

$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

Two things will affect this equation. The length of the time lag (τ) and the response time of the population – this is inversely related to the intrinsic rate of increase (i. e., 1/r). The ratio of the time lag to the response time $\tau/1/r$ (which is simply r τ) controls population growth.

Stochastic Models of Population Growth

The balance of birth, death, and age-at-maturity determines a population's dynamics and responsiveness to environmental change, and there have been numerous attempts to mathematically model populations based on these features. In a stochastic model, unpredictability is added for one or more of the model's processes. As a result, the model produces a different result each time it is run. Running it several times yields a measure of the model's variability in results. There are three types of stochastic processes: demographic, environmental, and individual stochasticity.

There are two fundamental techniques to generate stochastic models. Starting with a deterministic model and recasting the model parameters as random variables derived from various probability distributions is one way. This option requires the specification of probability distributions for each model parameter, although it makes little to no difference to the core model structure. The expected or mean values of model outputs such as population size differ from the result of a deterministic

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model using mean parameter values in nonlinear models. The mistake of expecting that the outcomes of deterministic models utilizing point estimates will be directly equivalent to those of a correctly constructed stochastic model is illustrated by this finding, which arises from Jensen's inequality. Because deterministic relationships are still stressed, the deterministic model with random parameters is theoretically weak. In such models, stochasticity is merely noise that obscures a deterministic signal. Nature, on the other hand, is essentially stochastic rather than deterministic. As a result, it seems reasonable to incorporate more fundamental stochasticity into models. This can be accomplished by concentrating on the model's state variables rather than its parameters. The likelihood or probability of all possible future states at time t + 1 are evaluated given the state of the system at time t. A probability distribution is the essential building component of a stochastic process model, and it defines the range of possible future states as well as their probabilities.

Time Lag Models of Population Growth

This is basically defined as the interval of time between two related phenomena. Because organisms rarely respond instantly to a change in the system, time-lag models aim to build population growth forms that better match natural conditions. Depending on the length of the time delay, introducing a time lag into a model might destabilize the model and create dramatic variations in population size.

In a continuously growing population, adding new individuals into the population causes a continuous decrease in the per capita rate of population growth [(1/N)(dN/dt)]. However, in many populations there are time lags (τ) in response to changes in population size

Two things will affect this equation. The length of the time lag (τ) and the response time of the population – this is inversely related to the intrinsic rate of increase (i. e. 1/r). The ratio of the time lag to the response time $\tau/1/r$ (which is simply rt) controls population growth.

If $r\tau$ is small (between 0 to 0. 368), the population increases smoothly to a carrying capacity.

If $r\tau$ is moderate (0. 368 to 1. 570), the population first overshoots then undershoots carrying capacity, followed by dampening oscillation to reach carrying capacity over time.

If $r\tau$ is large (>1. 570), the population goes into a stable limit cycle of oscillations above and below carrying capacity that go on indefinitely.

1.3.3 Stable Age Distribution

Stable age distribution is generally defined as the probability density of the age of a randomly selected individual in a large population, which is growing exponentially in a constant environment. When a population's growth rate and relative age distribution do not alter over time, it is said to be stable. There is a consistent share in the group. Each age group's size grows/diminishes at the same (constant) rate as the population as a whole.

Age distribution refers to the proportionate number of people in each age group in a particular population. Due to variance in fertility counts and trends, age

distributions change between countries. A population with persistently high fertility, for example, has a large number of children and a small proportion of elderly people. A population with fewer children and a greater proportion of the old, such as France's, has fewer children and a larger proportion of the elderly. Changes in fertility have an immediate effect on the number of children, but it takes many years for the change to affect numbers beyond childhood. As a result, a population with a recent drop in fertility tends to have a limited number of children and elderly people, as well as a big proportion of adults in their middle years.

Migrations, war losses, and variances in mortality have all had an impact on age distributions, albeit these impacts are often minor compared to the influence of fertility fluctuations. However, migration of young adults who bring children or will soon have children in the area to which they move is likely to increase the number of middle-aged adults and children in the receiving country, while the proportion of elderly people remains low, having the opposite effect on the population of an area where there is a large net outflow.

The stable age distribution is in which the proportion of individuals in each age class remains constant over time, and a stable (unchanging) time-specific growth rate. The proportionate numbers of people in each age category in a given population is known as age distribution. Disparities in age distributions exist between countries due to differences in fertility numbers and trends. For example, a population with consistently high fertility has a big number of children and a small proportion of the elderly. A population with a lower proportion of children and a higher proportion of elderly people, such as France's, has a lower proportion of children and a higher proportion of elderly people. Changes in fertility have an immediate impact on the number of children, but it takes many years for the shift to have an impact on numbers beyond childhood. As a result, a population with a recent drop in fertility tends to have a limited number of children and elderly people, as well as a big proportion of adults in their middle years.

Age distributions have also been influenced in varying ways by migrations, war losses, and differences in mortality, though these effects are generally less important than the influence of variations in fertility. Yet the migration of young adults, who bring children with them or soon have children in the area to which they move, is likely to swell the number both of adults in the middle ages and of children in the receiving country, while the proportion of aged persons remains low, with reverse effects on the population of an area from which there is a large net out movement.

Check Your Progress

- 1. Define demography.
- 2. What is population growth?
- 3. Define life tables.
- 4. Define exponential growth of population.

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1.4 LIFE HISTORY STRATEGIES

Life history strategy is defined as the age and stage specific pattern which involves the timings of events that helps in making up of an organism's life such as birth. The life cycle of a species, and in particular the lifecycle elements associated to survival and reproduction, can be characterized as its life history. Natural selection shapes life history, which represents how members of a species distribute their limited resources among growth, survival, and progeny production. Thus, the events in between usually include birth, childhood, maturation, reproduction, and senescence, and together these comprise the life history strategy of that organism. The major events in this life cycle are usually shaped by the demographic qualities of the organism. The examples of plants and animals that use strategies of different types are as follows:

• **Parental Care and Fecundity:** The quantity of offspring vs a parent's investment in each individual offspring is a fundamental tradeoff in life history strategies. Essentially, this is a 'quantity vs quality' question: an organism can have a big number of offspring with a small amount of energy invested in each, or a small number of offspring with a large amount of energy invested in each.

To put it another way, we can argue that fecundity is inversely proportional to the amount of energy spent each offspring. The reproductive capability of an organism (the number of offspring it can produce) is known as fecundity. The higher an organism's fecundity, the less energy it'll put into each offspring, both in terms of direct resources (such as fuel reserves stored in an egg or seed) and parental care. Organisms that generate a high number of offspring invest a modest amount of energy in each one and usually do not provide much parental care. The kids are left to fend for themselves, with the hope that enough will survive (even if the odds for any one are low). Organisms that have a small number of offspring invest a lot of energy in each one and often provide a lot of parental care. These organisms are effectively 'placing their eggs in one basket' and are deeply involved in each offspring's survival. These are general patterns, not universal principles, as in so many examples in biology. The fundamental issue is that when creatures have a large number of offspring, they can't devote as much energy to each one. When they have fewer offspring, they may (and must) devote more energy to ensuring their survival.

Example: Many Offspring, Low Investment/Parental Care

A normal sea snail (whelk) can lay hundreds of eggs at a time, and these eggs hatch into baby snails that are self-sufficient right away. In fact, the hatchling snails will eagerly devour their slower-hatching siblings. Aside from the cannibalism, this case is a good example of a prevalent type of parental investment approach. Sea snails and many other marine invertebrates give their babies little (if any) attention. Instead, they spend the majority of their energy budget on producing a large number of little offspring. When it comes to numbers, the sea snail isn't even that impressive, a female sea urchin may spawn 100,100,000,000,000 eggs in a single spawning.

Offspring in species that use this method are generally self-sufficient at a young age. Nonetheless, because little energy is invested in each child, they tend to be little and have limited energy reserves when they enter the world. As a result, the progeny are vulnerable to predation, and many, if not all, will perish; instead, the population's survival is ensured by their sheer numbers.

Example: Few Offspring, High Investment/Parental Care

To see a strategy at the opposite end of the spectrum, let's consider the giant panda. Panda females typically have just one cub each time they reproduce, and the young cub is far from self-sufficient. Animal species like the panda, which have few offspring during each reproductive event, often give extensive parental care. They may also produce larger, more energetically 'expensive' offspring. The newborn panda above may look tiny, but compared to a hatching sea snail, it's massive! Species with this type of high-investment strategy use much of their energy budget to care for their offspring, sometimes at the expense of their own health.

This type of strategy is common in mammals, including humans and kangaroos as well as pandas. The babies of these species are relatively helpless at birth and need to develop quite a bit before they become self-sufficient.

- Fecundity and Investment Tradeoffs in Plants: Plants follow the same broad patterns that mammals do. Plants, on the contradictory will not provide parental care in the same manner that mammals do. They can, however, generate huge quantities of energetically 'cheap' seeds or small quantities of energetically 'expensive' seeds. Low-fecundity plants, such as coconuts and chestnuts, generate a tiny number of energy-rich seeds, each of which has a strong chance of developing into a new creature. Plants with a high fecundity, such as orchids, use the opposite approach: they produce a large number of little, energy-poor seeds, each with a slim chance of survival.
- Timing of First Reproduction (Early vs. Late): Another key component of a species' life history is when it begins reproducing, and another place where we witness trade-offs and a lot of variety among species. Some plants and animals reproduce quite quickly, while others take considerably longer. What are the advantages and disadvantages of these strategies?

Organisms that reproduce early have a lower chance of producing no offspring, but this may come at the sacrifice of their growth or health. Small fish, such as guppies, utilize all of their energy to reproduce early in life, but because they devote all of their energy to reproduction, they never grow to the size that would allow them to defend themselves against predators.

Organisms that reproduce later in life have higher fecundity and are better able to care for their offspring. On the other hand, they have a higher chance of not reaching reproductive age. Larger fish, such as bluegills and sharks, for example, spend their energy to develop to a size that provides them with more security. As a result, they postpone reproduction, increasing the likelihood that they will die before reproducing (or before reproducing to their maximum). Demography, Population Growth and Life History Strategies

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In general, a species' longevity is connected to its age at first reproduction. Short-lived species are more likely to reproduce early, whereas long-lived species are more likely to reproduce later. This serves as a useful reminder that a life history strategy is a comprehensive 'solution' to the problem of producing as many offspring as feasible, and that each component (e. g., age of first reproduction) only makes sense in the context of the others (e. g., lifespan).

• Single vs. Multiple Reproductive Events: Another essential aspect of life history is the number of times an organism reproduces over its lifetime. For certain species, reproduction is a one-time, all-or-nothing affair, and the creature does not survive much beyond that. In other species, possibilities for reproduction arise several times, if not many times, over the course of the organism's life.

To apply a little ecology vocab, we can split species into two groups:

- Those that can reproduce only once (semelparity)
- Those that can reproduce multiple times over their lifetime (iteroparity)

The ability to survive and reproduce are two important aspects of fitness. Organisms seek to achieve optimum fitness by focusing on survival and reproduction in a variety of ways, some of which are odd. Such life cycles abound in nature, leaving many perplexed and even seeking explanations. The solution to such perplexing puzzles is quite easy. Organisms that are poised to begin life have a plethora of alternatives. Organisms choose a particular life design based on the physical circumstances of their habitat and other selection factors. Many components of life, or 'traits,' go into making a design decision. 'Life history strategy' refers to the rules followed and decisions made while pursuing a life design. Thus, life history strategy refers to the alternatives that have been exhausted in terms of affecting features related to an individual's survival and reproduction schedule.

Ecology revolves around life history strategies. It is the only field that allows you to come near enough to the delicate thread that connects the diversity and intricacies of living beings. The study of life histories uncovers the underlying simplicity that unites and explains the incredible diversity of living beings on the planet, as well as their strange life cycles. A detailed examination of these life histories demonstrates how well they are tailored to the species' lifestyles. Life history research also considers the numerous tactics or patterns that influence both survival and reproduction. These techniques are nothing more than adaptations that have evolved to improve fitness through resource efficiency. In fact, different life stories might be viewed as different fitness techniques. The study of life history traits is one topic that can help you comprehend other fields. The study of life histories, traits, and strategies contributes to a better understanding of natural selection, evolution's driving force.

The male blue-headed wrasse, which is large and beautifully coloured, warrants a second glance, especially since the females are bland and smaller in comparison. His blue head is distinguished from his green body by two black bars separated by a white band. On the small reef where it dwells, it has a harem of females. It is adept at attracting females by displaying its vibrant coloration and sophisticated courtship behaviour. While it is busy releasing sperms, it copulates with each of the females

and causes them to release a batch of eggs. As the eggs and sperms drift away with the water current, the cloud of eggs and sperms disappears. The majority of the eggs will not hatch into larva and will be eaten by a predator waiting in the wings. The larvae of the survivors hatch. Only a few are fortunate enough to make it to the reefs. The little larva continues to feed and grow after reaching a small reef where another single male, like its father, big and colorful, lives with his harem of females. After one year of age, this blueheaded wrasse matures into a female, as do the majority of blueheaded wrasses. The yellow-colored (initial phase) female, which is ten cm long, mates with the identical blue-headed (final phase) male, which is twice its own size. It is the largest female on the reef after three years. The lone guy on the reef becomes a predator's feast one fateful night. Within 24 hours, the reef's largest female decides to take command and develops the blue-green coloration. Its ovaries shrink, and for the first time in its life, it mates as a male the next day (a phenomenon called as protogyny - starting life as female and then changing sex to male). A different scenario was unfolding on another reef. A larva had grown large enough on the reef to be defended by a single male. Holding territories isn't a good idea here because the reef is too big to be guarded alone. The lucky survivor grows, feeds, and develops into a little, dull male after a year. In fact, it looks like a female. It doesn't waste any energy on useless mating attempts. It merely waits for the appropriate moment, which occurs when a huge, vividly coloured blue-headed male starts mating with a female. It infiltrates the nest and releases its sperm into the spawn. This little, uninteresting male has several such opportunities during his life. The reproductive success (offspring surviving) of this is as much those of few large males on the reef which started off life as females.

Without a sure, the tale of the blue-headed wrasse is fascinating. Nature is full of such perplexing stories to tell. The question that arises in all of these stories is why does an organism have a specific life cycle? The solution is straightforward: nature knows best. Nature has created all species to suit the environment they live in through natural selection. When the set of environmental conditions changes, the form and function of the object changes as well. The only reason to survive biologically is to reproduce and contribute to the gene pool. This is a metric of evolutionary fitness that characterizes reproductive success. The differences we see between populations or species are essentially adaptive adaptations that help them evolve more successfully. On small reefs where territories may be maintained, the majority of young blue-headed wrasse mature as females, with only a few small, dull males. Large reefs, on the other hand, see more baby fish mature into little, dull males who never change sex. The fish mature into an adult form that is appropriate for the reef where they first arrive. As a result, the ecology and evolution are inextricably linked. Organisms respond to and adapt to the physical conditions of their surroundings. The ultimate goal of all living beings, regardless of their design, is to reproduce and leave as many successful progeny as possible.

1.4.1 Evolution of Life History Traits

The features or combinations of traits that are directly or indirectly related to an individual's reproductive success and are thought to represent an adaptive response to the organism's environment are referred to as life history traits. The various different kinds of life history patterns are discussed below:

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- 1. After 5 years of feeding in the broad waters of the North Pacific, a salmon reaches a river and swims 2,000 metres upstream to a tributary without eating. It has digested its muscles and organs along the travel. It reproduces, lays eggs, and then dies.
- 2. In the Australian outback, a Red Kangaroo looks after three offspring at different phases of development. The oldest has left its mother's pouch, the second is linked to a pouch teat, and the third is a fertilized egg unattached to the placenta (where it will remain for 204 days).
- 3. In a little stream, a mayfly egg hatches. The nymph swims to the top and hatches into the first adult stage after a few weeks of feeding. The winged creature flies away and hides among the bushes near the stream's edge. It sheds its skin and matures sexually in a matter of hours. Both sexes fly over the water and mate shortly after. The female subsequently lays her eggs on the water's surface, and both sexes die as a result.
- 4. A bamboo plant reproduces vegetatively (asexually) for 100 years. Along with other individuals, it forms dense stands of plants. Then in one season, all the individuals in the population flower simultaneously, reproduce sexually and die. One hundred years later the process is repeated.

These examples serve to point out that there exists a wide array of life history patterns among plants and animals. The essential premise of this theory is that life-history features evolve to optimize fitness (i.e. genetic representation in the next generation) within development and/or genetic restrictions. Fitness = number of offspring in next generation. Arguments of this theory are grounded in the assumption that there are trade-offs. Traits represent the 'optimum' state and represent a compromise between 'costs' and 'benefits'.

Note: Potential lag time between environmental change and genetic response.

1.4.2 Longevity and Theories of Aging

Let us discuss longevity

Longevity

Longevity is a term for a number of different actuarial constructs, the two most common of which are life expectancy which is an empirical concept referring to the average age of death in a cohort and life span (or maximum life span) which is a theoretical concept referring to the highest age attainable by any member of a population.

It is the outcome of the individual's subject to the risk of death at each age expressed as age-specific mortality rate—the probability that an individual currently alive will die in the next time period (e. g., one year).

Longevity can be altered by changing mortality in one of three ways, all of which are under genetic control:

- (a) shifting the age of maturity—this is one of the most common ways in which fruit fly longevity is increased in population genetics selection experiments;
- (b) reducing mortality over part of the life course—this can occur through disease prevention or cure and reductions in accidental deaths; and
(c) reducing the actuarial rate of aging—this effectively reduces the rate of change (slope) of mortality with age.

Lifespan, often known as longevity, is a fundamental life-history feature that varies greatly between and within species or it can be defined as the duration of individual's life. The bowhead whale (*Balaena mysticetus*) has a maximum longevity of 211 years, while the pygmy goby has a maximum lifespan of only eight weeks (Eviotasigillata). Lifespan varies greatly with body size, as it does with most other life-history features, with giant animals living longer than smaller species. Many animals, however, live significantly longer, or even shorter, lives than one might assume based on their body mass. Understanding the factors that cause these departures from expected lifespans may hold the key to treating and preventing human ageing.

Low extrinsic mortality (i.e., a low risk of death due to external causes such as disease, predation, food shortages, or accidents) will, on average, select for longer lifespans than when extrinsic mortality is high, which is one explanation for species living longer than expected given their body size. Because untimely mortality is more likely, early and frequent reproduction is prioritized above long-term maintenance and survival. As a result, given their body mass, species with modifications that lower the risk of extrinsic mortality should live longer than expected. These principles have spawned a slew of taxon-specific speculations regarding features that may lower extrinsic mortality and lengthen lifespan.

The capacity to fly, and so more readily avoid predators and unfavourable conditions, is possibly the most successful technique for a terrestrial animal to evolve in order to reduce extrinsic mortality and extend its longevity. The lifespans of volant (flying) and non-volant (non-flying) vertebrates are strikingly different; on average, bats live 3. 5 times longer than non-volant placental mammals of equal size, and birds live up to four times longer than similar-sized mammals. Flight, on the other hand, may not be the only way to reduce extrinsic mortality and thus extend lifetime.

Theories of Aging

Why do we get older? When do we begin to age? What exactly is an ageing marker? Is there a limit to the number of years we can live? In the last few hundred years, mankind has often pondered over these concerns. Despite recent discoveries in molecular biology and genetics, however, the secrets that govern human lifetime remain unsolved.

Many ideas have been presented to explain the ageing process, but none seem to be completely satisfactory. Traditional ageing theories claim that ageing is neither an adaptation nor a genetically predetermined process. There are two types of modern biology theories on human ageing: planned and damage or mistake theories. According to the programmed hypotheses, ageing follows a biological timetable, maybe similar to that which governs infant growth and development. Changes in gene expression that alter the systems responsible for maintenance, repair, and defense responses would be required for this regulation. Environmental assaults on living organisms that generate cumulative harm at various levels are highlighted as the cause of ageing in the damage or error hypotheses. Demography, Population Growth and Life History Strategies

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The programmed theory has three sub-categories:

- 1. **Programmed Longevity:** Senescence is described as the moment when age-related deficiencies show, and ageing is the result of a sequential switching on and off of particular genes. Certain scientists discuss the importance of genetic instability in the ageing process as well as the dynamics of ageing.
- 2. Endocrine Theory: Hormones regulate the rate of ageing by acting on biological clocks. Recent research confirms that ageing is hormonally regulated, with the evolutionarily conserved insulin/IGF-1 signaling (IIS) pathway playing a significant role in hormonal ageing regulation.
- **3. Immunological Theory:** The immune system is designed to deteriorate with time, increasing vulnerability to infectious disease and, as a result, ageing and mortality. It is well recognized that the immune system's efficacy peaks at puberty and then gradually declines with age. Antibodies, for example, lose their potency as people age, and the body is able to resist fewer new diseases successfully, resulting in cellular stress and death. Cardiovascular disease, inflammation, Alzheimer's disease (AD), and cancer have all been related to a dysregulated immune response. Although direct causal relationships have not been established for all these detrimental outcomes, the immune system has been at least indirectly implicated.

1.4.3 Energy Apportionment between Somatic Growth and Reproduction

Apportionment can be defined as the process of dividing up the total consumption of an organism or other entity and allocating it to individuals. There are numerous possible strategies to determine how this should be carried out and different strategies will suit different individuals. Nevertheless, there are certain desirable characteristics that all apportionment approach should exhibit:

- 1. Completeness: the sum of the energy apportioned to all individuals should be equal to the total energy to be apportioned and
- 2. Accountability: actions by an individual should have a maximal effect on their own allocation and a minimal effect on others.

In theory, growth and reproduction are two separate processes that compete for the same finite amount of bodily resources. A variety of factors influence growth, some of which are solely dependent on the environment, such as temperature. Others, such as the food supply, are subject to human intervention. Individual fish growth can be influenced in four different ways by exploitation, both short and long term:

- 1. by reducing population abundance (giving rise to density dependent responses),
- 2. by altering the density of the different preys (incl. switch to non optimal feed),
- 3. by diminishing the abundance of predators/competitors, and
- 4. by systematic, selective removal of individuals growing at rates deviating from the average for the original population as a whole.

As more interacting populations are affected by the fishing effort, the prey predator interaction becomes more complex. Individual growth will be improved by reducing intraspecific competition if the environmental factors remain constant if a single species is targeted. However, because numerous species are exploited in practice, changes in interspecific connections may be just as important as changes in intraspecific relationships, resulting in a very complex scenario. Leaving aside the possibility that fisheries can cause adaptive changes in populations, the most basic idea is that increased fishing pressure will result in increased individual growth due to a better predator-prey relationship. Growth may, however, be unaffected if prey availability is reduced as a result of changes in the environment or the equivalent amount of exploitation. While environmental fluctuations cause changes in age at maturity over time, fisheries can induce a rapid reaction in age at maturation by modifying population abundance and individual development rate, as documented for various fish stocks, such as the Flemish Cap cod. The onset of maturation indicates that particular needs, either in terms of size or energy storage accumulations, or both, have been met at a specific point in life. Growth is thus a requirement for maturity, but once started, maturation has a negative impact on subsequent somatic growth. Because fecundity and survivability of children are inversely proportional to maternal size, any decrease in growth rate after maturation may have a negative impact on the individual's reproductive success. Atresia and skipped spawning can be explained in terms of both survival tactics (when the fish is in poor health) and resource conservation (when the fish has a bigger body mass and better environmental conditions). Furthermore, due to the inherent energetic tradeoff between growth and maturation, changes in growth rate prior to maturation frequently result in considerable variations in maturation age schedule. If the growth rate of juvenile fish is slowed, maturation will occur at a later age. Accelerated growth, on the other hand, should result in quicker maturation. However, under different ecological or physiological conditions, the ideal size at maturation is not the same. Fisheries, or more especially, population reductions, are usually thought to be one of the principal reasons of observed changes in maturation age (and growth rates). Accelerated growth should imply a reduction in age at maturation, but not necessarily in size at maturation, if maturation occurs when a given body size is reached. However, as this research shows, the majority of recorded maturation alterations do not only pertain to age, but also to size. Under these conditions, the smaller fish appear to have stored enough spare energy to successfully support the expense of reproduction, see plasticity and reaction norm for size at maturity.

Age at maturation, on the other hand, is a heritable feature, and the shift to a younger age and larger size at maturation is a function of changes in genotype frequencies in the population over time. Fish genotypically designed to late maturation (at large size) are unavoidably far less likely to spawn before being fished out in an intensively exploited population, which is characterized among other things by excessive removal of larger individuals. Individuals who are predisposed to mature early and at a lesser size, on the other hand, may reproduce at least once. This principle should be represented in a higher relative abundance of fish genotypically predisposed to early, small-size maturation over generations. Such population modification may have an impact not only on the composition of the commercial catch, but also on ecological fitness. The long-term ramifications Demography, Population Growth and Life History Strategies

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of this remain unknown, but if it occurs, it could have a significant impact on the productivity of harvested fish stocks.

Growth and Reproductive allocation are the terms used in ecology and evolutionary biology that refers to the proportion of an organism's energy budget allocated to growth and reproduction at any given time. Reproduction must be balanced (or traded off) against opposing expenditures such as growth, survival, maintenance, and future reproduction. The term also covers division of resources among offspring size and number. Animals show a vast degree of variation in reproductive allocation.

- Kiwis, for example, famously lay a single egg that is up to 20 percent of body weight. As if this were nothing, caecilians (amphibians) can bear live litters of offspring that are up to 65 percent of the mother's body weight. Egg numbers vary enormously and can reach spectacular numbers: tsetse flies bear as few as six live offspring in a lifetime, whereas ghost moths can lay more than 50,000 eggs.
- Social insects have truly mind-boggling fecundity: driver ants can lay several million eggs per month, and can live for decades; ocean sunfish release about 300 million eggs at a time, more than any other vertebrate. At the other extreme, very many organisms have one offspring at a time.
- Usually this goes hand in hand with repeated breeding, but perhaps the most puzzling of allocation decisions is found in dung beetles, which have only one ovary; some species lay as few as five to ten eggs.
- Careful parental care ensures that more than 90 percent of offspring survive, explaining why these species have not become extinct.
- In Drosophila and Daphnia, where traits of reproductive allocation (body size, egg size, egg number, etc.) have become model traits for modern genetic analyses. Modern approaches to reproductive allocation typically involve elucidating genetic bases for trade-offs expressed across a range of environments.

1.4.4 Parental Investment and Offspring

In general, the meaning of parental investment is portioning in offspring by the parent that increases the chances of survival of the offspring. Any sort of parental behaviour that improves the fitness of the offspring is defined as parental care. Preparation of nests and burrows, production of large, heavily yolked eggs (which are generally associated with increased hatchability and young survival), care of eggs or the young inside or outside the parent's body, provisioning of young before and after birth, and care of the offspring after nutritional independence are all included in this definition of parental care. There are two types of parental care: depreciable and non-depreciable. Depreciable care, such as food provision, reduces the benefits of parental care for individual offspring as the broodor litter size grows; non-depreciable care, such as parental vigilance to detect potential predators, does not decrease the benefits of parental care for individual offspring as the broodor litter size grows. Parental investment, on the other hand, is defined as any expenditure by parents on a single child that diminishes their ability to invest

in other children, both current and future. The definition of parental investment is up for debate, and there are often disagreements over what should and should not be included. Today, the word refers to any activity taken by parents to improve the fitness of their kids at the expense of their own future reproduction. This concept emphasizes the dilemma posed by parental investment, as parents must choose between spending resources in their own survival or future reproduction and investing these resources to improve the odds of their current offspring surviving and reproducing. It's vital to remember that there's no required link between the size of a parent's investment in a child and the child's gain; the currency of interest is the cost to the parent of future reproduction. Parental care is widespread in the animal kingdom, yet there is a wide range of how parents care for their children, as well as the amount of resources they devote to it. For example, the relative parental investment by the sexes varies significantly - in some species, mothers invest more, in others, males invest more, and in others, investment is more or less equally split. Varied hypotheses have been presented to explain patterns of parental investment between sexes and species, and work is still on to develop an overarching hypothesis that may explain the various patterns seen.

Perhaps as a result of human newborns' complete reliance on parental care throughout their early years, we don't think of parents devoting important resources to feeding and caring for their children as an evolutionary riddle. However, the subject of why parents spend resources that could be utilized to improve their own health and survival chances on their children is far from inconsequential. Indeed, there is a vast variety in the type of care and resources that parents devote to their kids among animals. In many species, investment is limited to producing eggs or live offspring, which are then left to fend for themselves – for example, in the herring (Clupeaharengus), whereas in others, such as several bird species and some mammals, including humans, both parents invest in substantial periods of parental care, sometimes even after nutritional independence.

Parental Investment Patterns across Species

Care of eggs or progeny is uncommon in invertebrates, such as terrestrial arthropods, and only a few orders provide care of eggs or young. Parental care after the eggs or young are removed from the parent's body is missing in early vertebrates, such as chondrichtyans (sharks and rays). In contrast, about 21% of the 422 families of bony fish (Teleostei) show some sort of egg care, such as the development of eggs or offspring inside the female's body (ovoviviparity and viviparity), while only 6% show guarding of newly hatched young. Approximately 71 percent of amphibians families have some form of parental care (including ovoviviparity and viviparity), and 66 percent of them have one of the parents caring for the eggs or offspring. In reptiles, 56 percent of all families show some form of egg care (including viviparity), although egg guarding by females is seen in only 3% of egg-laying snakes and 1% of egg-laying lizards. All bird species provide parental care for their eggs, though some brood parasites (e.g. cuckoos) have other species brood their eggs and feed their young, whereas megapodes (Megapodiidae) do not incubate eggs and instead build mounds or bury them, and the chicks hatch at an advanced stage of development and are generally self-sufficient.

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Finally, all mammals take care of their young ones. There is a lot of variety in which sex is the primary caregiver across species having parental care. In mammals, the vast majority of species provide female-only care, with only about 5% providing bi-parental care. Bi-parental care is far more widespread in birds, with around 90% of species presenting care from both parents, despite the fact that females invest more in care than males. In fishes, diversity is significantly higher, with paternal care accounting for 61% of caring species, maternal care for 39% of caring species, and bi-parental care for around 20% of caring species (note that the species with bi-parental care are also represented in the species with maternal and paternal care). In fish, whether fertilization is internal (which is linked with female-only care) or external (which is associated with male-only care) has been postulated to influence sex differences in relative investment in care (more generally associated with male-only care). Furthermore, male territoriality, which is frequent in fish, has been suggested as a factor in the evolution of male care since it allows for a transition to also defending eggs inside the territory. In the humid tropics, parental care of eggs or young is most prevalent among terrestrial amphibians, with egg guarding, often by the male, being the most common type of care. The legless amphibian Boulengerulataitanus provides a magnificent example of parental care, with females producing a modified outer skin to give a plentiful supply of nutrients for developing larvae to feed on. In reptiles, some lizard species care for eggs and pythons incubate the eggs for some time. Only crocodiles and their relatives care for both eggs and hatchlings.

1.4.5 Reproduction Strategies: Ecology and Evolution of Sex and Mating System, Optimal Body Size, R- and K-Selection

Evolution of Sexual Reproduction and Mating: Sexual reproduction is an adaptive feature which is common to almost all multi-cellular organisms (and also some single-cellular organisms) with many being incapable of reproducing asexually. Prior to the advent of sexual reproduction, the adaptation process whereby genes would change from one generation to the next (genetic mutation) happened very slowly and randomly. Sex evolved as an extremely efficient mechanism for producing variation, and this had the major advantage of enabling organisms to adapt to changing environments. Sex did, however, come with a cost. In reproducing asexually, no time nor energy needs to be expended in choosing a mate. And if the environment has not changed, then there may be little reason for variation, as the organism may already be well adapted. Sex, however, has evolved as the most prolific means of species branching into the tree of life. Diversification into the phylogenetic tree happens much more rapidly via sexual reproduction than it does by way of asexual reproduction. Evolution of sexual reproduction describes how sexually reproducing animals, plants, fungi and protists could have evolved from a common ancestor that was a single-celled eukaryotic species. The origin of sexual reproduction can be traced to early prokaryotes, around two billion years ago, when bacteria began exchanging genes via conjugation, transformation, and transduction. Though these processes are distinct from true sexual reproduction, they share some basic similarities. In eukaryotes, true sex is thought to have arisen in the Last Eukaryotic Common Ancestor (LECA), possibly via several processes of varying success, and then to have persisted.

A mating system is a way in which a group is structured in relation to sexual behaviour. Mating systems include monogamy, polygamy (which includes polygyny, polyandry, and polygynandry), and promiscuity, all of which lead to different mate choice outcomes and thus these systems affect how sexual selection works in the species which practice them. (Detail Discussion is given in unit 4 of this book)

Optimal Body Size: Body size is one of the most fundamental properties of an organism. It is related to lifespan, habitat and other aspects of life history of an organism and its ecology, the relationship between body size and abundance is an important link between the individual and population level traits of species and the structure and dynamics of ecological communities. Body size is considered as one of the primary determinants of metabolism and resource used by it. The relationship between size and quantity also reveals how resources are partitioned in ecological systems.

Body size varies considerably between species and among populations within species, it shows many repeatable patterns. For many animals, resource quality and intraspecific competition may mediate selection on body size producing largescale geographic patterns. On average, large-bodied species live at lower densities than small-bodied ones. Early studies suggested that population densities might scale so that the energy use of a population is independent of body size. However, recent work shows that, at the scale of local communities, this is rarely true and that the pattern varies among taxonomic or ecological subsets of those communities. Energetic considerations may only be relevant to the densities of more abundant species. Within many animal taxa there is a trend for the species of larger body size to eat food of lower caloric value.

Reproductive Strategies: The word 'reproductive strategy' refers to an animal's approach to mating and/or raising offspring. It could refer to sexual vs. asexual reproduction, for example. It could also apply to semelparous reproduction, which occurs once in a lifetime, vs iteroparous reproduction, which occurs several times over an organism's existence. It could even imply the animal's traits and the habitat in which it lives.

Two Approaches

Let's look at an example to better comprehend reproductive techniques. Assume you're a graphic designer who's been entrusted with designing a logo for a company using one of those crowdsourcing websites. What type of graphic designer do you think you'd be?

- i. Taking a Shotgun Approach: You must create as many logos as possible in the shortest amount of time. You're hoping that one of them will continue with the customer despite the fact that none of them are particularly good. The benefit is that you don't have to spend as much time on design, but the disadvantage is that you're less likely to win the competition.
- **ii.** Careful Approach: You design one, maybe two logos, and it takes you a long time. But you know they are higher quality. The upside is a much higher chance of winning the design contest but the downside is, if you don't, you would've wasted a lot more time than in A.

So which graphics designer would you be? Believe it or not, both A and B are a reflection of two general types of reproductive strategies animals use. The

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level of investment in offspring varies between and within species when it comes to sexual reproduction tactics. According to life-history theories, the rate of sexual maturation is closely tied to reproductive strategy, with high investment being linked to fewer children and later maturation. Puberty and first sex age are two developmental milestones for humans that have been linked to reproductive choices.

Understanding how organisms invest resources in reproduction, as well as the dynamic selection forces and tradeoffs that affect this, is one of the most enduring study topics in evolutionary biology. Natural selection has produced a huge variety of reproductive techniques, but there is always a tradeoff between offspring size and number (fecundity). This tradeoff has been the subject of a huge body of theoretical and empirical studies, although the focus has typically been on plants (by botanists) or animals (by zoologists), rather than both. Despite the fact that both plants and animals have evolved a wide range of reproductive techniques, their fitness is inevitably determined by the quality and quantity of their progeny, as well as resource availability. As a result of the underlying similarities in evolutionary forces and constraints, the reproductive strategies of these widely diverse lineages may have converged.

The SF model predicts a conflict between parent and offspring due to maternal and offspring-specific optimum sizes, which raises the fundamental question of maternal vs. zygotic control over reproductive resource allocation. When there is 'sibling rivalry,' or competition among numerous offspring of the same mother for maternal resources, as might occur during offspring development on the parent or after delivery in animals with parental care, the parent-offspring conflict becomes even more complex. While competition between animal offspring can be vigorous, even leading to direct fratricide, competition between sibling seeds in plants is more likely to be passive, as the maternal resource pool is depleted. Importantly, a seed's ability to draw nutrients is a function of its size: larger seeds can devote more energy to resource drawing, potentially bypassing maternal constraints and causing a resource scarcity for smaller seeds. When the demands on the children grow too great, the parent plant may abort 'inferior' embryos to ensure the survival of a few offspring and therefore improve parental fitness. When nutrients become few after oviposition or delivery, several animals selectively starve the weakest young.

The parent will lose some control over the size of the remaining offspring by selectively aborting or starving inferior children (by exerting direct control over offspring number). This is because the surviving offspring will obtain more resources, grow larger, and so increase their nutrition drawing capabilities (in the case of seeds), implying that zygotic control will become stronger. Changing resources from inferior to superior kids, on the other hand, is in the parents' best interests.

The SF model depends on two critical assumptions-

- **a.** an optimum fraction of available total resources should be invested in reproduction such that it maximizes lifetime reproduction of a parent and
- **b.** the resource pool is a homogenous entity, which parents invest to determine offspring size.

While point (a) is intuitively true, resources are often heterogeneous. For example, plants require both carbon and nitrogen, and the availability of these two components may vary over the course of a season. The terms *r*-selection and *K*-selection are used by ecologists to describe the growth and reproduction strategies of organisms

- *r*-selected species have a high growth rate but low survivability ('cheap' offspring)
- k-selected species have a low growth rate but high survivability ('expensive' offspring)

R-selection

- Occurs in unstable environments where there are ecological disruptions and resources are used for maximizing reproduction
- There are usually many offspring per brood, which require little parental care and have a high rate of mortality
- The body size of offspring is typically small and they have an early onset of maturity (short developmental span)
- Population size is typically variable (highly fluctuating) and an example of a *r*-selected organism is a pioneer species

K-selection

- Predominates in stable or predictable environments where resources are used for maximizing long-term survival
- There are usually very few offspring per brood, each requiring high levels of parental care (resulting in low mortality)
- The body size of offspring is typically larger and they have a late onset of maturity (long developmental span)
- Population size is typically stable (reaches carrying capacity) and an example of *K*-selection is a climax species

It's tough to tell whether a species is using an r-strategy or a K-strategy because they represent opposite extremes of a spectrum. In actuality, most species choose a strategy that falls somewhere in the middle of the spectrum (e. g. type II growth). Depending on the environment, certain species may even change their selection method. In volatile conditions, the optimum strategy is to generate a huge number of offspring, many of whom will perish but just a few will survive. In stable conditions, it is preferable to produce fewer children but invest more in each one, increasing the chances of offspring survival. As a result, r-selected species are short-lived, reproduce quickly, exploit open niches, and are prone to population booms and busts depending on the environment. K-selection refers to organisms that live longer, reproduce more slowly, and are less susceptible to environmental fluctuations. K-strategists are larger than r-strategists, have a high energy cost to produce one offspring, produce few offspring, have a long life expectancy, can reproduce multiple times, sexual maturity is slow to arrive, and offspring survival should be fairly high—with most offspring living to their full potential lifespan.

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Fig 1.5 Population Size and Time

According to our lengthy lifetimes, slow maturation, few offspring, and high offspring survival rate, humans are near the K end of the continuum. However, some scientists believe that strategy varies even within a species, and have used the concepts of r and K strategies to characterize human mating tactics, reproduction, and parental investment. In unstable situations, humans may choose to increase their pace of reproduction while spending less in each individual kid, resulting in offspring reaching sexual maturity and beginning their own reproduction sooner than humans raised in stable environments. Unstable conditions throughout development may influence reproductive choices, such as partner selection.

Check Your Progress

- 5. Define r-strategy.
- 6. What is parental care?
- 7. Define longevity.
- 8. What is aging?
- 9. Define life history strategies.

1.5 ANSWERS TO 'CHECK YOUR PROGRESS'

- 1. Demography is the statistical study of human populations. It examines the size, structure, and movements of populations over space and time.
- 2. Population growth is the increase in the number of people in a population. Global human population growth amounts to around 83 million annually, or 1.1% per year.
- 3. A life table is a table which shows, for each age, what the probability is that a person of that age will die before their next.
- 4. In exponential growth, a population's per capita (per individual) growth rate stays the same regardless of population size, making the population grow faster and faster as it gets larger. In nature, populations may grow

exponentially for some period, but they will ultimately be limited by resource availability.

- R-selected species, also called r-strategist are species whose populations are governed by their biotic potential (maximum reproductive capacity, r). Such species make up one of the two generalized life-history strategies posited by American ecologist Robert MacArthur and American biologist Edward O.
- 6. Parental care is a behavioural and evolutionary strategy adopted by some animals, involving a parental investment being made to the evolutionary fitness of offspring.
- 7. Longevity is defined as 'long life' or 'a great duration of life. The term comes from the Latin word longaevitâs. In this word, you can see how the words longus (long) and aevum (age) combine into a concept that means an individual who lives a long time.
- 8. Ageing or aging (see spelling differences) is the process of becoming older. The term refers especially to humans, many other animals, and fungi, whereas for example bacteria, perennial plants and some simple animals are potentially biologically immortal.
- 9. A life history strategy is the 'age- and stage-specific patterns' and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc.

1.6 SUMMARY

- Demography is the statistical study of human populations.
- A life table is a table which shows, for each age, what the probability is that a person of that age will die before their next.
- In population ecology and demography, the net reproduction rate, R0, is the average number of offspring (often specifically daughters) that would be born to a female if she passed through her lifetime conforming to the age-specific fertility and mortality rates of a given year.
- In population biology and demography, generation time is the average time between two consecutive generations in the lineages of a population.
- Reproductive value is a concept in demography and population genetics that represents the discounted number of future female children that will be born to a female of a specific age.
- Population growth is the increase in the number of people in a population.
- A life history strategy is the 'age- and stage-specific patterns' and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc.
- Reproductive strategies represent a set of behavioral, morphological, and physiological adaptations that facilitate access to potential mates, improve the chances of mating and fertilization, and enhance infant survival.

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1.7 KEY TERMS

- Demography: It refers to the statistical study of human populations.
- **Population growth:** It refers to the increase in the number of people in a population.
- Life history strategy: It is a life history strategy is the 'age- and stagespecific patterns' and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc.
- Cohort or Generation Life Table: It refers to the table that summarizes the age-specific mortality experience of a given birth cohort (a group of people born at the same time) over the course of their lives, which might span many calendar years.

1.8 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

- 1. What is the importance of demography?
- 2. What do you understand by the term 'life expectancy at birth'?
- 3. What is the relevance of the discipline of demography to public health practitioners?
- 4. Name the five processes which determine population size, its composition and distribution.
- 5. What causes population to grow?
- 6. What are life history strategies of animals?

Long-Answer Questions

- 1. Write a detailed note on the foru main challenges of population growth.
- 2. Identify the different life history strategies.
- 3. Explain life history strategy of humans.
- 4. What are the reproductive strategies for animal reproduction? Discuss.

1.9 FURTHER READING

- Preston, Samuel. Patrick Heuveline and Michel Guillot. *Demography: Measuring and Modeling Population Processes*. London: Wiley-Blackwell.
- Begon, Michael, Martin Mortimer, and David J. Thompson BA. *Population Ecology: A Unified Study of Animals and Plants, Third Edition.* Hoboken: Blackwell Science Ltd.
- Vandermeer, John H. *Population Ecology: First Principles*. Princeton: Princeton University Press.
- ¹ Adam Lomnicki. *Population Ecology of Individuals. (MPB-25), Volume 25.* Princeton: Princeton University Press.

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UNIT 2 PREDATION AND MUTUALISM

Structure

- 2.0 Introduction
- 2.1 Objectives
- 2.2 Predation
 - 2.2.1 Models of Prey-Predator Dynamics
 - 2.2.2 Optimal Foraging Theory
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- 2.3 Competition and Niche Theory
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- 2.7 Answers to 'Check Your Progress'
- 2.8 Summary
- 2.9 Key Terms
- 2.10 Self-Assessment Questions and Exercises
- 2.11 Further Reading

2.0 INTRODUCTION

Organisms in a community have direct and indirect effects on one another. Under natural conditions, an organism never lives in complete isolation and, as a result, must communicate in order to carry out fundamental life activities such as development and reproduction. Organisms can impact individuals of the same species biologically (intraspecific interaction), such as pollination and grazing, or they can influence individuals of different species (interspecific contact), such as parasitism. Interactions between individuals of the same species are known as intra-specific interactions, and interactions between two or more species are known as inter-specific interactions. However, since most species occur within ecological communities, these interactions can be affected by, and indirectly influence, other species and their interactions.

They interact with other ecological elements in the environment, resulting in the ecosystem's optimal functioning. As a result, these intricate relationships are critical to an organism's existence. Interdependencies between species occur in spatial and physiological links, and interactions between species can result in widely separated individuals with taxonomic relationships, such as bacteria and plants, fungus and plants, bacteria and humans, and so on. Interactions can be neutral, useful, or destructive, and they can be further categorized based on the duration of

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the relationship, which can range from casual to permanent, as well as the strength or mechanism of the organisms.

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Depending on the evolutionary context and environmental conditions in which they occur, the nature of these interactions can vary. As a result, ecological interactions between individual creatures and entire species are frequently difficult to identify and measure, and depend on the scale and context of the interactions. Nonetheless, there are various types of organism-organism interactions that can be observed in a variety of environments and ecosystems. When researching an ecological community, scientists can use these classes of interactions as a framework to characterize naturally occurring processes and forecast how human changes to the natural world would affect ecosystem features and processes.

Competition, predation, and mutualism are the interactions that will be covered in this unit. These aren't the only kinds of species interactions; they're all part of a bigger network of interactions that make up nature's intricate network of relationships.

2.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the concept of predation among animals, its basic model and role in nature.
- Understand how animals behave in a competition and mutual relationship, with the concepts of niche.
- Understand the intrinsic and extrinsic regulatory mechanisms of population.

2.2 PREDATION

Predation

Predation is defined as the ecological process in which an animal (or an organism) kills and feeds on another animal (or an organism). The animal that kills another animal to feed on is called a 'predator'. The one that is killed to be eaten is known as prey. The best example of predation is in carnivorous interaction. A carnivore is an animal that gets its energy only by eating meat or animal tissues. Thus, in carnivorous interaction, one animal feeds on another.

Examples are wolves hunting a deer or a moose, an owl hunting the mice, and the lion hunting various animals.

Predation – In the broad sense, when members of one species eat the members of another species.

A. Types of predation.

- 1. Carnivory–When animals feed on herbivores or other carnivores.
- 2. Herbivory When animals feed on plants. (Includes folivores, browsers, granivores and frugivores.)
- 3. Parasitism- a predator (parasite) that lives in or on its host. Moreover, it is dependent upon that host for it's development. Parasites can be categorized as microparasites and macroparasites.

- a. Microparasites include those organisms that cause disease. Also known as pathogens.
- b. Macroparasites includes parasitic worms and insects.
- c. Parasitoids parasitic activities are limited to the larval stage. Includes most insect parasites.
- 4. Cannibalism A special form of predation, where the predator and the prey are the same species.
- 5. Conceptual link- each interaction enhances the fitness of one organism, reduces the fitness of another- exploitation

Let us discuss the types in more detail

Types of Predation

Within the term *predation* there are specific kinds that are defined by how the predator-prey interactions and relationship dynamics work.

Carnivory: When we think of predator-prey relationships, this is the first sort of predation that comes to mind. Carnivory is a type of predation in which the predator consumes the meat of other animals or non-plant creatures, as the name implies. Carnivores are organisms that like to devour other animal or insect organisms. This type of predation and the predators that fall within this category can be further broken down. Some species, for example, require meat to survive. These types of animals are known as *Obligate* or *Obligatory carnivores*. Mountain lions, cheetahs, Africa native lions, and domestic cats are all examples of the cat family.

Facultative carnivores, on the other hand, are predators that can thrive on meat but do not require it. They may also thrive by eating non-animal foods such as plants and other creatures. Omnivores is another term for these carnivores (meaning they can eat anything in order to survive). Facultative carnivores include humans, dogs, bears, and crayfish. Examples of carnivory include wolves eating deer, polar bears eating seals, a Venus fly trap eating insects, birds eating worms, sharks eating seals and people eating meat from animals like cattle and poultry.

Herbivory: The predator consumes autotrophs such as terrestrial plants, algae, and photosynthetic microorganisms in this type of predation. Many people don't think of this as a typical predator-prey situation because predation is commonly connected with carnivory. Herbivory, on the other hand, is a sort of predation since one organism consumes another. The term herbivory is most commonly used as a descriptor for animals that eat plants. Organisms that eat plants only are called herbivores. As with carnivory, herbivory can be divided into subtypes. The two main subtypes of herbivory are monophagous and polyphagous herbivores. Monophagous herbivory is when the predator species eats solely one type of plant. A common example would be a koala bear that only eats leaves from trees.

Polyphagous herbivores are species that eat multiple kinds of plants; most herbivores fall under this category. Examples include deer eating multiple types of grasses, monkeys eating various fruits and caterpillars that eat all types of leaves.

Parasitism: Both herbivory and carnivory necessitate the death of the prey organism in order for the predator to obtain nutrients and energy. Parasitism, on the other hand, does not always need the death of the prey. Parasitism is a relationship

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in which one creature, the parasite, benefits at the expense of another organism, the host. Because not all parasites eat on their hosts, not all parasitism is considered predation. Parasites may exploit the host as a source of protection, shelter, or reproduction. This is a typical case of head lice. Head lice feed on the blood on the human scalp and use it as a host. This has bad health consequences for the host (itching, scabs, dandruff, tissue death on the scalp, and so on), but it does not kill the host.

2.2.1 Models of Prey-Predator Dynamics

There is a natural equilibrium between predator and prey populations. The population of the prey can grow exponentially if there are no predators. It has the potential to boost the environment's carrying capacity. Predators help to keep the population of prey under control by eating it. Because there is more food available when the population of prey grows, the number of predators grows as well. However, an increase in predator numbers could lead to a decrease in prey numbers. This, in turn, has an impact on the predator population, which is also declining due to food scarcity. Prey and predator populations experience cyclic changes as a result.

A predator-prey interaction tends to keep both species' populations in check. The graph in Figure 2.1 demonstrates this. Predators get more food as the population of prey grows. As a result, after a little pause, the predator population grows. More prey is taken as the number of predators grows. As a result, the number of prey begins to decline.



Fig 2.1 Predator-Prey Population Dynamics

2.2.2 Optimal Foraging Theory

Foraging is the basic activity of animals, this is the method through which they obtain food. Food is required for animals to maintain their metabolism, supply energy for a variety of tasks, and aid reproduction. Foraging takes up a large portion of available time in some settings, and because animals can't do two things at once, increasing the amount of time spent foraging may lower the amount of time available for other tasks like mating, resource defence, and predator avoidance.

Optimal foraging theory is a method of studying animal foraging behaviour that employs mathematical optimization techniques to generate predictions about this important component of animal behaviour.

Take a look at a hummingbird sipping nectar from flowers. Firstly hummingbird collects nectar fast, when it arrives at a new bloom, but as it spends more time there, nectar becomes more difficult to obtain since the hummingbird has depleted the quantity. This is how most food patches function. Fresh patches give food quickly, but as the forager depletes the patch, the rate of intake slows. Because it costs time and energy to go to a new patch, this simple observation creates a foraging challenge. How long should the forager stay in one patch before moving on to another? This is one of the classical problems of foraging theory. Figure 2.2 shows the idea of patch depletion graphically: the amount of energy extracted from the patch increases with the time an animal spends in the patch, but the instantaneous rate of food gain (given by the slope of this function) declines steadily; so this gain function increases but bends down. Now, it takes T units of time for the animal to travel from one patch to another; and t is the time the animal spends in each patch. The classic patch model finds the patch time, t, which gives the highest rate of food intake. Figure 2.2 shows how we can find this 'optimal patch time' graphically. The slope of the line that connects the point T on the x-axis (which is the time axis) to the point (t, e[t]) on the gain function gives the rate of energy intake an animal can expect if it spends time t. A bit of reflection shows that the highest slope (and hence the maximal intake rate) occurs at timetopt l when the line is tangent to the gain function. This simple graphical approach predicts that foragers should stay longer when it takes longer to travel to fresh patches. Compare t_{opt1} and t_{opt2} , which correspond to short (T) and long (4T) travel times. A number of early empirical studies support this prediction qualitatively.

Foraging creatures make a variety of additional decisions. They choose what types of food to eat and where and when to look for food, for example. The foraging behaviour we see is the product of these judgments. We will have a better grasp of these behavioural decisions if we can explain and anticipate them in terms of underlying processes, and the more quantitative (rather than qualitative) we can be in matching predictions with observations, the better.

At its most basic level, optimal foraging theory assumes that foraging decisions have evolved, and that as a result, the fitness associated with an individual animal's foraging behaviour has been maximized; as a result, the underlying processes are 'optimal.'



Fig 2.2 Graphical Representation of Optimal Departure Rule

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Optimal foraging models can and do come in a variety of shapes and sizes. Models differ in the behavioural decisions they consider (patch use, prey choice, habitat use), how they simulate the environment (e.g., sequential vs. simultaneous encounter with resources), and which currency they optimize (e.g., rate of net energy intake vs. probability of survival). Despite this diversity, we acknowledge a core group of foraging models that are critical because they serve as a foundation for continued growth.

These classic models use the currency of rate maximizing to analyse two basic decision issues (patch utilization and prey choice), assuming that the forager meets resources (prey or patches) sequentially. These traditional models understand that when an animal chooses one action over another, it may forego other options, and that a forager will often suffer an 'opportunity cost' when it chooses one action over another. Many optimal foraging models incorporate the concept of opportunity cost.

Diet choice: Foraging models can predict the optimal diet selection for an organism which has the goal of maximizing its net acquisition rate for energy while hunting and gathering. A simulation methodology is used to determine the optimal diet selection under the assumption that the forager's goal is to minimize the risk of an energy shortfall. The rate-maximizing and risk-minimizing diets are similar; that sharing is more effective than changes in diet in reducing risk; and that the riskreduction which can be obtained from sharing requires quite small numbers of participants. Food sharing may be an ancient and pervasive feature of hominid foraging adaptations. Species which exist today survived and reproduced effectively in the past. To do this, individuals had to meet competition from other species and from individuals of the same species. This may help to explain why wild animals often eat certain foods whilst ignoring others which seem to be nutritionally adequate and which are eaten by closely related species, or even by different populations of the same species. An individual presumably shows preferences based on archetypes which ensured the genetic survival of its progenitors. That an animal chooses foods which maximize its genetic fitness.

Prey Selectivity: According to optimal foraging theory, predators should prefer prey which provides the highest amount of energy per unit time. However, prey selectivity may also depend on previous diet and specific nutritional demands of the predator. From the long-term perspective, diet composition affects predator fitness. The existence of individual variation in prey selection, predation risk and functional responses effects the predator and prey population dynamics and impact predation on evolutionary trajectories of both predators and prey. Ecological communities are often characterized by many species occupying the same trophic level and competing over a small number of vital resources. The mechanisms maintaining high biodiversity depends upon prey selectivity. Prey selectivity by generalist predators plays an important role in promoting biodiversity. Intermediate levels of prey selectivity can explain a high species richness, functional biodiversity, and variability among prey species. In contrast, perfect food selectivity or purely proportion-based food consumption leads to a collapse of prey functional biodiversity.

Foraging Time:

While the animal is within a patch, it experiences the law of diminishing returns, where it becomes harder and harder to find prey as time goes on. This may be because the prey is being depleted, the prey begins to take evasive action and becomes harder to catch, or the predator starts crossing its own path more as it searches. This law of diminishing returns determines energy gain per time spent in a patch. With time it becomes harder to find prey. Another important cost to consider is the traveling time between different patches and the nesting site. An animal loses foraging time while it travels and expends energy through its locomotion. It is important for an animal that amount of time it should spend in a patch before leaving, this depends upon the amount of energy an animal receives per unit time, more specifically, the highest ratio of energetic gain to cost while foraging. Foraging theory predicts that the decisions that maximize energy per unit time.

2.2.3 Role of Predation in Nature

This is a situation where one organism, the predator, kills another, the prey, for nourishment. This is an important process not only in natural ecosystems, but also in man's life, because he is either a direct predator (as when he catches fish in the sea or hunts game animals in the forest) or has to cope with natural predators that are directly harmful to him or destroy useful prey.

Let us consider the importance of predation in nature. Following are its important roles:

- (i) Predation aids in the distribution of energy fixed by photosynthetic plants through different trophic levels. The 'grass-deer-tiger' food chain would not exist if not for predation! Remember that the grass sees deer as a predator; similarly, a plant sees a sparrow that consumes its seeds as a predator.
- (ii) By selectively preying on competitively superior species and keeping their populations low, predators can reduce the intensity of intraspecific rivalry in a community. This allows the weaker species to survive in the environment.
- (iii) In many biological communities, predators appear to be responsible for sustaining high species variety. The removal of all predators from a population has been shown to result in the extinction of some species and a general decrease in species variety in experiments.
- (iv) Predators have the ability to control the population density of their prey in some circumstances. Predation is obviously not helpful to the individual organism that is killed and eaten as food, but the predator could be quite useful to the prey population as a whole.

In an ideal scenario, prey and predator populations exhibit what are known as 'coupled oscillations' over time. For example, in a habitat with abundant resources, prey populations increase, and predators have more food and generate more offspring as a result. As the predator population in the area grows, more prey is killed, eventually reducing the size of the prey population. Predators are now unable to acquire adequate food due to low prey populations in the habitat, Predation and Mutualism

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and their numbers are beginning to decline. Both prey and predator numbers oscillate as a result of these events. It is vital to note that if the predator is not 'prudent' or 'too efficient' in killing the prey, the situation could turn out to be quite different. Under these circumstances, the predator will hunt out and kill every prey individual, causing the prey species to go extinct, and then starve to death!

If a predator is picky and specialized to the point of relying nearly entirely on a single prey species, we can anticipate the evolution of both prey and predator to be related. In this type of 'co-evolution,' the prey develops defenses to avoid the predator, while the predator develops adaptations to fight those defenses and become more efficient at catching the prey.

2.3 COMPETITION AND NICHE THEORY

Competition is an aspect of life for most organisms. At a bird feeder, seed-eating birds compete for seed, and weeds compete for space in a sidewalk crack. It's a situation in which multiple individuals or populations compete over a restricted resource. As a result of the competition, each individual has less access to the resource. Within and between species, competition can arise. Because they demand the same resources—they occupy the same niche—members of the same species must compete with one another. When members of different species compete, it's because their niches overlap, meaning they share part of the same resources in the same area.

Indirect Competition: Even if they never come into close contact with each other, species can compete. Assume that one bug species eats a particular plant during the day and another species eats the same plant at night. The two species are indirect competitors because they share the same food supply. Similarly, even if the plants do not compete in any other manner, two plant species that flower at the same time may compete for the same pollinators. Although humans rarely contact with the insects that consume our food crops, they are still vying for food with us.

Niche: Because it's difficult to delve into one niche completely, most observations focus on certain aspects of it. It includes everything (e.g. resources an organism needs to meet its energy, nutrient, and survival demands) and every aspect of the way an organism lives with the environment (e.g. the environmental features it needs to hunt and escape successfully). Because an organism's niche is influenced by both abiotic (such as climate and habitat) and biotic (such as competition, parasites, and predators) elements at the same time, ecologists normally look at two types of niches: basic niches and realized niches. The realized niche of an organism is the set of conditions in which it can potentially live and reproduce; the fundamental niche is the set of conditions in which it can potentially survive and reproduce in nature.

Other ways of splitting a niche among groups of similar species have been observed by ecologists. We could expect one species to be more successful than the other when two species with similar niches are placed together in the same ecosystem. The species with stronger adaptations would be able to occupy more of the niche. Adaptations that reduce competition, on the other hand, will benefit species whose niches overlap in the long run. Competition between species can be lessened by splitting the niche in time or space. When each species uses less of the niche than they are capable of using, this is known as niche restriction. Closely related species that share the same resources within a habitat exhibit niche limitation. In the intertidal zone of rocky shorelines, for example, two similar barnacle species compete for space. When the other species are present, one of the species, *Chthamalus stellatus*, is exclusively found in the top level of the zone. *C. stellatus*, on the other hand, is discovered at deeper levels when the other species are removed from the region. When there is competition, a species' actual niche may be less than its potential niche.

2.3.1 Intraspecific and Interspecific Competition

In ecology, competition is a class of relationship in which the presence of another creature influences or reduces the fitness of one organism. The immediate supply of nutrients for development and reproduction for a population of organisms of its own kind or species may exceed the immediate supply of those resources, resulting in competition amongst the connected organisms.

Competition can take both direct and indirect forms, and it is not necessarily a simple relationship. The linked species usually support this form of interaction by sharing shared resources such as nutrients, water, and territory, as well as competing for it. When resources become scarce or insufficient to meet the needs of all those who want it, interactions become more harmful. The magnitude of competition depends on many interacting a-biotic factors and biotic factors in the same ecosystem that affects the structure of the community.

Two types of resources can act as limiting factors:

- (a) Raw materials like organic nutrients and water, which comes under heterotrophs and inorganic food, light and water in autotrophs,
- (b) Habitat to grow hide, from predators etc.

Competition is an area of population ecology involving members of same species as well as members of different species, hence classified either on the basis of species specific competition or on the basis of mechanism involving direct or indirect competition Fig 2.3.



Fig 2.3 Types of Competition

Types of Competition on the Basis of Species

On the basis of type of interacting organisms whether belonging to same species or different species, broadly two types of competition exist.

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i. Intraspecific Competition

In an ecosystem, competition can develop between individuals of the same population fighting for the same type of resources. This interaction, which is also known as scramble competition, explains the availability of resources rather than competition. For example, *Cyprinus carpio*, a type of freshwater fish, compete for food resources in the pond of the Palace of Marrakech in Morocco, resulting in intraspecific rivalry.

Intraspecific competition is usually more harmful and intense than interspecific rivalry. Although the exact process varies between species, populations are governed by a density-dependent regulatory factor. In population ecology, scramble competition causes variations around a specific density of a population. Interference is a type of competition in which one creature prevents another from exploiting resources within a region of the environment. This can be seen, for example, in animals that defend their territories. Space can be viewed as a finite resource, resulting in lower survival, development, and reproduction rates.

ii. Interspecific Competition

Interspecific competition, often known as contest competition, involves interference competition. Interspecific competition occurs when individuals from two different species interact and compete for limited resources. Spotted hyenas and male lions, for example, share the same ecological niche and hence compete with one another.

In honor of the founders of the classical mathematical models of interspecific competition, the logistic model is called as Lotka-Volterra competition equations predicting four possible outcomes based on the assumptions of (a) fluctuation free stable environment, (b) instantaneous effects of competition, (c) migration is not important, (d) stable equilibrium leads to coexistence; (e) and the only important biological factor is competition. The possible outcomes of two interacting species occupying same space as competitors are:

- a. Species A survive and competes with species B leading to its elimination.
- b. Species B survive and competes with species A leading to its elimination.
- c. Both the species survive and eventually co-exist indefinitely. This happens when interspecific competition is less intense then intraspecific competition in both species.
- d. Depending upon the ecological variables at one time, either species can survive leading to extinction of other species.

2.3.2 History of Niche Concepts

The ecological niche has its roots in the more general observation that no two species are alike. In the latter half of the nineteenth century, many naturalists focused on documenting the characteristics that separate one species from another. When two species appeared to be quite similar, it was assumed that differences would eventually emerge that would differentiate each species' particular role in the community. This concept may be found in Darwin's writings, and it has since grown into a fairly wide theory: the principle of competitive exclusion. For much of the twentieth century, the study of ecology has been dominated by the ramifications of this very simple concept.

Throughout the early 1900s, the notion of competitive exclusion and the principle of competitive exclusion grew in lockstep. Volterra (1926) demonstrated that only one species should be able to thrive on a single resource provided certain conditions are met. With two species of Paramecium feeding on a shared supply, Gause (1934) confirmed this idea experimentally. Two species that eat the same resource in the same way can't live together. Grinnell, a renowned naturalist of the North American west, used the term niche in the context of competitive exclusion in 1914. Grinnell's study of the California thrasher illustrates some of the most basic components of a niche

- (a) Type of food consumed (mostly insects, berries at some times of the year),
- (b) Microhabitat preference (beneath shrubby vegetation),
- (c) Physical traits and behaviors used in gathering food (a long beak thrashed through the top layers of soil and leaves), and
- (d) Resources required for shelter and breeding (dense shrubs for night roosting and nesting).

These four basic factors allow one to characterize the basic niche of most animals, and most animals differ with respect to one or more of these factors.

Temperature, substrate type, salinity, pH, and wave exposure are all important niche dimensions for marine organisms. The publication of Elton's Animal Ecology text (1927), thirteen years after Grinnell, cemented the term niche in the ecology lexicon. The concept of the niche, however, was not thoroughly developed as a cornerstone of ecological theory until Hutchinson's (1957) work. Hutchinson's niche is an n-dimensional hyper volume, suggesting that the role of a species in a given habitat is usually defined by a number of parameters, or dimensions. Grinnell's basic niche parameters were mentioned, but they went well beyond that. This foundation spawned a slew of other ecological ideas. A species' core niche includes the resources it would need if it were separated from all potential competitors. The realized niche is a subset of the fundamental niche that comprises the resources that the species in nature really consumes. Competition from other species in the community accounts for the discrepancy between the realized and basic niche.

Niche as the Description of a Species' Habitat Requirements

The ecological niche was characterized by a place a species can take in nature, determined by its abiotic requirements, dietary preferences, microhabitat characteristics (for example, a leaf layer), diurnal and seasonal specialization, or predation avoidance, in the early formulations of the idea. Joseph Grinnell, who coined the word, is largely credited with popularizing it. He was particularly interested in the elements that determine where a species might be found and how niches created by the environment are filled. Understanding and even predicting a species' geographic distribution requires knowledge of its niche, which is dictated by its habitat 3 requirements; consequently, the niche idea is more relevant in biogeography and macroecology than in community or ecosystem ecology.

Niche as Ecological Function of the Species

According to this concept of niche, each species plays a certain role in the dynamics of an ecosystem, and one of these roles can be completed by various species in

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different regions. The observation of distant species adapted to equivalent ecological roles (the resemblance between jerboa and kangaroo rat, many eutherian and marsupial species, or Galapagos finches diversifying to highly specialized roles including those normally taken by woodpeckers) clearly influenced Charles Elton, who emphasized species functional roles. There is a niche for burrowing detritivores, a niche for creatures that specialize in cleaning ticks or other parasites, and a role for pollination, according to Elton. Elton's niche can be applied to a variety of animals, such as 'the niche occupied by birds of prey that consume small mammals.' As a result, the term 'functional niche' refers to a species' location in food webs and trophic chains, and it's especially important in ecosystem ecology.

Niche as a Species Position in a Community

In the second half of the twentieth century, an emphasis on the diversity of biological communities and interspecific competition within them led to the formalisation of the niche concept and an emphasis on the qualities of niches that enable species coexistence within a habitat. Niche, according to George Evelyn Hutchinson, is a 'hypervolume' in multidimensional ecological space dictated by a species' need to reproduce and survive. Each dimension of the niche space indicates an environmental variable that may or may not be relevant for a species' survival. These biotic and abiotic variables can be represented by simple physical values like temperature, light intensity, or humidity, as well as more complex quantities like soil texture, terrain ruggedness, vegetation complexity, or numerous resource attributes. This may simply be seen of as a formalisation of the original Grinnellian niche, i.e. the precise descriptions of species habitat requirements. Ecological niches, on the other hand, are dynamic in the Hutchinsonian view, because the existence of one species constrains the presence of another species through interspecific competition, altering the position of species' niches within the multidimensional space. This concept therefore combines the ecological requirements of the species with its functional role in the local community.

2.3.3 Theory of Limiting Similarity

According to Hutchinson, a species' realised niche is exclusive, meaning that no two species can share a single niche and that given a stable environment, no overlap in realised niches is feasible. In other words, if there is overlap in one dimension of the niche, such as trophic 'dimension,' species will differ in other dimensions, such as abiotic factor tolerance or predator avoidance. Now, the general consensus is that a small overlap between niches is acceptable for cohabitation, but a bigger overlap is not.

The theory of limiting similarity, developed by Robert MacArthur and Richard Levins, predicts the resource consumption curve's minimal allowed degree of overlap (Fig. 2.4). They demonstrated that cohabitation between species using a continuous resource is conceivable when the niche width to distance between species' optima ratio is around unity or smaller. (The competition coefficients were found by the proximity of species' bell-shaped usage curves, and this was derived using the Lotka-Volterra equations explaining the growth rates and thus stability of populations of competing species.) The result, however, is sensitive to assumptions about the resource utilization function's shape and population growth rate: for

example, highly peaked resource utilization functions show almost no limits to coexistence (because their overlap is always minute), and niches can overlap widely when fitness increases as the frequency of individuals carrying the respective trait decreases (negative frequency-dependence). Coexistence of species can also be aided by environmental oscillations that cause frequency or density dependent selection, or when rivals' responses to common variations are nonlinear.



Fig 2.4 Concepts of Distances between Niches, Niche Overlap and Limiting Similarity

Note: The predictions of the limited similarity theory cannot be directly validated by observation since, by definition, if a species pair is close to limiting similarity, the population density of one of the species is close to zero, and so the utilization functions are not observable. Finding a similarity that is larger than expected, on the other hand, would clearly show that some of the model's assumptions have been broken. Between sexually and asexually reproducing species, the spacing between species in niche space, which results from distributing the available resources, vary significantly. Because clones with favourable combinations do not recombine in asexual organisms, those adapted to varied resource combinations can be spaced arbitrarily in the niche space. Individuals in sexual groups have a same gene pool, preventing divergence in adaptive responses to varied resource combinations.

Check Your Progress

- 1. Define competition.
- 2. Mention two types of predation.
- 3. Define niche.
- 4. What is intra-specific competition?
- 5. Define predation.

2.4 MUTUALISM AND ITS EVOLUTION

Another predator-prey interaction that does not result in the prey's death is mutualism. These are more reciprocal exploitations than cooperative connections between individuals, and both interacting species benefit from each other's survival, growth, and reproduction. When it comes to mutually beneficial interacting species, interspecific interactions are more widespread in the tropics, and they are

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characterized by intimate, mandatory contact and often permanent affiliation, which is required for each interacting species' survival, growth, and reproduction.

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As we observed with the ant-acacia system, many plant-animal relationships involve some type of physiological exchange that benefits both species. Ants and acacias is a mutualistic interaction between ants and plants, especially in tropical settings, or with herbivore insects like homopterans. Live American ants can be found in the swelling thorns of acacia trees, providing shelter and nourishment to the ants at all phases of development. Ants defend plants against herbivores that graze on them. Additional interactions that can benefit both plants and herbivores include pollination and fruit dissemination.

Mutualism can be symbiotic or non-symbiotic, and it can be obligatory or voluntary. An obligate non-symbiotic mutualist is reliant on one another, although they live separate lives. Interaction among guilds of species involved in pollen and seed dispersion, where plants reward animals with food, fruit, nectar, and oil, is an example of non-obligatory facultative mutualists. The following are some examples of mutualism:

(a) Obligate Symbiotic Mutualism

Obligate symbiotic mutualists are physically reliant on one another, with one living within the tissue of the other, such as lichens. Some types of relationships are so enduring and obligatory that they blur the lines between interacting populations.

(b) Non-obligatory mutualism / Proto co-operation

A non-symbiotic mutualism, according to earlier literature, is proto-cooperation in which both members of the pair benefit each other but do not dwell together. They frequently have a facultative or opportunistic relationship, and they can thrive without each other. Sea anemones (coelenterates) linked to Pagurus prideauxi shells are an example of proto co-operation (Hermit crab). Crab is used by sea anemones to get to feeding locations, and in exchange, crab is shielded from its predators.

2.4.1 Theory of Mutualism

Mutualistic behaviour improves an individual's inclusive fitness in a species 1 if the benefits of members of species 2 surpass the costs of benefiting species to me. 2. Similarly, mutualistic behaviour improves the fitness of an individual j of species 2 if the advantages of species 1 outweigh the costs of benefiting species for j. 1. This is more likely if the advantage each species delivers to the others is low-cost to donors while high-value to recipients.

To be specific, let the inclusive fitness W_{1i} of member i of species 1, and the inclusive fitness W_{2i} of member j of species 2 be

 $W_{1i} = W_{10} - c_{1i}P_{1i} + b_2P_2(i);$ $W_{2j} = W_{20} - c_{2j}P_{2j} + b_1P_1(j);$

Here, W_{10} is the inclusive fitness of individual i if it does not cooperate, assumed the same for all members of the species: this is the 'base fitness.' P_{1i} is the level of cooperation of i's phenotype, 1 if it cooperates and 0 if not, c_{1i} is the cost of cooperating, $P_2(i)$ is the sum of the levels of cooperation of the members of species 2 with which i interacts, and b_2 is the benefit to i from each individual that cooperates. Likewise for individual j of species 2 Mutualism spreads if

$$b_2 Cov[W_{1i}, P_2(i)] > /c_1 Cov[W_{1i}, P_{1i}],$$

 $b_1 Cov[W_{2i}, P_1(j)] > /c_2 Cov[W_{2i}, P_{2i}],$

In other words, mutualism spreads if

 $b_2r_{21} > c_1, b_1r_{12} > c_2,$

where r_{21} is the regression of the sum of the levels of cooperation of the members of species 2 interacting with i on i's level of cooperation, and r_{12} is the regression of the sum of the levels of cooperation of members of species 1 interacting with j on j's level of cooperation.

Costly mutualism (c1>0, c2>0) only evolves if, on the average, an individual i of species 1 benefits from providing goods or services to species 2 and an individual j of species 2 benefits from providing services to species 1. In other words, the bread an individual casts upon the waters must return to it, or its relatives.

2.4.2 Plant-Pollinator and Animal-Animal Interactions

Mentioned below are the types of interactions:

Plant-Pollinator Interactions

When a flower receives pollen from another flower of the same species, pollination takes place. Our survival depends on pollination. Without pollinators, most of the foods we eat would be impossible to grow. Pollinators are essential for the reproduction and survival of natural fibers, fruits, vegetables, forest products (wood, rubber, vanilla), and flowers. To explain the relationship between a plant and its pollinator, the concepts of coevolution and mutualism need to be understood.

Coevolution happens when two organisms evolve in tight ecological interaction with each other and adapt to the changes in each other. These types of relationships occupy very specific niches in nature. For example, the Andrenid bee is the only pollinator of death camas and is immune to the poisonous nectar. **Mutualism**, on the other hand, is a relationship between two species in which both parties gain. Flowers benefit from having their pollen efficiently dispersed to other flowers of the same species, allowing them to reproduce, in mutualistic connections between flowers and their pollinators. Pollinators benefit from the nourishing pollen and nectar provided by flowers. Flowers and their pollinators are often at odds with one another, despite the fact that they rely on and benefit from one another. Bees, for example, try to transport as much pollen back to their colony as possible for sustenance, whereas flowers must ensure that part of the pollen on the bee's body is transferred to another flower. Some flowers have evolved intricate mechanisms to dust pollen on a visiting bee's back, where it can't reach with its legs to clean itself.

The more exclusive the relationship between a plant species and its pollinator, the better for the plant; if a pollinator only visits one kind of flower, that flower may rest assured that its pollen will reach another of its kind. Many flowers have evolved

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Predation and Mutualism to attract only one type of pollinator while keeping other creatures away from their pollen and nectar. A pollinator may profit from an exclusive partnership since it will not have to compete with other animals for pollen or nectar provided by its flower spouse.

The examples discussed below outlines the typical characteristics of flowers dependent on various types of pollinators:

- (a) Bee-Pollinated Flowers –Red is invisible to bees. Flowers that rely on bees as pollinators are typically yellow, purple, or blue in colour. Furthermore, flowers fertilized by bees often have unique UV reflectance patterns that bees can see well. These patterns are undetectable by humans. The lower lip of bilateral flowers with an upper and lower lip (such as monkey flower, blue-eyed mary, and *Cascade downingia*) may serve as a landing place for pollinators. Bees are the only insects strong enough to pry apart the lips and reach the pollen in some flowers, where the stamens (pollen-producing structures) are contained by the two lips.
- (b) Fly-Pollinated Flowers –Because most flies lack specialized sucking mouthparts, they are limited to feeding from shallow blooms with easily accessible nectar. Bee flies and hover flies, on the other hand, have lengthy mouthparts that are specialized for eating on tubular flowers. Many flypollinated flowers (including the world's largest flower, *Rafflesia arnoldii*, which reaches up to a metre across in Indonesian jungles) smell like faeces or decaying flesh. Flowers of this type are usually a dull brown, purple, yellow, or speckled colour. Flies looking for rotting material to lay their eggs in are drawn to their aroma.
- (c) Butterfly- and Moth-Pollinated Flowers The petals (collectively known as the corolla) of many butterfly-pollinated flowers are fused together to create a tube, and the nectar-producing glands are concealed deep within the flower. Other butterfly-pollinated blooms feature long, backward-pointing spurs, the tips of which produce nectar. The nectar is largely hidden from most would-be nectar-feeders in either arrangement, but it is available to butterflies via their long tongue, which acts as a drinking straw. In fact, there appears to be a strong link between the depth of a flower's corolla tube or spurs and the length of a butterfly's tongue when it visits it. The tongues of many butterflies are nearly as long as their bodies. Butterfly-pollinated flower frequently stretch out at the lip to provide a handy perch for the butterflies. Moths, like butterflies, have lengthy tongues (in fact, some tropical moths have tongues as long as 25 cm). Flowers pollinated by moths resemble those pollinated by butterflies in shape. Moths, on the other hand, are nocturnal, and the flowers they pollinate frequently open at night, are pale in colour, visible in low light, and create powerful scents that appeal to moths' excellent sense of smell.
- (d) Beetle-Pollinated Flowers Beetle pollination is one of the simplest and least specialized forms of animal pollination. Beetles don't have the necessary mouthparts to probe deep inside blooms, therefore they stick to superficial blossoms with easy-to-reach pollen. Beetles rely on their sense of smell more than their eyesight, and their preferred flowers have a sweet perfume but aren't always highly coloured.

- (e) **Bat-Pollinated Flowers** Flowers pollinated by bats typically bloom only at night, when bats are most active. These blooms have a powerful smell and are drab or pale in colour. To withstand the weight of a clinging bat, they are usually huge and strong. Bat-pollinated flowers are uncommon in our area, but they are prevalent in the tropics and deserts.
- (f) Wind Pollinated Plants- Pollen is blown from one plant to another during the process of wind pollination. Pollen is typically light, silky, and produced in large quantities to maximise pollination chances. Plants that rely on wind for pollination have long stamens and pistils to capture the pollen floating in the air. They don't need to support or attract pollinators, thus they don't have petals or colourful flowers.
- (g) Water Pollinated Plants- This sort of pollination is less prevalent than the others mentioned. In nature, it occupies a considerably smaller niche. Water pollination happens when pollen floats from one flower to another on the surface of a stream, pond, or vernal pool.
- (h) Human Pollinated Plants- Humans play an important part by acting as pollinators for agricultural and horticultural plants. Humans may also come into contact with wild plants, allowing pollen to become airborne or carry pollen on their clothing from one location to another.

Animal-Animal Interactions

A mutualistic relationship is when two organisms of different species 'work together,' each benefiting from the relationship. Examples of mutualism among animals are:

- (a) The oxpecker (bird) and the rhinoceros or zebra. Ticks and other parasites that dwell on rhinos and zebras are eaten by oxpeckers. The oxpeckers get fed, and the creatures get rid of the pests. The oxpeckers also fly upward and shout a warning when there is danger, which aids the symbiont (a name for the other partner in a relationship).
- (b) *Heteractis magnifica* are one of ten species of anemones to host anemone fish, most coming from the genus Amphiprion. Mutualism is the term used to describe a connection in which both organisms benefit. The clownfish will benefit from the anemone's protection, such as sheltering within its stinging tentacles, and laying its eggs beneath the oral disc overhang for added security. As a result, the clownfish will assist in chasing away any predators who might try to eat the anemone, as well as providing it with nutrients from its own waste.
- (c) The shrimp-crab symbiotic connection with *Heteractis magnifica* is limited. The shrimp and crab are limited to scuttling under the oral disc overhang because they are not 'immune' to the stinging tentacles. They clean the underside of the anemone and seek for microscopic pieces of food.
- (d) Human beings also interact with *Heteractis magnifica*. This anemone species is one of the most popular in home aquariums. They are frequently sold to distributors right from the water. The Ritteri Anemone is one of the most difficult kinds of anemone to keep healthy, despite their ability to thrive in aquaria. People like to own *Heteractis magnifica* because clownfish take to them so easily, despite the fact that it is a lot of labour.

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(e.g., *Leidyopsi sp.*) synthesize cellulose and, as a result, digest the wood consumed by the host. The chemicals excreted as a byproduct of the flagellates' metabolism are used by the termites. The termites die even if they continue to eat wood if they are defaunated by exposing them to high temperatures or high oxygen concentrations, both of which are poisonous to the flagellates.

- (f) The relationship between the wood-roach Cryptocercus and its mutualistic flage-llates involves more than the dietary story. Here the roach's molting hormone ecdyson influences the sexual cycle of the flagellates.
- (g) Although blood-sucking leeches are unable to digest blood, their intestinal flora, which are restricted to the leech gut, assist their hosts in digestion. From the examples given above, it appears that mammals, bacteria, fungi, algae, and plants exhibit a remarkable diversity of mutualistic associations.
- (h) Humans and other mammals have bacteria in their intestines and on their bodies. The bacteria are provided with nourishment and a place to live, while their hosts benefit from digestive benefits and are protected from dangerous microorganisms. Humans and microbes, such as yeast and bacteria, have a mutualistic relationship. Countless bacteria reside on your skin in mutualistic or commensalistic relationships (helpful to the bacteria but not to the host). Bacteria that live in mutualistic symbiosis with humans protect humans from pathogenic bacteria by preventing harmful bacteria from invading their skin. The bacteria obtain nutrition and a place to live in exchange. Some bacteria found in the human digestive system coexist with humans in a mutualistic relationship. These bacteria help to digest organic molecules that might otherwise go undigested. Vitamins and hormone-like substances are also produced by them. These bacteria are vital for the development of a healthy immune system in addition to digesting. The bacteria profit from the collaboration because they have access to resources and a safe environment to flourish in.

2.4.3 Basic Models

Although mutualism is widespread in nature, the theoretical, mathematical work in this area is not quite as prolific as the theoretical work related to predation and competition. Early attempts at modelling mutualism included altering negative coefficients to positive coefficients in a Lotka-Volterra type model to depict mutualism rather than competition. Murray succinctly explains this, and gives the following model as one of the easiest attempts to convert a traditional Lotka-Volterra model to a mutualism model:

$$\frac{dx(t)}{dt} = ax(t) + bx(t)y(t),\tag{1}$$

$$\frac{dy(t)}{dt} = cy(t) + dx(t)y(t), \qquad (2)$$

where x(t) and y(t) are the population sizes of the interacting species at time t, and a, b, c, d are positive constants. The problem that can occur with this approach, as can be seen from this example, is that both dx/dt and dy/dt are positive, leading to unbounded growth.

To make these models more realistic, various constraints must be added, such as weak or asymmetric interaction strengths, to guarantee the presence of a positive steady state (the stable coexistence). While these criteria in Lotka-Volterra models can prevent unbounded growth, they also indicate that mutualism has little impact on population dynamics. Mutualism has been viewed as an interesting interaction, but one that is less important to ecological dynamics than predation or competition, as a result of these theoretical results.

A model is described where the mutualist decreases the density dependence in the per capita birth rate of the other species. Consider the existence of a species, whose population at a given moment in time is described by the continuous function $N_1(t)$. Suppose that the per capita birth rate decreases with density, so that it may be described by the relationship

$$B_1(t) = b_0 - bN_1(t),$$
 (3)

where both b_0 and b are positive constants. We also impose the restriction that $B_1(t) \ge 0 \forall t \ge 0$. Similarly, we suppose that the per capita death rate increases with density, and once again the constants we introduce are positive, with a restriction that $D_1(t) \ge 0 \forall t \ge 0$:

$$D_1(t) = d_0 + dN_1(t).$$
 (4)

Therefore a growth rate of $(B_1(t) - D_1(t))N_1(t)$ leads to the very familiar logistic differential equation

$$\frac{dN_1(t)}{dt} = rN_1(t) - \frac{r}{K}N_1^2(t),$$
(5)

Where $r = b_0 - d_0$, $K = \frac{b_0 - d_0}{b + d}$.

The introduction of r and K in this manner helpfully reduces the number of parameters. We now introduce a facultative mutualist, i.e. a second species given by $N_2(t)$ where, although interactions between members of $N_1(t)$ and $N_2(t)$ provide a benefit to both populations, the interactions are not essential to the survival of either species. The benefit that $N_2(t)$ provides to $N_1(t)$ is realized through its ability to decrease the density dependence in the per capita birth rate of N_1 :

$$B(t) = b_0 - \frac{bN_1(t)}{1 + \alpha_{12}N_2(t)}.$$
(6)

The interaction therefore has no effect on the per capita death rate of $N_1(t)$. Taking a symmetrical approach to constructing a differential equation for describing the $N_2(t)$ population yields the model discussed as:

$$\frac{dN_1(t)}{dt} = \left(r_1 - \frac{b_1 N_1(t)}{1 + \alpha_{12} N_2(t)} - d_1 N_1(t)\right) N_1(t),$$

$$\frac{dN_2(t)}{dt} = \left(r_2 - \frac{b_2 N_2(t)}{1 + \alpha_{21} N_1(t)} - d_2 N_2(t)\right) N_2(t). \tag{8}$$

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(7)

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Both models avoid the absurd scenario of reciprocal benefaction's emergence, which is found in many Lotka-Volterra-based mutualism models. They do, however, have diverse mutualistic mechanisms and biological meanings.

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Direct interactions are defined as physical interactions between two species, such as a plant relying on an animal or bird to transport its seeds to another location, thereby providing a food source for the animal and dispersing the seed to increase the plant's population level and geographic spread (positive interaction) (again, positive interaction). Instead of two species physically engaging, a third species (potentially more) delivers the mutualistic effects in indirect contacts.

2.5 POPULATION REGULATION: EXTRINSIC AND INTRINSIC MECHANISM

Every population on the planet has a growth limit. And, while humans are giving the concept of unlimited growth a run for its money, we, too, will eventually face environmental constraints on population numbers.

Extrinsic and Intrinsic Factors: Field studies of mechanisms involved in population regulation have tended to focus on the roles of either intrinsic or extrinsic factors, but these are rarely mutually exclusive and their interactions can be crucial in determining dynamics. While intrinsic factors act from within an individual, extrinsic factors wield their influence from the outside (i.e., they are environmental, cultural, or related to lifestyle). Ecosystems with low diversity and physically stressed or subjected to extrinsic perturbations populations tend to be regulated by physical components such as weather, Water currents, chemical limiting factors and pollution, etc. Among the extrinsic factors the most important role is played by weather.

These factors can act in two ways:

- (i) Density-dependent limiting factors
- (ii) Density-independent limiting factors

What are these environmental limiting variables, exactly? There are two types of factors that control population growth: density-dependent and density-independent.

Density-Dependent Limiting Factors

Consider a population of organisms—say, deer—which have consistent access to a fixed amount of food. When the population is tiny, the restricted food supply will be sufficient for all. However, if the population is large enough, the restricted food supply may become insufficient, resulting in deer competition. Some deer may die of famine or fail to have offspring as a result of the competition, lowering the per capita—per individual—growth rate and causing population numbers to level or fall.

Food rivalry is a density-dependent limiting factor in this scenario. In general, density-dependent limiting factors are those that have a varying effect on a population's per capita growth rate depending on how dense the population is already. As the population grows, most density-dependent factors cause the per capita growth rate to slow. This is an example of population growth being stifled by negative feedback.

The logistic pattern of growth, in which a population's size levels out at an environmentally determined maximum called the **carrying capacity**, can be caused by density-dependent limiting factors. This isn't always a smooth process; in some situations, the population may exceed carrying capacity and be pushed back down by density-dependent factors.



Fig 2.5 Logistic Growth

Density-dependent limiting factors tend to be biotic—living organismrelated—as opposed to physical features of the environment. Some common examples of density-dependent limiting factors include:

- Competition within the Population: When a population reaches a high density, more people are competing for the same limited resources. Competition for food, water, shelter, mates, light, and other resources required for survival and reproduction might occur as a result of this.
- **Predation:** Predators may be attracted to higher-density populations that would not bother with a sparse population. When these predators eat members of the population, they reduce the population's size while potentially increasing their own. This can result in cyclical patterns that are interesting to look at.
- **Disease and Parasites:** Disease is more likely to break out and result in deaths when more individuals are living together in the same place. Parasites are also more likely to spread under these conditions.
- Waste Accumulation: High population densities can lead to the accumulation of harmful waste products that kill individuals or impair reproduction, reducing the population's growth.

Behavioral or physiological changes in the creatures that make up the population can also be examples of density-dependent control. Lemmings, for example, respond to excessive population density by departing in large groups in pursuit of a new, less congested home. Because the lemmings occasionally drown while attempting to cross bodies of water, this procedure has been misconstrued in popular culture as a form of mass suicide. NOTES

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Density-independent Limiting Factors

The second group of limiting factors consists of density-independent limiting factors that affect per capita growth rate independent of how dense the population is. Take, for example, a wildfire that breaks out in a forest where deer live. Regardless of population size, the fire will kill any unlucky deer present. The likelihood of a deer dying is unaffected by the number of other deer present. Natural disasters, extreme weather, and pollution are common density-independent limiting factors.

Density-independent limiting factors, unlike density-dependent limiting factors, cannot maintain a population at constant levels on their own. That's because their strength is independent of population size, thus when the population grows too high, they don't make a 'correction.' Instead, they may result in irregular, sudden population changes. Small populations may be vulnerable to rare, density-independent shocks that wipe them off.

Population Fluctuations

Many density-dependent and density-independent limiting variables can interact in the actual world to produce the patterns of change we witness in a population, and they typically do. For example, density-dependent factors may keep a population near carrying capacity for a while before a density-independent event, such as a storm or fire, causes a sharp decline in population.

Even in the absence of natural disasters, populations do not always remain constant at carrying capacity. In truth, population density can fluctuate or vary in a variety of ways. The numbers of some people fluctuate erratically. Algae, for example, may flourish if an input of phosphorus causes population growth that is unsustainable. Other populations experience boom and bust cycles on a regular basis. Let's look at these cycles in more detail.

Population Cycles

Some populations have cyclical size fluctuations. Cyclical oscillations are periodic increases and decreases in the population size. If we plotted population size with time for a population with cyclical oscillations, we'd get something like this.



Fig 2.6 Population Size with Time

Where do these oscillations come from? In many cases, oscillations are produced by interactions between populations of at least two different species. For instance, predation, parasite infection, and fluctuation in food availability have all been shown to drive oscillations. These density-dependent factors don't *always* create oscillations. Instead, they only do so under the right conditions, when populations interact in specific ways.

2.6 CASE STUDIES IN POPULATION DYNAMICS: FISHERIES, WILDLIFE AND BIOLOGICAL CONTROL OF AGRICULTURE PESTS

Following are the case studies in population dynamics:

1. Population Dynamics of Fish Species in a Marine Ecosystem: A Case Study in the Bohai Sea, China

For many fish species, coastal environments provide essential spawning, feeding, and nursery grounds, as well as vital fishing grounds for humans. These ecosystems account for around a quarter of global primary productivity and 90 percent of global catch. More than 90% of China's marine fisheries catch has been caught in its coastal seas since the 1950s. The Bohai Sea is a Chinese inland sea that served as the 'fisheries cradle' for both the Bohai and Yellow Seas. Overfishing has drastically reduced fisheries in the Bohai Sea during the last 30 years. Furthermore, the fast expansion of the Bohai Sea's coastal industry has exposed the coastal ecosystem to a variety of stressors, including large-scale reclamation throughout the whole coast. This reclamation, which is being caused by the construction of the Caofeidian Industrial District, will cover 310 km² by 2020, directly affecting wetlands, intertidal zones, and the gulf, as well as creating further loss and fragmentation of vital fish habitat. Most of the coastal waters in the Bohai Sea have seen eutrophication, increasing exposure to elevated concentrations of heavy metals, persistent organic pollutants, and other emergent contaminants as a result of land-based pollution. There is evidence that these contaminants have resulted in a significant decline in the hatching and survival rates of fisheries-targeted fish (referred to as 'fishery species'), resulting in lower population growth rates and abundance. Furthermore, reduced flow from the Yellow River, Liao River, Hai River, and other rivers has harmed fish habitat along the Bohai Sea coast, producing changes in water temperature and salinity, as well as reduced sedimentation. Furthermore, large-scale mariculture has had a direct influence on important fish habitat and the food base for some fish species, as well as eutrophication and accompanying algal blooms. Changes in the Bohai Sea have put more stress on the coastal ecology and lowered fish harvests. The fish and fisheries of the Bohai Sea have been the subject of numerous research. Retrospective studies in the Bohai Sea demonstrate that the fishing resources have shown signs of depletion. (1) abrupt shifts in species dominance; (2) decreased species abundance; (3) juvenation of spawning populations; (4) reductions in the size at age in some species; and (5) a decrease in both the species diversity and trophic structure. In this study, we conducted a retrospective analysis of fish data from surveys in the Bohai Sea to (1) evaluate the temporal population dynamics of fish species; (2) document changes in the fish community; (3) identify shifts in species dominance; and (4) describe changes in the sizes of ecological niches. The results provide scientific information related to the conservation and management of fishery resources in coastal waters.

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2. Population Dynamics: The Foundation of Wildlife Damage Management for the 21st Century

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The global population is growing at an unprecedented 90 million people per year. Similarly, due to land-use changes and effective management programmes by public and private agencies, dramatic increases in populations of many wildlife species such as Canada geese (*Branta canadensis*), gulls (*Lams spp.*), white-tailed deer (*Odocoileus virginianus*), double-crested cormorants (*Phalacrocorux auritus*), and beaver (*Castor canadensis*) have occurred in North America over In an increasingly crowded world, these simultaneous population booms ultimately lead to confrontations between wildlife and humans.

Managing these conflicts is an intricate, difficult process because of four factors: 1) The science of wildlife management is complex, particularly understanding and predicting the behavior, population dynamics and economic/health impacts of wildlife species. 2) Wildlife biologists study and manage sentient, adaptable and secretive organisms, requiring the development of many complex, labor-intensive tools and techniques to census, monitor, and measure. 3) The sociological aspects of wildlife management are diverse and emotional, particularly the oftentimes polarized views of society regarding the killing and management of wildlife species. 4) The regulatory aspects of wildlife management can be almost overwhelming, particularly regarding the legal status of wildlife, National Environmental Policy Act (NEPA) processes, and the registration of chemicals as management tools.

3. Case Study: Hymenoptera Parasitoid Agent for the Control of *Agrilus Planipennis*

Agrilus planipennis Fairmaire (Coleoptera: Buprestidae) originates from Far-East Asia and is primarily a pest of Fraxinus (ash). It was detected in North America (USA and Canada) in 2002 and in the European part of Russia (Moscow region) in 2005. It is a serious pest of Fraxinus where it has been introduced outside its native range. It has caused extensive ash mortality in North America and in the Moscow area and is spreading in all introduced areas.

Agrilus planipennis: normally it oviposits on live trees and has been found ovipositing on freshly cut ash logs on rare occasions, albeit larvae developing from such eggs seldom complete their development. There are four instars in the larval stage. The larvae of the first instar crawl through the bark to the cambium. The larvae then feed on the inner bark and sapwood of the tree. They make S-shaped tunnels (up to 26-32 cm long) that are packed with frass. Pupal cells are found at the end of the larval gallery in the outer sapwood or outer bark. Pupae are mostly found in the sapwood when the bark is thin. When the bark is thick, however, the outer bark contains more pupal cells. Adults remain under the bark for 1-2 weeks after eclosion ('callow adults') before exiting through D-shaped apertures. Adult emergence normally occurs after a period of 230-260 degree-days at a temperature of 10°C.

All life stages (except adults) are difficult to detect since they are hidden (eggs in bark fissures; larvae, prepupae, and pupae in the bark or sapwood; callow adults in the bark or sapwood). Trees that are infested do not show obvious symptoms until they have been badly harmed. Symptoms may not appear for another 2-3 years or longer after the initial attack, especially if the infestation starts
in the upper section of the tree. Although emerging adult-produced D-shaped exit holes are evident after the first year of infection, they are usually few in number and located high in the canopy (i.e., not clearly apparent) on bigger trees. First emergence, and therefore the appearance of D-shaped holes, will be delayed if the individuals develop over more than one year.

Under this scenario, a parasitic hymenoptera has been collected from the native range of the pest and scientists tentatively identified the species to facilitate its import into quarantine. Apart from this no additional research has been conducted.

Based on this scenario answer the following questions:

- i. Which legislation applies to this scenario?
- ii. Which international or regional standards are relevant?
- iii. What additional information is needed to make a decision? In what format should that information be provided and by whom?
- iv. Who carries out the analysis and using what methodology?
- v. Who evaluates the analysis?
- vi. Who should make the decision and who should be consulted?

Check Your Progress

- 6. Define pollinator.
- 7. What is population growth?
- 8. Define mutualism.
- 9. Define obligate symbiotic mutualism.
- 10. What is population fluctuation?

2.7 ANSWERS TO 'CHECK YOUR PROGRESS'

- 1. Competition is an interaction between organisms or species in which both the organisms and species are harmed. Limited supply of at least one resource (such as food, water, and territory) used by both can be a factor.
- 2. The two commonly recognized types of predation are: (1) carnivore, (2) parasitism
- 3. Niche is the match of a species to a specific environmental condition. It describes how an organism or population responds to the distribution of resources and competitors and how it in turn alters those same factors.
- 4. Intra-specific competition is an interaction in population ecology, whereby members of the same species compete for limited resources. This leads to a reduction in fitness for both individuals, but the fitter individual survives and is able to reproduce.
- 5. Predation is a biological interaction where one organism, the predator, kills and eats another organism, its prey.
- 6. A pollinator is anything that helps carry pollen from the male part of the flower (stamen) to the female part of the same or another flower (stigma).

Predation and Mutualism

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- 7. Population growth is the increase in the number of individuals in a population.
- 8. Mutualism is defined as an interaction between individuals of different species that results in positive (beneficial) effects on per capita reproduction and/or survival of the interacting populations.
- 9. Obligate symbiotic mutualism is a type of mutualism in which the species involved are in close proximity and interdependent with one another in a way that one cannot survive without the other.
- 10. Populations rarely grow smoothly up to the carrying capacity and then remain there. Instead, fluctuations in population numbers, abundance, or density from one time step to the next are the norm.

2.8 SUMMARY

- In predation, one organism kills and consumes another. Predation provides energy to prolong the life and promote the reproduction of the organism that does the killing, the predator, to the detriment of the organism being consumed, the prey.
- In ecology, predators are those animals that live by preying on other organisms for food.
- Optimal Foraging Theory (OFT) is a behavioral ecology model that helps predict how an animal behaves when searching for food.
- Competition is a relationship between organisms in which one is harmed when both are trying to use the same resource related to growth.
- Intraspecific competition occurs when members of the same species compete for the same resources in an ecosystem.
- Interspecific competition, in ecology, is a form of competition in which individuals of different species compete for the same resources in an ecosystem (e.g. food or living space). This can be contrasted with mutualism, a type of symbiosis.
- The natural world is filled with plants and animals, each with their own special job or niche. A niche is the role played by an organism in the natural world.
- A mutualistic relationship is when two organisms of different species 'work together,' each benefiting from the relationship. One example of a mutualistic relationship is that of the oxpecker (a kind of bird) and the rhinoceros or zebra.

2.9 KEY TERMS

- **Foraging:** This behavior includes all the methods by which an organism acquires and utilizes sources of energy and nutrients.
- **Mutualism:** It is defined as an interaction between individuals of different species that results in positive (beneficial) effects on per capita reproduction and/or survival of the interacting populations.

- **Competition:** It is an interaction between organisms or species in which both the organisms and species are harmed. Limited supply of at least one resource (such as food, water, and territory) used by both can be a factor.
- **Predation:** In predation, one organism kills and consumes another. Predation provides energy to prolong the life and promote the reproduction of the organism that does the killing, the predator, to the detriment of the organism being consumed, the prey.
- Inter-specific competition: Interspecific competition, in ecology, is a form of competition in which individuals of different species compete for the same resources in an ecosystem (e.g. food or living space). This can be contrasted with mutualism, a type of symbiosis.
- **Pollinator:** A pollinator is anything that helps carry pollen from the male part of the flower (stamen) to the female part of the same or another flower (stigma).

2.10 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

- 1. Which groups of natural enemies are better for biological control, predatorparasitoid or pathogen?
- 2. How can predators cause problems?
- 3. What is the concept of prey selectivity and the effect of diet on growth?
- 4. What factors affect optimal foraging?
- 5. Does food availability in a certain area affect the bee's swarming?
- 6. How do flowers and pollinators interact? How well understood is the contribution of wasps, hover-flies and other insects to pollination?
- 8. How do plants and pollinators benefit each other?
- 9. What is meant by population regulation?

Long-Answer Questions

- 1. Explain how animals deal with storing food in another experimental patch?
- 2. How to check if the data follows the Lotka-Volterra (predator-prey) model distribution? Describe.
- 3. What are two important factors that animals should consider when foraging? Explain.
- 4. Explain how the environmental condition affect the foraging activity of honeybees?
- 5. Describe the reasons why animals make better choices in patch-leaving problems?

Predation and Mutualism

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- 6. Discuss the different ways to regulate the population amongst animals.
- 7. Write a detailed note on the four controls that regulate population size.

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|2.11 FURTHER READING

- Preston, Samuel. Patrick Heuveline and Michel Guillot. *Demography: Measuring and Modeling Population Processes*. London: Wiley-Blackwell.
- Begon, Michael, Martin Mortimer, and David J. Thompson BA. *Population Ecology: A Unified Study of Animals and Plants, Third Edition.* Hoboken: Blackwell Science Ltd.
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UNIT 3 INTRODUCTION TO ANIMAL BEHAVIOUR

Structure

- 3.0 Introduction
- 3.1 Objectives
- 3.2 Historical Perception of Animal Behaviour
- 3.3 Types of Animal Behaviour
 - 3.3.1 Innate or Inherent Behaviour
- 3.4 Perception of the Environment
- 3.5 Neural and Hormonal Control of Behaviour3.5.1 Nervous Systems and the Study of Behaviour
 - 3.5.2 Behavioral Endocrinology
- 3.6 Genetic and Environmental Components in Development of Behaviour
- 3.7 Communication
- 3.8 Answers to Check Your Progress
- 3.9 Summary
- 3.10 Key Terms
- 3.11 Self Assessment Questions and Exercises
- 3.12 Further Reading

3.0 INTRODUCTION

The word 'ethology' comes from two Greek words: 'ethos,' which means 'culture,' and 'logos,' which means 'study.' In order to survive and reproduce, an animal's behaviour might be defined as the visible behaviours that it engages in in response to diverse stimuli. Signs/symbols or releases can be used as a trigger. Signs might take the form of visual, aural, chemical, or other sensory models. There can be two different types of behaviour-1. Innate: this is inherent or these are genetically determined fixed action patterns; 2. Learned: these types of behaviour are flexible and can be modified by practice or experience. Innate behaviors are rigid and predictable and usually involve basic life functions, such as caring for offspring, so they often are necessary for successful reproduction. Even if the stimulus is no longer there, once a predetermined action pattern is activated by a stimulus, the sequence continues until it is finished. As a result, most behaviour is stimulusresponse focused. An organism's behaviour is fundamentally an expression of its neurological system's capabilities. While the type of the stimulus is decided by the environment, the response is determined by the body, particularly the neurological system of the organism, which is genetically determined.

Animals' most fundamental life processes rely heavily on communication. This viewpoint emphasizes that communication is one of two mechanisms by which all animals adapt to and thrive in their surroundings. Communication takes numerous forms and has many roles, but there is still a lot of similarities in terms of basic communication dynamics and the services they provide for biological systems.

> Self - Learning Material

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In this unit, you'll learn how behaviour is best understood as the consequence of evolutionary processes that sometimes establish behavioural instructions for animals through genetic coding and other times develop flexible mechanisms that allow animals to handle challenges unique to their environment.

3.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand innate behaviour
- Discuss environmental perception on animal behaviour
- Explain neural, hormonal, genetic and environmental control of animal behaviour
- Understand communication and its types amongst animals

3.2 HISTORICAL PERCEPTION OF ANIMAL BEHAVIOUR

The history of ethology is as old as mankind because human beings were hunter gathers and they have revealed the animal behaviour in the paintings on the walls of excavated caves of pre-historic times. Aristotle (372BC), a brilliant Greek philosopher, was the first to write an accurate explanation of animal behaviour in his work '*Historia Animalium*,' which means 'The History of Animals.' He meticulously observed animal behaviour, yet the conclusions he made from his findings were erroneous. Because of the near resemblance between the two species, he claims that Redstarts transform into robins in the winter. During the winter, Redstarts did migrate. Another keen observer of animal behaviour was William Harvey, a 17th century scientist who studied the breeding, nesting and incubation behaviour of many birds.

Gilbert White (1720-1793), an English vicar, meticulously recorded human and animal behaviour, particularly that of swallows. He, like Aristotle, was unable to use a scientific technique to interpret his findings. During the winter, he believed swallows buried themselves in the muddy bottom. As the swallows congregate in the reef beds before migrating at night, he came to this conclusion.

In his book, '*The Expression of Emotions in Man and Animals*,' Charles Darwin (1809-1889) is credited with being the first to do a scientific study of animal behaviour. This book described animal behaviour in detail and is now considered a classic. He claimed that the same natural selection laws that regulate the physical evolution of creatures applied to phylogenies of behavioural development. After Darwin's theory of natural selection was published, it provided the study of animal behaviour a fresh drive and a new direction. The application of natural selection laws to ethology opened up new avenues for bettering our understanding of animal behaviour. John Romanes, Darwin's student, wrote an excellent book on 'Animal Intelligence' after his death.

Early ethological research was based on observations of pets, domestic animals, and farm animals. Oskar Heinroth (1871-1945), a German zoologist who spent his life to researching water fowls, ushered in a fundamental shift in the way we study behaviour in the wild. In his work '*Ethology of Anatidae*,' he enumerated his findings. The writings of three famous ethologists, Karl Von Frisch of Germany, Konrad Lorenz, an animal Psychologist in Vienna, Austria, and Niko Tinbergen, a Zoologist in Holland, brought ethology to its pinnacle of fame. In 1972-73, these three were awarded the Nobel Prize in Physiology or Medicine for their outstanding contributions to animal behaviour. They are also acknowledged with introducing a completely new branch of science to Zoology and popularising it among the general public. I. P Pavlov (1849-1936), a Russian physiologist, achieved worldwide acclaim for his work on condition reflex observations in psychological studies on learning before Fischer, Konrad, and Tinbergen.

Karl Von Frisch (1886-1982), a German scientist, revealed his well-known research on honeybee communication. He explained how foraging bees use the bee dance to communicate distance, location, and kind of food items.

Konrad Z Lorenz (1903), founding father of ethology developed a theory on animal behaviour which stressed its inherited aspects and relative fixity. He formulated imprinting behaviour in goselings. His books, 'King Solomon's ring' and 'Man meets dog' demonstrates his deep understanding on animal behaviour.

Niko Tinbergen (1904), a Dutch ethologist who co-founded contemporary ethology with Lorenz, is known for his research on instinctual behaviour. He studied stickleback fish courting behaviour, food begging in sea gull chicks, and digger wasp nesting behaviour.

B. F. Skinner (1904), an American psychologist, conducted considerable research in caged rats on learning by reward or reinforced learning. Skinnerian Psychology was born as a result of this.

3.3 TYPES OF ANIMAL BEHAVIOUR

Animal behaviour, the concept broadly considered, referring to everything animals do including movement and other activities and underlying mental process can be categorized into two main types:

- 1. Innate or inherent behaviour or
- 2. Learned or acquired behaviour

Learned or acquired behaviour can be defined as an adaptive change in individual behaviour as a result of experience. The degree of permanence of newly acquired learned behaviour patterns depends on memory storing information gained from the experience. Learning alters the range of behaviors shown by an individual, and allows it to adapt to and control its environment. Introduction to Animal Behaviour

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Let us discuss innate behaviour in more detail

3.3.1 Innate Behaviour

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It's also referred to as innate behaviour. It entails a predictable, species-specific, genetically controlled, and experience-independent sequence of actions. This form of behaviour is known as stereotyped behaviour because it follows a fixed pattern (FAP) that is predictable and found in all individuals of a species.

Characteristics of Innate Behaviour

- 1. Pattern of behaviour is inherited. It is passed on from parents to offsprings.
- 2. It is unlearned behaviour.
- 3. It occurs in all the members of a species hence it is species specific and predictable.
- 4. It is not dependent on past experience as it is an inborn response to a stimulus.
- 5. It takes place in individuals even when kept in isolation away from their fellow members.
- 6. Innate behaviour has high adaptability and survival value.

Types of Innate Behaviour

There are different types of innate or stereotyped behaviour:

- 1. Taxis
- 2. Kinesis
- 3. Reflexes
- 4. Instincts

1. Taxis

Taxis are the most basic form of innate behaviour. It is an animal's response to a stimulus source in which it is oriented (either towards or away). Positive taxis are those that are oriented towards the stimulus, whereas negative taxis are those that are oriented away from the stimulus.

The taxis are usually named after stimuli. As a result, we have phototaxis, chemotaxis, thermotaxis, geotaxis, and so on. Positive phototaxis occurs when a plant or animal moves towards light. Negative phototaxis is seen in burrowing animals such as rats and planaria that migrate away from the source of light.

Example for positive phototaxis: The protozoan, Euglena response to a variety of stimuli and is very sensitive to light. It swims towards light, hence it shows positive phototaxis. It is able to respond positively to the source of light stimulus due to the presence of the paraflegellar body, a photoreceptor located in front of the eyespot or stigma. This behaviour is of distinct advantage to the animal because light is necessary for assimilation of CO_2 by the chlorophyll. If a dish containing Euglena is covered on one half and the other half is exposed to light it is seen that euglena will avoid the dark region and will aggregate in the bright region of the dish.

Example for Negative Phototaxis: Maggots that are about to pupate moves away from light source towards a dark location hence they show negative phototaxis. When maggots are kept on a surface illuminated by a beam of light, it will move away from the source of light more or less in a straight line.

2. Kinesis

Kinesis is a type of locomotory behaviour in relation to the source of stimulus. The animal responds to the variation in the intensity of the stimulus and not the source of direction of the stimulus. To respond to such stimulus the animal only requires sense organs sensitive to variation in stimulus intensity.

There are two types of kinesis:

a) **Orthokinesis:** It is a response that involves changes in the speed of movement of the whole body in response to stimuli like humidity, preserve and diffused light.

Eg: Wood louse, *Porcellerio scaber*, a small crustacean that live in damp areas, and they tend to lose water from their body fairly rapidly when exposed to low humidity. When wood lice are kept at the junction in a choice chamber where one side has high humidity and the other half has low humidity. It is noticed that after a short while the wood lice begin to move and the speed of movement and the rate of turning is greatest in the driest part of the chamber and least in the humid part. This increased and apparently random movement is an attempt by the animal to remain in the most favorable environment.

b) Klinokinesis: In this the speed of locomotion remains constant but the rate at which the animal changes direction depends on the intensity of the stimulus.

Eg: A **planaria** changes its direction ever so often as it crawls. If the light intensity above the animal is increased it changes direction more frequently but moves at the same speed. The increase in rate of turning falls after sometime but increases again with a further increase in the intensity of light.

3. Reflexes

A simple movement of a part of the animal in response to a stimulus is called reflex. It is a quick, innate and immediate response of a part of the body to an external or internal stimulus, which has great adaptive and survival value to the organism. Reflexes are inherited and unlearned behaviour found in all members of the species. The knee-jerk, constrict of pupil of eye in the bright light, blinking of eye, peristalsis, coughing, etc., in man, flight in birds, web spinning in spiders are all examples of reflexes. The main advantage of reflex is it enables the animal to respond immediately to harmful stimuli hence it has great adaptive and survival value

4. Instinct

Instinct is the most complex type of stereotyped behaviour which is unlearned, predictable, genetically controlled and species specific and it is in response of a sign or releaser stimuli. It is the result of both external stimuli and inner environmental conditions. External stimuli represent environmental factors like temperature,

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photoperiods, suitable nesting material, food sources. The internal conditions refer to the levels of hormones in the blood. Eg: building of nest by birds, singing to attract males, territoriality, migration, parental care, etc.

Check Your Progress

- 1. Define ethology.
- 2. What is innate behaviour?
- 3. Define orthokinesis.
- 4. Give three examples of innate behaviour.
- 5. What is an instinctive behaviour?

3.4 PERCEPTION OF THE ENVIRONMENT

Environmental perception is the process of analyzing and storing information about the environment, as well as the method in which an individual experiences the environment. Individuals make decisions based on how they perceive the environment rather than how it actually is. Warm feelings for an environment, information sorting, and an understanding of the world, however subjective, are all characteristics of such perception. The sensory system detects signals from the environment and relays them to the nervous system, which then sends them to the body. External inputs are translated into changes in membrane potentials by specific sensory receptor cells in the sensory system. If the changes in membrane potential are sufficient to elicit an action potential, the action potentials are subsequently conveyed to the CNS for processing through neurons in the afferent division of the PNS. Through the efferent division of the PNS, the CNS integrates and analyses incoming signals in order to affect a response to the appropriate bodily systems.

(a) Mechanical

Mechanoreception, an animal's ability to perceive and respond to particular types of stimuli in its surroundings, such as touch, sound, and changes in pressure or posture. Animals have a shared gift of sensitivity to mechanical stimuli. As a result, some mechanoreceptors alert the animal to changes in body posture, while others aid in the detection of painful stimuli, and yet others aid in hearing.

Special mechanoreceptors called lateral-line organs are found in the outer skin (epidermis) of all predominantly aquatic vertebrates, including cyclostomes (e.g., lampreys), fish, and amphibians. These organs are particularly sensitive to small, localized water displacements, such as those caused by other creatures moving in the water. Approaching creatures are recognized in this manner. As a result, the lateral lines are thought to act as touch receptors at a distance, allowing the animal to detect and identify prey, approaching adversaries, or members of its own species (e.g., in sexual display behaviour).

(b) Electrical

Although we cannot see electricity, it acts as a traffic signal for some creatures, guiding them to their destination. Sharks and other fish can detect it thanks to

channels filled with a gelatinous substance that are exposed to the outside through skin pores. Lorenzini blisters are the organs that sharks have on their heads. Platypuses have a similar system in their beaks that allows them to detect their prey in deep, muddy waters. It is the sole case of a mammal capable of perceiving electricity that has been discovered so far.

(c) Chemical

Chemoreception is the process by which organisms respond to chemical stimuli in their environments using primarily their senses of taste and smell. To regulate cell function, it relies on molecules that act as signals. While many chemicals found within animals, such as hormones and neurotransmitters, regulate specific physiological functions, chemicals found in the environment are also recognized by and elicit responses from entire species. This latter type of chemoreception is found in all animals and microbes such as bacteria, although the two most wellknown chemosensory systems are the senses of taste (gustation) and smell (olfaction).

Chemoreceptor cells are found in separate structures called sensilla on the outside of the body of many invertebrates. In nematodes, the number of chemoreceptor cells is quite low. Only 34 chemosensory cells are grouped in eight sensilla at the head of *Caenorhabditis elegans*, a small soil-dwelling species. The tail of this organism has four sensory cells, although it is unknown if these cells function as chemoreceptors.

(d) Olfactory

The ability to perceive heat, also known as thermoregulation, is a crucial sense that allows animals to recognize their surroundings. Vampire bats sense temperatures of 30°C at a distance of up to 20 centimetres using their nose and upper lip, which are equipped with heat receptors. This allows them to pinpoint their prey's location, as well as the patches of skin that line the blood vessels, allowing them to determine the optimum spot to pierce in their search for blood. Some vipers and boas use unique facial pit organs to detect the heat of their prey. The direction of the source is given by the part of the pit that perceives the heat and the presence of pits on both sides of the head allows them to measure the distance.

(e) Auditory

One of the best researched examples of animal senses is bats' capacity to map their environment using sound. These flying mammals are not blind, contrary to popular perception, but their eyes are useless when they catch insects in flight at night. Bats' shrieks, which are inaudible to humans, reverberate off their surrounds and their flying victims. They can hunt with great precision thanks to the Doppler Effect, which causes the return signal's timing, direction, and frequency to fluctuate as it passes by, similar as when an ambulance with a wailing siren passes by.

(f) Visual

When we think of photoreception, we usually think of visual receptors or eyes; however, invertebrates have extraocular photoreceptors, which are not related with the eyes at all. These receptors, like the main eyes, are known to alter circadian Introduction to Animal Behaviour

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rhythm expression in many circumstances, therefore they could be engaged in the systems that control photoperiodic events.

Photoreceptors, especially eyes, are designed to provide animals with a variety of information. Complex eyes may supply the data concerning the following features of the visual field: light intensity, spectral distribution, spatial distribution (images), polarization pattern, and temporal distribution (movement, flicker, or duration).

Some insects' eyes, as well as those of other animals like octopuses, have a feature that we don't: they can discern polarized light, or light with a definite vector direction in space. It would be useful for navigation to be able to take use of these varying orientations of light in the sky, and that is exactly what those ants or bees capable of travelling long distances to return to their anthills or hives do.

3.5 NEURAL AND HORMONAL CONTROL OF BEHAVIOUR

In the history of study into the proximal physiological origins of animal behaviour, two types of mechanisms, neural and hormonal, have been prominent. During the early stages of this history, the neurological and endocrine systems were thought to be independent systems that were examined by various research groups. This survey's structure reflects the survey's multiple origins. Several discoveries beginning in the twentieth century led to the recognition that the neurological and endocrine systems are physiologically integrated to a large extent, which is critical for animal behaviour. Hormones are synthesized and secreted by nerve cells, and their behavioural effects are mediated by their activities on neurons. The brain regulates the endocrine axes, allowing hormone levels to respond to both social and physical contexts.

3.5.1 Nervous Systems and the Study of Behaviour

Our current understanding of how neural systems govern animal behaviour owes a lot to a group of scientists who pioneered an experimental strategy to studying behaviour in the mid-twentieth century. Niko Tinbergen was one of the first proponents of ethology, and he was one of the most thoughtful of its early proponents. Tinbergen defined ethology simply as 'the biological study of behaviour' in an important paper titled 'On aims and methods of ethology' (Tinbergen, 1963). Tinbergen had a significant impact on ethology by focusing on field observations or elegantly basic experiments on intact animals. However, he expected the results of this effort to be combined with a neurological analysis as soon as one became available. This is evident in his synthesis of ethology, The Study of Instinct (1951), in which he resorted to current findings in neurophysiology and articulated his notions as closely as possible in terms of the neurological system. He predicted that ethology's biological approaches would produce 'real problems that can be addressed by both the ethologist and the physiologist,' and he talked of 'the basic unity of the neurophysiological and the ethological approach.' The long-term goal of this method is to examine behavioural patterns in terms of the activity of the underlying brain components. As a result, this field of study is sometimes referred to as neuroethology, a term that initially appeared in the 1960s. Neuroethology aims to study the brain foundation of behaviour by combining ethological and neurobiological methodologies. Often, this entails looking at groupings of receptors or nerve cell networks to figure out how they interact in order to understand behaviour. As Tinbergen predicted, it is sometimes possible to apply both neurobiological and ethological analysis to a single phenomenon.

The activity in an animal's neurological system is largely responsible for its behaviour. The patterns of behaviour identified in ethological investigations may thus represent the neurological system's fundamental organisation. Consider the classic case of ground-nesting birds' egg-retrieval behaviour, which was first examined in the greylag geese (genus Anser) by Lorenz and Tinbergen in the 1930s. To collect an egg that has been moved from the nest, a nesting goose follows a predictable pattern of movements. The bird leans out of the nest, extends its beak beyond the egg, and then brings it back to its chest, rolling the egg back into the nest. Little side-to-side motions of the beak are superimposed on this movement towards the breast, which aid to maintain the egg in place. For egg retrieval, all members of the species perform this series of movements; none use a different strategy. Other species, such as the herring gull (Larus) on which many studies have been conducted, have a very similar pattern of movement (Fig. 3.1). Stereotyped movements of this kind were originally called fixed action patterns; nowadays, more general terms like motor pattern are used instead by most ethologists.



Fig 3.1 Early Ethological Concepts of the Mechanisms Involved in a Simple Behaviour Pattern Such as Egg Retrieval

These and other findings showed that only some aspects of the natural stimulus are required to elicit a response. These key characteristics were dubbed sign stimuli or social releasers when they appeared in the context of social behaviour. Ethologists were correct in hypothesizing brain mechanisms in the responding animal to account for the fact that animals often respond to only a small subset of accessible stimuli. Although the capacity of the sense organs may play a role in response selectivity, it was already recognized that an animal may respond to a certain sensory cue in one behavioural situation but not in another. Hence, the occurrence of sign stimuli must also be due to stimulus selection by more centrally located mechanisms processing the information received from the sense organs.

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3.5.2 Behavioural Endocrinology

It is the scientific study of hormones and behaviour interactions. Hormones can influence behaviour, and actions can change hormone concentrations in a bidirectional manner. Hormones are chemical messengers that are secreted by endocrine glands and influence the neurological system to govern an individual's physiology and behaviour. Hormones that regulate physiological processes have been co-opted to alter behaviours that are linked to these processes throughout time. Hormones are organic chemical messengers created and released by endocrine glands, which are specialized glands that manufacture and release hormones. The term endocrine is derived from the Greek root words endon, which means 'within,' and krinein, which means 'to release,' whereas hormone is derived from the Greek word 'hormon', which means 'to excite.' Hormones are released into the bloodstream (or the tissue fluid system in invertebrates) and act on target organs (or tissues) at a distance from their source, coordinating an animal's physiology and behaviour by regulating, integrating, and directing its bodily function. Estrogens, for example, which are connected with gamete maturation, are now widely linked to the regulation of female sexual activities. Mating behaviour only occurs when mature gametes are ready for fertilization, owing to these dual hormonal activities. Hormones accomplish this through influencing the sensory systems, central integrators, and/or peripheral effectors of humans. It's critical to track hormone levels as well as receptor interactions in the brain to fully comprehend hormonebehaviour relationships. Because certain chemicals in the environment can imitate natural hormones, they can have a significant impact on human and animal behaviour.

Effect of Hormones on Behaviour

All behavioural systems, including animals, are made up of three interconnected components: (1) sensory input systems, (2) integrators (the central nervous system), and (3) output systems, or effectors (e.g., muscles). Hormones have little effect on behaviour. Hormones, on the other hand, impact these three systems, making particular stimuli more likely to evoke specific reactions in the right behavioural or social setting. Hormones, in other words, alter the likelihood that a specific behaviour will be emitted in the suitable situation. This is a crucial distinction that influences how hormone-behaviour interactions are seen. Female rats, for example, must adopt a tight mating posture (known as lordosis) in order to copulate successfully. Females only adopt this posture when blood oestrogen levels are high, which coincides with ovarian maturation. In response to tactile impulses delivered by a mounting male, females adopt the lordosis position. Estrogens increase the receptive field size of sensory cells in the flanks, which affects sensory input. Estrogen alters the speed of processing and connection of neurons via affecting protein synthesis, neuron electrophysiological responses, and the development of growth-like processes on neurons in the central nervous system. Finally, oestrogen influences muscle output, which causes lordosis, as well as chemosensory impulses that help attract a mate.

Effect of Behaviour on Hormones

The female rodent mating posture example demonstrates how hormones can affect behaviour, but, as noted previously, the reciprocal relation also occurs, that is, behaviour can affect hormone concentrations. For example, chemosensory cues from males may elevate blood estradiol concentrations in females, and thereby stimulate proceptive or male-seeking behaviors. Similarly, male mammals that lose an aggressive encounter decrease circulating testosterone concentrations for several days or even weeks afterward.

Similar results have also been reported in humans. Human testosterone concentrations are affected not only in those involved in physical combat, but also in those involved in simulated battles. For example, testosterone concentrations are elevated in winners and reduced in losers of regional chess tournaments.

Check Your Progress

- 6. What are hormones?
- 7. Define visual perception.
- 8. What is mechano-reception?
- 9. Define environmental perception.

3.6 GENETIC AND ENVIRONMENTAL COMPONENTS IN DEVELOPMENT OF BEHAVIOUR

How do genes and environment interact to influence animal behaviour? Both have vital roles to play. Prior populations' evolutionary reactions to selection on behaviour are captured in genes. Environmental flexibility allows animals to adapt to changes throughout the course of their lives. The mechanics of heredity, DNA, and the translation of genetic information into morphology, physiology, and behaviour were unknown to early humans. They intuitively realized, however, that conduct is influenced by genetics. Herds and flocks of animals beneficial to humans were tamed by managing mating. The domesticated animals that resulted, such as cattle, horses, and dogs, behave significantly differently from their wild ancestors. Even though the underlying science was not grasped until the Darwinian and Mendelian revolutions in the nineteenth century, selective breeding was a major breakthrough in human history.

We now understand that both genes and the environment influence behaviour, and scientists researching behaviour concentrate on the relationship between the two. Genes, through their effects on morphology and physiology, form a framework within which the environment shapes an individual animal's behaviour. The environment can influence morphological and physiological development, and the shape and internal workings of an animal behaviour. Learning, memory, and cognition are extraordinary capabilities that allow animals to acquire and store information about their environment for use in influencing their behaviour, and genes provide the framework for these remarkable mechanisms. Introduction to Animal Behaviour

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Instinct and Behaviour

Instinctive, or hard-wired (i.e., genetically determined) behaviour piqued Charles Darwin's interest, as well as that of later ethologists like Niko Tinbergen. The term 'instinct' refers to a conduct that is carried out without deliberation and cannot be changed via learning. Simple behavioural patterns, expressed in reaction to a given stimuli or within a specific environment, are examples of instinctual behaviour. When a species' environment varies little from generation to generation, or when clear messages need to be delivered and received, genetic (innate) information is the best predictor of behaviour.

When a light is turned on, a cockroach, for example, runs to the safety of a dark nook. Before settling down to sleep, a dog may circle its bedding numerous times, as if trampling grass. A rattlesnake will strike a moving, warm object the size of a mouse. When designing its reaction, the animal in none of these circumstances engages in learning or thought.

Imprinting and Development

Imprinting refers to the ability to learn a specific piece of information at the appropriate developmental stage. Konrad Lorenz and his geese are the most renowned example of imprinting. Goslings learn to recognize their mother (and distinguish her from other geese) quite early in life, according to him. He could induce the goslings to imprint on him and obediently follow him wherever he went by replacing himself for the mother goose at the appropriate developmental period. It's fascinating to see how open goslings are to learning from a leader, even if it doesn't seem like a goose. Imprinting shows how genes mostly control behaviour, but evolution can open a window for learning vital information about environmental diversity.

Learning about Specific Environments

Many creatures acquire vital information in order to survive. These abilities are frequently context-dependent. A species may be highly good at learning information that are important to its survival, but it may not be able to apply that knowledge to a wide range of scenarios that have never occurred in its evolutionary past. Guam's native birds, for example, were utterly unprepared to learn how to avoid brown tree snakes, which were brought to the island about 1950. Animals that store (or cache) food are another good illustration of this. Caching is a strategy for coping with food supplies that are plentiful for a limited period of time, such as fruits and tree nuts. Food is stored in a central location by some animals. Honeybees storing honey are an example of this, and centralized stores can necessitate strong protection against robbers, which honeybees are known for. Alternatively, cached food can be dispersed across the area; tree squirrels and grey jays are particularly adept at this (this is sometimes called scatter hoarding). Food scatter caching stands out as a particularly difficult environment for learning complicated information about places, and birds and mammals that cache food frequently have outstanding recall abilities. Another set of examples comes from animals that leave their nests to forage and must learn enough about their surroundings to find their way back home. The site of a nest or burrow is unlikely to remain constant over many generations; the

capacity to return home necessitates the ability to integrate a great deal of environmental data. Some species, such as the desert ant *Cataglyphis cursor*, use path integration to incorporate learning into navigation. Path integration is the ability to recall distances and directions travelled, total them, and then compute their return path. To integrate a navigational path, you'll need strong learning and calculation skills. Other animals learn their outward course by observing markers such as the position of the sun, which they then reverse to return home. The innate mechanisms for combining learned environmental information in cache retrieval and homing have been provided by evolution.

Environment, Genetics and Cognitive Development

Cognition was once assumed to be what distinguished humans from animals, but scientists today acknowledge that cognitive talents are not unique to humans. Cognition allows animals to be more adaptable in their social and physical contexts, yet even cognition is limited by genetic constraints. One fascinating feature of cognition is that it allows an animal to distinguish itself as a distinct individual. Some researchers take this as proof of cognition if an animal recognizes 'self' in a mirror rather than identifying the image as that of another species. A popular test involves changing an animal's visual appearance (for example, dyeing a patch of hair) and then observing the animal's reaction to its mirror image. If it comes into contact with the dyed patch, it is assumed that the animal has a concept of 'self.' Mirror experiments show that apes, some monkey species, elephants, and dolphins all respond positively, indicating that cognition is vital in behavioural development in a wide range of animals.

Check Your Progress

- 10. What is animal learning?
- 11. Define instinct.
- 12. What is imprinting.
- 13. Define cognition.

3.7 COMMUNICATION

Information is passed on or exchanged through communication. It happens when one person's actions send out a signal that causes another person's behaviour to change. As a result, the evolution of communication is influenced by changes in the fitness of the sender and receiver of a signal. A change in fitness refers to the rate at which genes that influence an individual's actions spread across the population. This rate is determined by the survival and reproduction of people who possess these genes. An individual should only produce signals that boost its fitness as a result of natural selection in previous generations. Similarly, a person should only respond to signals in ways that improve his or her fitness.

Communication is a two-person phenomenon in which signals are exchanged between them. The introduction of a nonparticipant observer, here the ethologist,

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who monitors the behaviour and characteristics of the signaler (also called the source or sender), the receiver, and the signal is required for an objective examination of this system. (Fig 3.2).

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Fig 3.2 The nonparticipating observer, by recording the behaviour of the signaler and the receiver and the characteristics of the signal, acts like a privileged receiver 'tapping the wire' of communication between nonhuman animal

Even in the seemingly quiet world of plants, communication has been discovered; trees, for example, have been discovered to pass on information about approaching predators via chemical signals. Animals communicate so efficiently with one another and with people that they are often referred to as having a language of their own. However, the terms communication and (human) language are not interchangeable. Human language is a distinct mode of communication; yet, not all modes of communication qualify as language.

Forms of Animal Communication

Animals communicate using many different types of signals, such as visual, tactile, olfactory, gustatory, and auditory messages and they also use these signals in a wide range of contexts. Some of the most common forms of communication are:

(a) Chemical

Pheromones are chemicals produced by animals for the purpose of communication. They are chemical substances produced by an animal and released into the environment that impact the behaviour or physiology of other animals in the same species. Pheromones are employed by a wide range of organisms, including moulds, insects, and mammals.

A female moth releases a pheromone into the air to announce her reproductive readiness. A male moth just has to detect a couple of these chemicals to begin zigzagging upwind towards its probable partner.

Dogs and other canines mark their territory with a urine-based pheromone as an identity mark.

The female silkworm moth secretes one termed pheromone bombykol: males are sensitive to just a few molecules of this substance and may be attracted from distances of several kilometers.

Anal glands in mammals are known to add characteristic pheromones to faeces in over 100 species, and many animals have multiple specialized scent

glands. A deer, for example, can transfer odours in the air from glands on its legs and head, can use the same glands to mark trees and twigs, and has additional glands on its feet for leaving scent trails on the ground.

Although the possible functional roles of natural social smells are culturally limited in modern human communities, humans, like other animals, nonetheless have apocrine sweat glands. These are not vital for cooling (as they are in nonprimates; in primates, the epicrine glands are responsible for thermoregulation), but they are responsible for unpleasant body odours. The apocrine glands are only active during puberty, are extremely responsive to stress and excitement, and are larger in males, implying that they had some social and thus communication functions in the past.

(b) Visual

Humans value visual messages above all else, but they are also essential in the lives of many other species. Facial expressions, bodily movement, spacing and posture, attire, and other types of decoration are examples of visual communication. Printed words or graphics, a grin, a handshake, a tear, a new blue suit, or a stop sign are all examples of visual communications that are useful in human communication. Animals respond to movements, gestures, and colours in a similar way. Birds and butterflies' colours, fireflies' rhythmic light, and primates' head, ears, and tail movements are all useful sources of information.

There can be fast changes in skin colour or markings in fish, reptiles, and cephalopods (octopus and squid). Visual displays in mammals, particularly carnivores and primates, include variations in face expression, which are frequently accompanied by vocalization.

In a wide range of vertebrate and invertebrate species with the ecological and perceptual opportunities for visual message detection, posture, gait, and gestures via movements of the extremities can be detected as social signals.

There are specific types of communicative gestures. A male baboon that yawns, bares his fangs, and retracts his brows is suggesting that he is eager to fight. Experiments have revealed that humans are capable of accurately classifying the meanings of these utterances. Humans, for example, usually indicate cooperation by drawing back the corners of their mouths into a smile. The smile of nonhuman primates also suggests that they are not hostile.

(c) Light

The firefly or lightning bug is probably the most well-known light user in North America. This little flying insect communicates its identification, sex, and location by flashing light in different patterns. These insects have distinct light patterns that differentiate them from one another.

(d) Audio

Sounds made by speaking, whistling, drumming, or striking a part of the body against an object, the ground, or another part of the body are examples of auditory messages. When auditory messages are detected by receptors and then processed by the brain, they become significant to animal and human systems, just like other

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forms of communication. In the case of lower-order living systems, the response is usually either approach or avoidance; that is, animals can respond to auditory information by approaching or avoiding the source of the message.

Sounds can be used to attract mates, deter dangers, and express joy or suffering. Animal auditory communication includes barking, growling, hissing, and purring. When a stranger approaches, for example, dogs will bark. Intruders are warned away by red squirrels using a series of rattles, screeches, and yips. And dolphins use auditory communication to distinguish themselves from others, emitting a distinct whistle that also assists them in finding food.

(e) Species Specificity of Songs

Birds maintain breeding territories and actively defend them. Birdsong differs from calling in that calls are made all year, whereas singing occurs primarily in the spring, summer, and autumn, and only male birds sing. As far as we know, the primary functions of singing are to declare and delimit the male's territory, as well as to attract a mate. Male birds utilize song to create and keep territory without having to patrol and battle constantly. Furthermore, once a bird has established its territory, its song is used to attract and keep a mate. Because its aims necessitate identification of both species and individuals, birdsong varies from species to species and even from bird to bird within the same species. Songs are nothing more than a series of repeated sounds in certain species. In others, songs are made up of complicated patterns of pitches—sometimes referred to as syllables—that are repeated in lengthier units or themes. The song structure reflects individual variance among singers and serves a specific function.

Insects like crickets make a lot of noise for their size, and a cicada may need to increase its resting metabolic rate in order to sing; certain small frogs that increase their metabolic rate while calling have been estimated to spend more than 80% of their total calorific intake on this activity. This contrasts with the use of chemical signals, where minute amounts of pheromone are needed to have dramatic effects because the recipient can be sensitive to just a molecule or two and airborne transmission is free. This begs the question of why the auditory channel should ever be favoured for broadcast transmission over the chemical. The acoustic channel's presumed advantages include its high carrying capacity for rapid serial transmission and the possibilities for quick and accurate source identification, which, while not as direct as for visual signals, are in general much better than for dispersed chemicals.

Even in the mating cries of male frogs, particularly in sub-tropical species that reproduce opportunistically after big rains, some of the intricacies carried by the auditory channel are visible. Many of these species' males congregate in choruses to make basic noises, and multiple species frequently use the same space. Females must consequently be able to distinguish between species-specific signals using their hearing. If mating locations are scarce, male aggregations may be fortuitous, but there is evidence that the groupings are systematic, with the notion that the greater volume or longer length of a chorus puts dispersed individuals at a disadvantage. The discovery of highly ordered sub-groups within choruses supports this hypothesis. Individuals in a chorus alternate calling in duos, trios, and quartets at specific intervals in some species. There are leading individuals in the sub-groups, and leading sub-groups within choruses. As a result, chorusing is purposefully synchronized rather than occurring as a result of people' coincidental proximity. The individual-to-individual advantage balance that enables this collectively coordinated type of communication is certainly difficult to determine, but this is characteristic of most animal social behaviour. Thus, audio communication appears to be strongly associated with nocturnality in amphibians and reptiles, but not in other taxonomic groups.

Diurnal sound production is seen in grasshoppers and cicada among insects, and the most elaborate use of the auditory channel is found in birds, almost all of which are diurnal but are too small to be seen from afar. Owls and nightingales sing at night, and songbirds sing loudest at dawn and dusk. However, enough avian (and mammalian) vocalization occurs during daylight hours to dispel the concept that nocturnality is the only factor favouring acoustic communication. However, depending on visibility, there may be a trade-off between visual and audible communication.

Mammals, with the exception of primates, have little or no colour vision and no retinal fovea for high visual acuity, limiting their ability to use colour signals and their ability to show or mark very fine details. Reptile communication is olfactory and visual, with limited use of vocalization save in night lizards, birds have highly developed visual and acoustic channels, and mammals employ all four channels with a focus, if any, on the chemical.

(f) Evolution of Language

A continuity approach and its opponent, a discontinuity approach, have dominated recent discussion of the origins of language (Table 3.1). The Darwinian continuity method has often been defined as looking for precursors of language in animal communication systems. It asserts that language is such a complex system that it could not have arisen spontaneously (de novo). We can't imagine the eye appearing out of nowhere, and we can't imagine language appearing out of nowhere, either. The opposing viewpoint contends that language is unique among the biosphere's communication systems, and that claiming continuity between, for instance, bee talk and human language is tantamount to claiming 'evolutionary growth from breathing to walking,' as Chomsky pointed out.

 Table 3.1 Theories of Language Origin, Classified By Their Assumed Evolutionary Models and Modes of Language Acquisition

Evolutionary model acquisition	Continuity	Discontinuity	
mode			
Innate	Bickerton, Pinker, the present	Chomsky	
	author, and others		
Learned	'Behaviourism'	Culturalism	

The study of animal communication has yielded little insight into the evolution of human language. However, if human language is no longer thought to be wholly culturally driven, or b) assumed to be largely and vitally innate, but for fortuitous

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and non-Darwinian causes, marginally more relevant comparisons may be conceivable. The case has recently been made that the innate capacities that underpin human language must have evolved through Darwinian processes, and accepting this implies that there may be points of commonality between the evolutionary biology of human language and animal communication systems, even though the end-products are vastly different. So, it can be concluded that:

- 1. Language evolved, by a wholly Darwinian process, out of animal cognition, not out of animal communication.
- 2. The function of language in modern *Homo sapiens* and in the species' language-using ancestors is to communicate thoughts.
- 3. In so far as language entails sharing information, it might be considered disadvantageous to the individual, while cognitive intelligence is clearly advantageous. Accordingly, intelligence is the rule across species, language the exception.
- 4. Language evolved in the Homo lineage not because of superior hominid intelligence, but because of special social conditions: the development of reciprocal altruism as a way of gaining fitness by sharing and helping.

Functions of Communication

Some of the most common functions of communication are:

(i) Courtship and Mating

Across animal groups, there are significant differences in courtship and mating practices. Regardless, communication is essential for all species. Some aspects are simple to understand. The identification of a suitable mate is an important aspect of courtship and mating. This identification process may require the processing of visual, tactile, olfactory, gustatory, and/or auditory information, depending on the species. Attracting potential mates, as well as persuasion and negotiation, are all part of the courtship and mating process, which is a communication process. For example, grasshoppers and crickets use song, moths use pheromones, and fireflies use the visual messages created by their flashing light.

(ii) Reproduction

The biological components of reproduction can also be viewed as a process of communication. The reproductive process begins with the union of a sperm cell and an egg cell at the moment of conception. These cells contain all of the information needed to create a new living creature with striking similarities to its parents. Thus, genetic transmission ensures the formation of new children and, in a larger sense, the species' continuance through the union of these cells and the development that follows.

(iii) Parent-offspring Relation

Many offspring are quite dependent on adults for survival. For example, the survival of social insects, birds, and mammals depends on interaction with their parents. This interaction may take the form of food providing and physical guidance from one point to another.

(iv) Navigation

The goal-directed movement across space of an animal is referred to as 'navigation.' Whether the goal is to get food, avoid an opponent, follow a colleague, or arrive at a specific location, the activity necessitates the processing of messages in some way. The manner in which these processes occur varies substantially from one species to the next. Visual signals are widely used by humans. Ants navigate by following an olfactory trail left behind by other ants. Dolphins utilize echolocation to navigate as well; they send clicking signals through their forehead and receive and 'understand' returning signals through their jaw and throat.

(v) Self Defense

Communication is frequently used by animals in order to defend themselves. When an animal detects the presence of a predator, for example, it mobilizes in order to flee the situation. This detection-mobilizing-flight activity relies heavily on communication. Furthermore, the animal's departure may serve as a signal to other nearby animals—as well as the predator—who may all react in response to the signals they perceive and analyze.

(vi) Territoriality

Communication can also aid in the formation and maintenance of home territory. Many animals, including humans, are drawn to the places and spaces where they were born, spent their formative years, or mated. This bond leads to a need to mark, maintain, and occasionally defend the territory against invaders. Communication is a technique through which animals designate their territory, as well as a way for them to detect and respond to invasions. Birds are an excellent example of the necessity of territoriality and how territories are formed, maintained, and defended. Some birds take over a patch of land, a hedgerow, or a section of a meadow. Once this has happened, male birds will go to considerable lengths to keep out rival males by singing.

Check Your Progress

- 14. Which chemicals are produced by animals for the purpose of communication?
- 15. Which is the most well-known light user in North America?

3.8 ANSWERS TO CHECK YOUR PROGRESS

- 1. Ethology is the scientific study of animal behaviour, usually with a focus on behaviour under natural conditions, and viewing behaviour as an evolutionarily adaptive trait.
- Innate behaviour is behaviour is behaviour that's genetically buit-in in an organism and can be performed in response to a cue without prior experience.
- 3. In orthokinesis the speed of movement of the individual is dependent upon the stimulus intensity.

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- 4. The three examples of innate behaviour are: web making in spiders, nest building in birds, cocoon spinning in insects such as moths.
- 5. An instinctive behaviour is an action in an organism that is performed by all members of their species.
- 6. Hormones are chemical messengers that are secreted directly into the blood, which carries them to organs and tissues of the body to exert their functions.
- 7. Visual perception is the ability to perceive our surroundings through the light that enters our eyes.
- 8. Mechanoreception is an ability of an organism to detect and respond to certain kinds of stimuli-notably touch, sound and changes in pressure and posture in its environment.
- 9. Environmental perception is the way in which an individual perceives the environment, and the process of evaluating and storing information received about the environment.
- 10. Animal learning, the alternation of behaviour as a result of individual experience. When an organism can perceive and change its behaviour, it is said to learn.
- 11. An instinct is the ability of an animal to perform a behaviour the first time it is exposed to the proper stimulus. For example, a dog will drool the first time—and every time—it is exposed to food.
- 12. Imprinting is a form of learning in which a very young animal fixes its attention on the first object with which it has visual, auditory, or tactile experience and thereafter follows that object.
- 13. Cognition includes all ways in which animals take in information through the senses, process, retain and decide to act on it.
- 14. Pheromones are chemicals produced by animals for the purpose of communication.
- 15. The firefly or lightning bug is probably the most well-known light user in North America.

3.9 SUMMARY

- Behavioral biology is the study of the biological and evolutionary bases for changes in the activity of an organism in response to stimulus.
- Innate behaviors rely on response to stimuli and the simplest example of this is a reflex action, an involuntary and rapid response to stimulus.
- Nervous and hormonal system coordinates the physiology and behaviour of individuals by regulating, integrating, and controlling bodily functions.
- Over evolutionary time, hormones have often been co-opted by the nervous system to influence behaviour to ensure reproductive success.
- Genes, via their influences on morphology and physiology, create a framework within which the environment acts to shape the behaviour of an

individual animal. The environment can affect morphological and physiological development; in turn behaviour develops as a result of that animal's shape and internal workings.

• Animals communicate with each other using stimuli known as signals. An example of this is seen in the three-spined stickleback, where the visual signal of a red region in the lower half of a fish signals males to become aggressive and signals females to mate.

3.10 KEY TERMS

- **Pheromone**: It is a chemical that an animal produces which changes the behaviour of other animals of the same species.
- **Navigation:** It is the ability of many animals to find their way accurately without maps or instruments.
- **Communication:** Communication in animal occur when an animal transmits information to another animal causing some kind of change in the animals that gets the information.
- Animal behaviour: It includes all the ways animals interact with other organisms and the physical environment.
- Mechanoreception: It is the ability of an animal to detect and respond to certain kind of stimuli-notably touch, sound and changes in pressure or posture in its environment.

3.11 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

- 1. What is territoriality? How do animals defend their territory?
- 2. List the various types of animal behaviour.
- 3. What are the uses of communication in animals?
- 4. List the characteristic features of animal behaviour.
- 5. Write a short note on the evolution of language.
- 6. What is visual perception of the environment?
- 7. Mention the characteristics of innate behaviour.

Long-Answer Questions

- 1. How common are innate behaviors in the animal kingdom? Which animals tend to have a greater number of innate behaviors?
- 2. How can innate behaviors sometimes be disadvantageous for an individual in terms of reproduction? Give an example based on the graylag goose.
- 3. What kind of innate behaviors do humans exhibit?

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- 4. Describe how behaviour of an organism can affects the hormone?
- 5. How the nervous system of an organism is responsible for controlling the behaviour of organisms? Discuss.
- 6. Explain the environmental factors that control the behaviour of an organism.

3.12 FURTHER READING

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Various Aspects of Animal Behaviour

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UNIT 4 VARIOUS ASPECTS OF ANIMAL BEHAVIOUR

Structure

- 4.0 Introduction
- 4.1 Objectives
- 4.2 Ecological Aspects of Behaviour
 - 4.2.1 Habitat Selection
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 - 4.2.4 Aggression
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- 4.7 Answers to 'Check Your Progress'
- 4.8 Summary
- 4.9 Key Terms
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- 4.11 Further Reading

4.0 INTRODUCTION

Simple optimization models were used to start behavioural ecology in the mid-1970s. Number of partners, food obtained, or a more direct measure such as number of offspring are all used to correlate behaviour with reproductive success. The bird that fights the hardest is more likely to mate than the bird that fights the

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least. The wild dog that hunts with others eats more than the wild dog who hunts alone. Any behaviour is part of a pattern that forms the animal's ecology, hence behavioural processes produce ecological effects. As a result, behavioural ecology studies the ecological conditions that influence behavioural adaptations, such as how individuals locate food and avoid predators. Animals also refer to the set of interactions that occur when two or more individual animals, usually of the same species, create basic aggregations, engage and take part in sexual behaviours, participate in territorial disputes and also dispute over potential mates, or simply communicate across space.

Biological rhythm is a basic homeostatic system that influences animal behaviour and physiology. The circadian system, which regulates day-night cycles, matures gradually after birth. The period of sleep and waking is synchronized with the sleep cycle's rhythm regulation in natural conditions. The light/dark cycle regulates these rhythms, but they also remain during constant daytime conditions. The most important environmental factor impacting animal physiology and behaviour, as well as the timing of migration, hibernation, production, and reproduction, is the change in photoperiod (day-length).

Many researchers believe that practically everything we encounter is learned and stored in the brain, based on a number of surprising findings. Although we may have entered the minutest things of our lives into our minds computer, we are not able to consciously recall much of it. Sometimes, we can't even recall what we have tried to memorize, but apparently the information is there, the fault lies with our recall techniques. Classical animal learning studies have been dominated by the works of Watson, Hess Lorenz, Harlow, Niko Tinbergen Skinner, Pavlov and Thorpe. Learning occurs in a great number of different animals under a wide variety of circumstances. All animals learn from ants to elephants and from protozoa to primates.

In this unit, you will study behaviour of organism with respect to the ecology i.e. how the animals are going to select places for their food, survival and reproduction and how they defend their habitats from other animals. How the environmental factors affect the physiology and behaviour, timing of migration, hibernation, production and reproduction etc of animals and how the animals perceive and changes its behaviour.

4.1 **OBJECTIVES**

After going through this unit, you will be able to:

- Understand the ecological concepts of behaviour such as habitat selection, territoriality etc.
- Discuss how animals behave socially and their reproductive behaviour and strategies involved
- Analyze the concept of biological rhythm
- Discuss animals learning and memory

4.2 ECOLOGICAL ASPECTS OF BEHAVIOUR

Animal behaviour ecology is a branch of animal biology. It is concerned with the behavioural adaptations and interactions of animals within a population in response to selective forces in a given ecological context. It is engaged with determining whether or not an animal's behaviour is adapted, and if so, how it becomes adaptive. There are two categories of inquiries: proximal questions (also known as 'how') and ultimate questions (also known as 'why'). The proximal queries try to figure out how a specific behaviour arises and develops. The triggers in the environment that triggered a behaviour are identified. It also considers the genetic, physiological, and structural factors that influence ones behaviour. The final questions try to figure out how important that behaviour is for the animal's evolution, survival, and reproduction.

4.2.1 Habitat Selection

Habitats are the resources and conditions in a specific location that allow a given creature to survive and reproduce. Food, cover, water, and other specific elements are among the resources that a species requires for life and reproductive success. Habitat selection is a progressive cycle of behavioural reactions including a progression of inborn and learned behavioural choices made by a creature about what natural surroundings it would use at different scales of the environment, with reproductive achievement and species endurance being a definitive elements that impact an animal group or species' habitat choice.

It is linked to a comprehension of complicated behavioural and environmental systems. To comprehend the adaptive importance of unbalanced habitat use, two components of habitat selection are required: demonstration of choice and assessment of the fitness consequences of that decision.

Cover availability, forage quality and quantity, and resting or denning sites are all factors to consider while choosing a habitat. Seasonally, each of these may change. Individual habitat selection is influenced by a number of interconnected elements (e.g., competition, cover, and predation). Because each organism is involved in intraspecific and interspecific connections that divide the available resources within an ecosystem, competition is present. Competition may cause a species to fail to choose a habitat that is suitable in terms of all other resources, or it may influence the geographic distribution of a species within a habitat. Predation makes choosing a habitat more difficult. Predators may make it very difficult for an individual to occupy a given region. The species' survival and future reproductive success are likely the motivating forces that lead an individual to examine these biotic elements. A person may pick a different site with less ideal resources if there is a lot of competition and predators. After predators have been eliminated, regions with sufficient resources can be populated.

Because birds are highly migratory, often travelling thousands of miles, and reproduce in very particular habitats, they are practically ideal models for investigations of habitat selection. Many studies have shown that various species have distinct habitat requirements. Indeed, little migrant songbirds have a plethora of habitat options - where to feed, where to look for a mate, where to build a nest, Various Aspects of Animal Behaviour

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where to stop to replace depleted fat stores while travelling, and so on. Habitat utilization is often varied between the sexes of a species since choices are so highly adjusted. Male Henslow's Sparrows forage farther from the nest than females in grassland, whereas female Red-eyed Vireos forage closer to the height of their nest (10-30 feet) in woodlands, while males forage closer to the height of their singing perches (20-60 feet).

4.2.2 Food Selection

All living organisms require food as one of their most important commodities. It is a source of energy that is required for mobility, migration, courting, other activities, and even foraging and digesting food. Animals are divided into 11 classes based on their feeding habits. viz. a. 1. Predators 2. Grazers 3. Browsers 4. Scavengers 5. Particle feeders 6. Filter feeders 7. Fruit eaters 8. Seed eaters 9. Flower feeders 10. Food borrowers 11. Parasites. Ecologically animals are classified as carnivores, herbivores, scavengers, and saprophytes depending upon their food types. No two species living together at the same time and place eat exactly the same staple food; this is called as phenomenon of competitive principle. The feeding electivity is a subject of major biological importance to find out relationship between the problems of interspecific competition for food and studies of their nutrition.

- i. **Carnivores:** Carnivores are at the top of the food chain. They make the majority of their living by killing and devouring other animals. Some predators are experts, while others are opportunists.
 - a. Specialists- Eagles, big cats, snakes, owls, and other predators prefer to be sedentary. Only a limited portion of a specialist predator's time may be spent in search of food. They prefer larger food that they can feast on for several days, allowing them to rest and digest the flesh, such as lions preying on large ungulates like beasts, deer, and antelope. When big cats begin hunting, they first study the surrounding prey population and select the easiest target from among them, such as a buffalo that is injured or weak.
 - **b. Opportunists-** Crows, mongoose, dogs, leopards, foxes are some examples of busy opportunists. They will kill and eat anything they can get their hands on. Opportunistic feeders require a diverse and complicated environment to thrive.
- **ii. Herbivores**: Grazers eat grass. Some examples of grazers are horses, deer, antelope, buffalo, giraffes, and zebras. They eat a lot of food and digest it slowly because it's primarily cellulose, thus they spend the most of their lives foraging.

Important Aspects of Food Selection

How do animals know where to look for food and how do they know what's edible and what's not? An animal's habitat comprises a wide variety of items, some of which are edible and others which are not. The challenge for hungry animals is to discern between non-edible and edible items and choose the best option. A specialist feeder eats only one or two types of prey, whereas an omnivorous feeder consumes a wide variety of foods.

- a. Competitive Principle-According to Lack (1954) and Mayr (1963), no two species living in the same period and area eat the same staple food. This prevents interspecific food competition, such as between four Serengeti species (wildebeest, Topi, Zebra, and Thomson's gazelle) and Galapagos finches.
- **b.** Learned Aversion- Many animals are protected from consuming harmful or risky foods due to learned aversion. Toxic compounds are found in the larvae and adults of several insects, such as the Monarch butterfly (Glycosides). Birds that consume them become ill as a result of this. The bird becomes nauseated and regurgitates the monarch butterfly or its larva that it has consumed. When a bird sees a monarch butterfly or its larva the next time, it equates the insect's appearance with the disease it caused and avoids eating it. Learned aversion is the term for this phenomenon.
- c. Energy budget in foraging strategy- The animal's choice of food is influenced by its foraging energy budget. The energy expended in searching, stalking, grabbing, and devouring food should always be less than the energy acquired from it. Because the zebra requires more food in proportion to its body size, it consumes more food. Thomson's gazelle, on the other hand, prefers a few nutrient-dense fruits due to its tiny body size. A lion approaching a large prey herd such as buffalo, zebra, or wildebeest first observes all individuals and then strikes the one that is crippled or sick. This conserve energy and reduces the likelihood of failure, similar to how lions conserve energy.

4.2.3 Anti-Predator Defences

Most organisms are at risk from predation. For this reason, many species have evolved certain traits or strategies that confer different degrees of protection. Such traits and strategies can be physical (morphological), chemical, or behavioural and can be exhibited by both individuals and groups. As a result, predator defences are very diverse and are widespread across the animal kingdom. However, several key strategies have evolved separately in multiple groups of animals.

Examples of Animal Defences against Predators

- a) Some animals use shelters or refuges within their home range;
- b) Many frog species avoid detection by displaying color patterns that match those of their background;
- c) Fish schools are an example of how some organisms move in groups to minimize the per capita risk of predation;
- d) Insects such as katydids avoid recognition by resembling inanimate objects, for example, leaves. Aposematic organisms display distinct color patterns that predators learn to associate with their unprofitability;
- e) Burnet moths (Family Zygaenidae) sequester cyanide compounds from their food plants, but are also capable to produce them de novo;
- f) The granular poison frog (*Oophaga granulifera*) uses its vivid colors to warn predators about its possession of toxic skin secretions;

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- g) Coral snakes (genus Micrurus) serve as models to some harmless colubrid snakes, which gain protection from predators by mimicking the coral snakes color patterns;
- h) Body inflation helps animals appear larger than they actually are and discourage attacks from predators, or can make subjugation more difficult;
- i) Weapons such as deer antlers may be used for purposes other than protection from predators, for example, during male-male competition;
- j) Eyespots in the wings of butterflies are thought to mimic vertebrate eyes and thus can startle predators, making them hesitate to attack;
- k) The defensive secretions of poison frogs contain mostly alkaloids that act as neurotoxins;
- 1) Blue tits (*Cyanestes caeruleus*), among other species of Paridae, produce mobbing calls when predators are nearby

4.2.4 Aggression

Aggression is a multifaceted notion that can be broadly described as behaviour that causes pain or harm to another person. Psychopaths engage in excessive amounts of this conduct for no apparent cause. Aggression in humans can be physical (e.g., hitting out) or verbal, whereas aggression in animals can take the form of a threat or an attack, resulting in a variety of 'kinds' of aggressive behaviour. Members of a group or individuals of different species frequently engage in aggressive displays or agonistic encounters. During aggressive displays, sounds that signal a readiness to fight can be heard. These sounds can be used by animals to assess an opponent's willingness to fight and fighting ability. Loud noises can also be used to frighten or repel a predator. There are several types of animal aggression:

- 1. Territorial defence when animals attack intruders who enter their 'territory'
- 2. Predatory aggression when a predator strikes its prey. This type of violence is thought to be caused by the lateral hypothalamus and certain 'trigger' inputs, rather than hunger (the animals it typically feeds on the prey).
- 3. Inter-male aggression It occurs when another (stranger) male is present. Androgen (hormone) is believed to be important in this form of aggression.
- 4. Fear-induced aggression Before this type of aggression is displayed attempts to flee are always present. When the animal is cornered and scared, this type of aggressive behaviour is most visible. Before attempting to flee, they will nearly always respond aggressively. The lateral hypothalamus is thought to play a role in this.
- 5. Irritable aggression this will be evoked by any attackable object or other animal. The ventromedial hypothalamus is believed to be the crucial brain structures here.
- 6. Maternal aggression when a female reacts with aggression in order to protect her young from harm.
- 7. Instrumental aggression When aggression has previously been successful in a certain situation, the animal will repeat the behaviour (in the same or similar situation therefore the behaviour has been reinforced via learning).

4.2.5 Homing

Homing is the capacity of certain animals to return to a specific location after being separated from it for an extended period of time. The main navigational clues utilized by homing animals appear to be the same as those used by migrants (sun angle, star patterns, etc.), but homing can happen in any compass direction and at any time of year. Birds, notably racing or homing pigeons, are the most well-known instances of exceptional homing ability; however, many other birds, particularly seabirds and swallows, are known to have similar or better homing abilities. In 12 1/2 days, a Manx shearwater (*Puffinus puffinus*) was transported in a closed container to a point roughly 5,500 kilometres (3,400 miles) from its nest.

- a. **Natal Homing-** The homing migrations of Pacific salmon (Oncorhynchus spp.) from marine feeding grounds to their native river to spawn are well-known. During their migrations, salmon pass through a variety of ecosystems (e.g., oceans, lakes, and rivers), each with its own set of orientation clues and, possibly, sensory requirements for navigation. Juvenile salmon imprint on odours linked with their natal place prior to their seaward migration and later utilise these odour memories for homing as adults.
- b. **Pigeon's Homing-** The ability is based on a 'map and compass' approach, with the compass helping birds to orient themselves and the map allowing them to locate themselves. Birds can detect a magnetic field and use it to navigate back to their nest. Scientists discovered a vast amount of iron particles on top of the pigeon's beak that remain oriented to the north like a constructed compass, acting as a compass that aids the pigeon in establishing its home. Low frequency infrasound waves as low as 0.1 Hz are also used by homing pigeons to navigate home land.

4.2.6 Territoriality

It's a sort of intraspecific or interspecific rivalry that arises from the behavioural exclusion of others from a territory-defended space. Songs and cries, intimidation behaviour (to frighten), assault and pursuit conduct, and scent marking behaviour are all examples of this well-defined behaviour. Animals must pay a high price for this type of defence. So, why do animals compete with each other across species? To grasp this issue, one must consider territoriality from a cost-benefit perspective. The immediate grounds for such a defence are numerous. Some animals engage in such elaborate defensive behaviour in order to obtain and safeguard food sources, nesting locations, mating areas, or simply to attract a mate. The greater likelihood of survival and reproductive success may be the ultimate reason of this behaviour. When an animal defends a territory, it is ensuring that it will have an environment in which to search for food and breed successfully, hence boosting the animal's total fitness. When one considers the circumstances under which territoriality grows, such as when resources are reduced, this final explanation becomes much more compelling. Due to territoriality, less fit animals are typically forced to reside in fewer than ideal settings, limiting their reproductive success. Territoriality has numerous reproductive and nutritional advantages, but it comes at a cost. It's not simple to defend one's land. Territoriality takes time and energy, and it can sometimes get in the way of other important tasks like parenting, eating, courting, and mating.

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As a result, territoriality may not be considered a benefit in all animals. Animals must be able to reap the benefits of territoriality with the least amount of effort possible. For these reasons, defending the region would be counterproductive if resources were plentiful and predictable. On the other hand, if resources are sparse and unreliable, territoriality would be favourable. An animal selects its territory by determining which portion of its home range it wants to defend. The size and quality of a territory are important factors in determining an animal's habitat. Because a rise in territory leads to an increase in energy expenditure, the size of the territory should not exceed the needs of the organism to survive. For some animals, the quality of defended territory, rather than the size of the area, is the most essential feature of territoriality. Due to the abundance of food and superior nesting sites, the quality is believed to be vitally significant. Animals rely on these characteristics to maintain their superior fitness. Animals devote a significant amount of time and energy to defending their territories, and as a result, they battle ferociously to protect their turf at all costs. Because of this, researchers believe that when a rival challenges a territory owner, the owner almost always wins. This phenomena could be explained by an evolutionary stable strategy in which the rules for behaviour are regulated by an inherited proximal mechanism, so that differences in tactics between individuals are similar to differences in genes.

Defending a Territory: Some animals defend their area by engaging in combat with intruders. Fighting, on the other hand, is not always the greatest option because it consumes a lot of energy and can end in harm or even death. Threats are communicated to most animals by vocalizations, odours, and visual displays. Bird melodies, woodpecker pounding, and monkeys' booming calls are all warnings that may be heard over long distances, alerting potential intruders that someone else's area is being approached. Many animals use fragrance to demarcate their territory, spraying urine, leaving droppings, or rubbing scent glands along the boundaries. Without ever coming into contact with the territory's defender, approaching animals will be told to leave. These warnings are occasionally disregarded, and an invader may wander into a neighbouring territory or two animals may collide on the border of their own territories. When two territorial species members meet, they usually threaten each other using visual displays. These demonstrations frequently fluff up an animal's feathers or hair to exaggerate its size, or show off the animal's weapons. Ritual fighting occurs when animals go through all the rituals of fighting without ever really touching each other. The displays are usually strongest towards the middle of an animal's territory, where it is more likely to attack an intruder, and become more fragmented near the edges, where retreating becomes more of a possibility. This range of behaviours leads in territorial borders, where neighbourly displays are roughly equal in intensity or where the tendency to attack and retreat are balanced. Actual conflict frequently occurs in overcrowded situations with few resources. Serious injury may occur, and elderly or diseased animals may succumb, resulting in a more balanced population size. Territoriality is an effective technique of maintaining a healthy population under most natural settings. The study of social behaviours of animals, such as territoriality, may aid our understanding of human society and how individual conduct influences human communities.

4.2.7 Dispersal

The mechanisms through which a species maintains or grows the distribution of its population are referred to as biological dispersal. Movement away from an established population (population expansion) or away from the parent organisms is referred to as dispersal (population maintenance). In the latter situation, dispersal could simply include the parent generation being replaced by the next generation, with only slight changes in the geographic region occupied. Dispersal is important in both cases because new life must replace old, and the two generations cannot easily share physical space during the changeover. More importantly, dispersal allows the population of a species to occupy a large portion of the available habitat, optimizing resources and increasing awareness of local adverse events. Competition avoidance, inbreeding avoidance, kin competition avoidance, breeding dispersal, and colonization dispersal are the five main causes of dispersal. Dispersal's main causes include:

- Competition Dispersal (habitat depletion)- This is most likely a major cause of plant dispersal, as the parental plant depletes resources such as light, root space, and nutrients. It is also important in many animal species, and it is a recurring subject in this framework. Infanticide is a typical response in rodents to habitat loss, and it can be regarded as a result of resource competition. Females and males who are unrelated to or unfamiliar with the puppies commit infanticide. Infanticide is substantially less likely in congested populations of related mice and voles.
- 2. **Inbreeding Avoidance-** It was observed in meadow voles that they were more likely to disperse from plots occupied by siblings than from plots occupied by non-siblings.
- 3. **Kin-Competition Avoidance-** This is really difficult to discriminate from inbreeding avoidance because the result is essentially the same; close kin end up not living near one another.
- 4. **Breeding Dispersal-** Gravid females may leave social groups or natal territories in order to give birth and nourish their progeny in more suitable locations. The rationale for this is similar to other causes of dispersal: habitat depletion may prompt movement, and colonization may be a goal of movement.
- 5. Colonization Dispersal- Selection may favor colonization of new habitats. Individual fitness can be enhanced for plants or animals that find a vacant habitat patch.

In most cases, organisms (especially sedentary animals) have evolved dispersal adaptations that take advantage of various forms of kinetic energy found in the environment, such as water movement, wind, and falling leaves (response to gravity). Animal species, like plant species, must disperse for a variety of reasons. There will be rivalry between members of a specific animal species if there are too many of them in the same location. Eventually, one or more of the following factors will contribute to the death of a large number of people: Food scarcity, oxygen deficiency, and waste accumulation can all lead to disease. Overcrowding, this would allow disease to spread quickly through the population.

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4.2.8 Host-Parasite Relations

A parasite is an organism that lives on or in the body of another organism, benefiting from the latter at the expense of the former. Only one of the partners benefit, while the other is hurt or injured. The parasite's host is the organism that hosts the parasite. In this connection, the parasite always benefits while the host is wounded or harmed. Parasites can be found in a variety of animal species. Ectoparasites are parasites that live on the surface of the host's body, such as head louse, ticks, mites, bedbugs, and leeches. Endoparasites are parasites that reside inside the host's body, such as malarial parasite or plasmodium in red blood cells. Liverfluke *Faciola hepatica* is a parasite found in sheep's bile ducts that causes liver rot. Certain parasites, such as *Entamoeba histolytica*, can complete their life cycle in a single host. The life history of many endoparasites, such as liver flukes and tapeworms, can be completed in two or more hosts.

The definitive host is the one in which the parasite reaches sexual maturity, while the intermediate host is the one in which the parasite is in the early stages of development. These parasites, particularly endoparasites, have a number of parasitic adaptations as a result of their parasitic lifestyle. These adaptations do actually take the shape of parasitism-related specializations. Many of the basic characteristics of the group to which these endoparasites belong have been altered as a result of parasitism, particularly in endoparasites. Endoparasites such as liver fluke (Trematoda) and tapeworm (Cestoda), for example, have a tough cuticle that can withstand the host's digestive enzymes. Suckers, in addition to the spines in the cuticle, are found in liver flukes for the function of attachment. Hooks and suckers can be found in tapeworms. Endoparasites lack locomotor organs and do not move about in quest of food because they acquire plenty of digested food from their hosts' digestive systems. These endoparasites lack sense organs as well. Because the parasite does not require digestive glands, liver-fluke does not have them. The digestive system of the tapeworm is completely missing. Food particles that have been digested are absorbed directly through the skin. In these endoparasites, the reproductive system is complex. Hermaphrodites are creatures that have both male and female characteristics. These endoparasites have a complicated life cycle that involves several intermediate hosts and a variety of dangers.

Check Your Progress

- 1. Define territoriality.
- 2. Mention two anti-predator defences in organisms.
- 3. Define habitat selection
- 4. What is competitive principle?
- 5. What is homing with respect to animals?
4.3 SOCIAL BEHAVIOUR

The interactions that occur between two or more individual animals, usually of the same species, when they form simple aggregations, cooperate in sexual or parental behaviour, engage in territorial disputes and access to mates, or simply communicate across space are all examples of animal social behaviour. Interaction, not the spatial distribution of organisms, determines social behaviour. Individual clumping isn't necessary for social behaviour, but it does improve opportunities for interaction. A lone female moth is engaging in social behaviour as she produces a bouquet of pheromones to attract male potential mates. When a male red deer (*Cervus elaphus*) roars to show authority and dominance to keep other males at bay, he's also being social.

General characteristics

Individuals' social behaviour can range from simple attraction to existence in complex communities defined by division of labour, cooperation, altruism, and a large number of people assisting in the reproduction of a small number of people. Interaction among aggregations or groups of persons, on the other hand, is the most commonly recognized form of social behaviour. Social organisms are frequently shown as intensely competitive and aggressive, which is consistent with Darwin's beliefs. If there aren't enough balls or swings on a playground, for example, amicable interactions might soon devolve into violent competition. Furthermore, even among family members, severe competitive encounters that result in bodily injury can occur. The goal of social behaviour is to improve an individual's ability to gather resources and build alliances that will help it live and reproduce. The current understanding of social behaviour is that it is the result of individuals' competing interests. Individuals develop the ability to act selfishly when it advantages them and to collaborate or compete when it benefits them. Animal societies are believed to have a delicate mix of cooperative and competitive behaviours.

4.3.1 Aggregation: Schooling in Fishes; Flocking in Birds; Herding in Mammals

Aggregation can be found in the tiniest species, such as bacteria, to the largest, such as whales. Territorial animals must share knowledge, but there is no need for a group structure. Human societies and honeybee hives are two examples of highly connected groups. Long-distance communication between known individuals (siblings, reciprocating group members) at predefined sites (the hive, the calving grounds, the dinner table, etc.) may supplement instantaneous sensory touch in these systems.

Schooling (Shoaling) in Fishes

A school of fish, also known as an aggregation of fish, is something that everyone has heard of. Schools of fish can be polarized (all fish facing the same direction) or non-polarized (all fish facing different directions) (all going every which way). There are a few things that can make hanging out with other fish beneficial.

Antipredator: By hanging out with other fish, each individual fish may gain an advantage in not being eaten by other fish.

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Confusion Effect: A large school of fish may be able to confuse a potential predator into thinking that the school is actually a much larger organism.

Dilution Effect: When a fish congregates with a large number of other fish and a predator approaches, the predator must usually choose one prey item. With so many options, there's a good chance it won't be you. This is referred to as the 'selfish herd.'

Predator Detection: Because a school of fish has many more eyes and other senses than a single fish, it may be better at detecting predators. However, because of its size, a school may attract predators.

Spawning Aggregation: Many fish species only form schools during mating season. They'll create a massive school and discharge massive amounts of eggs and sperm. Releasing a large number of fertilized eggs into the water, 56 may have advantages over releasing a single egg, because a large number of fertilized eggs may be adequate to combat egg predators. Although the predators will consume as many eggs as they can, some will surely survive.

Enhanced Foraging: A school of fish may have stronger food-gathering abilities. Many more eyes to detect food would mean many more meals, but it would also mean many more mouths to feed. The school may be able to capture greater food items by operating as a team than any single person could.

Migration: Because of improved navigation and other factors, fish in schools may be able to migrate more easily.

Hydrodynamic Efficiency: A fish may receive a swimming advantage by being in a school due to the complex hydrodynamic qualities of water. The slipstream (a movement of air/water behind a fast-moving object such as a car, an aeroplane, or a fish) from the fish ahead of it may make it simpler to pass through the water. Except for the ones in front, it's good for all the fish.

Flocking in Birds

'Birds of a feather flock together,' as the saying goes. You've probably seen a flock of birds flying through the sky, beautifully spinning this way and landing gracefully as a single unit, and wondered, 'How can they accomplish that?' Do they have a leader, and if not, how do they all decide to do the same thing at the same time in a democratic manner? With pigeons, you and a companion can do a small experiment in flocking behaviour. All you'll need is a lot of bread and a few pigeons. Toss the bread to the pigeons every five seconds, but have a friend do it every ten seconds. Half of the birds will go to you at first, and half will go to your friend. However, the pigeons will realize you're the better food source in two minutes, and two-thirds of the birds will be flocking around you. The flock of birds will then need another two minutes to readjust after you and your friend switch feeding rates, so your friend gives them twice as much food. After that, your acquaintance will own two-thirds of the birds. Without a leader, how do the birds know how to swarm from you to your friend and back? Birds, microbes, slime moulds, fish, whales, elephants, and wildebeest, as well as sheep, all flock. It turns out that being a part of a flock has a lot of benefits. Another benefit is that if you're small but there are a lot of you, you can occasionally join together against a larger common opponent and successfully repel it. The flock's 'collective

intelligence' is another benefit. People who spend a lot of time watching European starlings return to their California roost have found that a small flock gets lost more often than a large flock. There are suggestions that flocks of birds have higher aerodynamic efficiency. The spinning air flowing off the ends of the wings causes vortices (a mass of air or water that spins around very quickly and attracts items into its empty centre). The fact that most flocks of creatures don't appear to have a single leader is unusual.

Herding in Mammals

The term 'herd' refers to a big gathering of animals. The phrase is most commonly used to describe mammals, notably ungulates. In behavioural ecology, however, all of these types of assemblages are referred to as 'herds.' When a group of animals is referred to as a 'herd,' the inference is that the collective tends to act in concert, but not as a consequence of planning or coordination. Rather, each person chooses behaviour that is similar to that of the majority of other members, potentially as a result of imitation or because they are all reacting to the same external circumstances. A herd is distinguished from a coordinated group in which individuals have specific duties. The question of why animals group together is one of the most fundamental in sociobiology and behavioural ecology. As noted above, the term 'herd' is most commonly used of grazing animals such as ungulates, and in these cases it is believed that the strongest selective pressure leading to herding 58 rather than a solitary existence is protection against predators. There is clearly a tradeoff involved, since on the one hand a predator may hesitate to attack a large group of animals, while on the other a large group offers an easily detected target. Risk dilution is seen to be the most essential protective feature; even if a predator attacks the herd, the chances of any individual becoming a victim are greatly reduced. Because there may be some degree of coordination or job differentiation in group hunting, it is often unclear whether the term 'herd' is suitable in the case of predators. Predator packs are often smaller than grazing packs because, while a pack may be more effective at catching prey than a single animal, the prey must then be shared among all members. By definition, a herd is loosely organized. However, there may be one or a few animals who are more frequently mimicked by the rest of the herd than others. A 'control animal' is an animal that plays this job and predicts the behaviour of the herd as a whole. The control animal, on the other hand, cannot be considered to be acting as a leader on purpose.

4.3.2 Group Selection, Kin Selection, Reciprocal Altruism, Inclusive Fitness

When the qualities of groups that consistently out-produce competing groups eventually come to characterize the species, this is referred to as group selection. The effectiveness of group selection, that is, the degree to which social group features can be attributed to selection on these characteristics, has long been a source of debate among evolutionists. The intractable nature of this debate stems from three inconsistencies in the natural selection metaphor, which manifest when the metaphor is applied to groups: (1) doubt about what defines a group trait for the purposes of group selection; (2) uncertainty about how to identify the group 'parents' of offspring groups; and (3) uncertainty about what constitutes the Various Aspects of Animal Behaviour

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analogue for 'flock' in the group level metaphor. These difficulties resolve when group selection is defined as a hypothesis concerning the evolution of emergent qualities of groups via differential group productivity mediated by quantitative inheritance of group attributes. When the qualities of groups that consistently outproduce competing groups eventually come to characterize the species, this is referred to as group selection. Group selection would appear to be a reasonable explanation for seemingly altruistic tendencies in humans, such as group defence behaviours, which appear to promote the group's interests over the individual holding the trait. Most evolutionary psychologists, on the other hand, have shied away from group selection hypotheses. The most common reason is that group selection explanations are implausible—groups can only 'reproduce' through the production of individuals, and any costly behaviour of individuals that benefited groups would eventually be eliminated from the general population by virtue of being eliminated from every group that made up the population. This is not a selfevident conclusion.

Kin Selection

The first hypothesized explanation for the existence of altruism, kin selection, describes how altruism might develop among close relatives. This type of altruism is demonstrated when adult animals risk their lives to divert prospective predators away from their offspring. Because such behaviour reduces an animal's chances of surviving while increasing the chances of its offspring, it is evolutionarily stable. Kin selection can occur between any animals that are relatives in proportion to their coefficient of relatedness, though it is most visible in the case of direct offspring (the proportion of genes that two individuals share by common descent). When the exact link is unknown to the animals involved, it's likely that they use apparent similarities to assess the degree of relatedness. Kin selection is based on a simple concept. Consider a gene that leads its carrier to act altruistically toward other organisms, such as by sharing food. Organisms without the gene are selfish, keeping all of their food for themselves and occasionally receiving handouts from altruists.

Altruists will clearly be at a disadvantage in terms of fitness, hence we should expect the altruistic gene to be eliminated from the population. Assume, however, that altruists are selective in who they share their food with. They don't share with just anyone, but exclusively their family members. This quickly alters the situation. Relatives share DNA and are genetically similar to one another. When an organism with the altruistic gene shares its food, there's a good chance that the recipients will also have copies of the gene (how probable depends on how closely related they are). This suggests that natural selection can spread the altruistic gene. The gene allows an organism to act in a way that lowers its own fitness while increasing the fitness of its relatives, who have a higher than average probability of harbouring the gene. As a result, the behaviour's overall effect may be to increase the number of copies of the altruistic gene found in the next generation, and hence the incidence of altruism.

Though Haldane hinted at this argument in the 1930s, William Hamilton was the first to make it clear (1964). Hamilton proved that when a certain condition, known as Hamilton's rule, is met, an altruistic gene will be favoured by natural selection. The rule asserts that b > c/r, where c is the cost incurred by the altruist

(the donor), b is the benefit obtained by the altruist's recipients, and r is the relationship coefficient between donor and recipient. In terms of reproductive fitness, the costs and benefits are calculated.

The coefficient of relationship is determined by a genealogical link between the donor and the receiver; it is defined as the chance that donor and recipient share genes that are 'same by descent' at a specific location. The value of r for full siblings in a sexually reproducing diploid species is 12(0.5), for parents and offspring 12(0.5), for grandparents and grand offspring 14(0.25), for complete cousins 1/8(0.125), and so on. The higher the value of r, the more likely it is that the altruist's recipient will have the altruism gene.

So, according to Hamilton's rule, a gene for altruism can spread through natural selection if the cost to the altruist is offset by a substantial amount of benefit to sufficiently near related relatives. Despite the fact that Hamilton did not use the term, his concept was rapidly dubbed 'kin selection' for obvious reasons. According to kin selection theory, animals are more likely to act altruistically toward their relatives than toward unrelated species members.

These predictions have been fully validated by empirical investigation in the years since Hamilton's theory was devised. For example, it has been discovered that 'helper' birds are significantly more likely to assist relatives in raising their young ones than they are to assist unrelated breeding pairs in various bird species.

Similarly, studies of Japanese macaques have revealed that altruistic behaviours, such as defending others from attack, are mostly focused at close relatives. In most social insect species, a genetic anomaly known as 'haplodiploidy' means that females share more genes with their sisters than with their own children on average. So, rather than bearing kids of her own, a female may be able to pass on more genes to the next generation by assisting the queen in reproducing, so increasing the number of sisters she would have. As a result, kin selection theory offers a simple explanation for how sterility in social insects may have evolved through Darwinian processes.

Individual organisms are merely 'vehicles' that genes have constructed to aid their propagation, according to the 'gene's-eye view of evolution,' which sees organic evolution as the result of competition among genes for increased representation in the gene pool, and kin selection theory as a victory of the 'gene'seye view of evolution,' which sees organic evolution as the result of competition among genes for increased representation in the gene pool, and individual organisms as mere 'vehicles' that genes have The gene's eye-view is unquestionably the simplest way to comprehend kin selection, and Hamilton himself used it.

Altruism appears odd from the perspective of the individual creature, but it makes perfect sense from the perspective of the gene. A gene seeks to increase the number of copies of itself discovered in the future generation, and one way to do so is to encourage its host organism to act altruistically toward other gene bearers, as long as the costs and benefits fulfil the Hamilton inequality. However, Hamilton demonstrated that kin selection may be understood from the organism's perspective. Though altruistic behaviour spreads through kin selection, it diminishes the organism's own fitness while increasing its inclusive fitness, as Hamilton defined it. The sum of an organism's weighted impacts on the fitness of every other organism

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in the population, with the weights given by the coefficient of relationship r, is the organism's inclusive fitness.

Reciprocal Altruism

Though kin-directed altruism is common in nature, it is far from universal: there are several examples of animals behaving altruistically toward non-relatives, and even members of different species. We can't understand these behaviours using kin selection theory. Trivers' (1971) hypothesis of reciprocal altruism is one effort to explain the evolution of benevolence among non-kin. The underlying concept is simple: one animal may gain from behaving altruistically toward another if there is a chance that the favour will be returned in the future. The cost of acting altruistically to the animal is offset by the likelihood of this return benefit, allowing the behaviour to evolve through natural selection. Reciprocal altruism is the name given to this evolutionary mechanism for obvious reasons. It is not necessary for the two people to be related or even members of the same species for reciprocal altruism to occur. Individuals must, however, connect with one another multiple times and be able to recognize other individuals with whom they have previously interacted. There is no value to be obtained by acting altruistically if people only interact once in their lives and never see each other again. However, reciprocal altruism can emerge if people interact regularly and are capable of recognizing and punishing 'cheaters' who have previously refused to act altruistically. A non-altruistic cheater will be less fit than an altruist because, while he avoids the cost of acting altruistically, he also forfeits the return advantages - others will not act altruistically toward him in the future. The Tit-for-Tat method is strongly tied to the concept of reciprocal altruism. Where animals dwell in tiny groups, this evolutionary mechanism is most likely to work.

Trivers (1985) offers a striking example of reciprocal altruism between individuals of different species, a phenomenon known as 'mutualism' or 'synergism.' Various kinds of small fish operate as 'cleaners' for giant fish on tropical coral reefs, eliminating parasites from their mouths and gills. The cleaners aren't acting out of pure charity because they eat the parasites they're removing. As a result, the contact benefits both parties: the large fish is cleaned, and the cleaner is fed. However, Trivers observes that the large fish can be helpful to the cleaners at times. When a predator attacks a huge fish with a cleaner in its mouth, the fish waits for the cleaner to leave before fleeing the predator. This is obviously altruistic; after all, wouldn't the large fish be better off ingesting the cleaner and escaping right away? The larger fish's behaviour is explained by Trivers in terms of reciprocal altruism. Because the huge fish frequently returns to the same cleaner, it is advantageous to protect the cleaner's welfare by avoiding swallowing it, even if this raises the risk of being injured by a predator. In brief, the larger fish acts altruistically toward the cleaner by allowing him to flee before escaping, knowing that there would be a future benefit - being cleaned again.

Inclusive Fitness

Inclusive fitness describes how an organism's genetic success is thought to be based on cooperation and altruism. According to the idea, altruism among creatures that share a certain percentage of genes allows those genes to be handed along to future generations. In this approach, an altruistic act that helps a relative or other individual survive theoretically improves both the beneficiary of the act and the altruistic organism's genetic fitness. The transmission of shared genes was thought to be a key factor in the emergence of eusociality (cooperative behaviour characterized by division of labour and group integration that is found in certain species of animals, mainly social insects).

J.B.S. Haldane, a British scientist, initially suggested the concept of inclusive fitness in his book 'The Causes of Evolution' in 1932. Inclusion fitness was later termed and developed by British evolutionary biologist William Donald Hamilton, who used it to explain both direct (reproductive) and indirect (assisted by a relative or a colony member) transmission of altruistic genetic features. Hamilton introduced his inclusive fitness hypothesis in 1963, and the phrase 'kin selection' was created the following year by British evolutionary biologist John Maynard Smith to define Hamilton's idea. Inclusive fitness was eventually recognised as a foundation for kin selection theory, which aims to explain altruistic social behaviour in animals through genetic relatedness and the rewards and costs of altruistic behaviours. In contrast to inclusive fitness, which takes into account genetic features in both related and unrelated individuals, kin selection solely examines relatives. Many biologists believed that Hamilton's inclusive fitness theory, as well as kin selection, resolved the conflict between natural selection, in which 'selfish' genes perpetuate their own fitness through survival of the fittest, and selfless behaviour, in which eusocial genes shared by relatives and colony members influence cooperative behaviours that encourage the propagation of those genes.

Inclusive fitness theory has been used to explain cooperative breeding in animals such as birds and the adoption of orphaned young by social red squirrels. It is most commonly applied to eusocial organisms like bees and ants, but it has also been used to explain cooperative breeding in animals such as birds and the adoption of orphaned young by social red squirrels (Tamiasciurus hudsonicus). Some members of certain bird species, such as the Florida scrub jay (Aphelocoma coerulescens) and the groove-billed ani (Crotophaga sulcirostris), will linger around nesting sites and help rear related offspring. Individuals who do not disperse to their own territories are assumed to value the inclusive fitness gains of cooperative breeding over dispersal to possibly less-favourable territory. In these cases, inclusive fitness through cooperative breeding is the outcome of territorial quality limits, which are impacted by factors including food, mating attraction, and predation. Indeed, being close to relatives is less favourable in the absence of limitations, potentially restricting breeding options and so making kin selection and inclusive fitness less beneficial to reproductive success. Individuals who participate in cooperative breeding commit varying amounts of time and effort to raising kin. Eusocial species, on the other hand, have fixed and stereotyped labour divisions; castes such as sterile labourers, for example, are thought to acquire reproductive advantages by assisting their relatives in the cooperative nurturing of young.

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4.3.3 Social Organization in Insects and Primates

Following are the methods of social organization in insects and primates:

Social Organization in Insects

Many animals live in groups, but they are not always sociable (for example, a school of fish) because sociality has a very specific meaning. Three characteristics describe true sociality (eusociality): 1). There is cooperative brood-care, thus each individual is not responsible for its own progeny, and 2) The generations overlap in order for the group (the colony) to survive for a while, allowing offspring to help parents during their lives as well as 3). That there is a reproductive division of labour, i.e., that not every individual in the group reproduces equally; in the case of insects, this usually means that there is one or a few reproductive(s) ('queen,' or 'king'), and workers are more or less sterile.

Degrees of sociality: Obviously not all insects are eusocial. Michener (1969) provided some other classifications of various stages of social insects:

- a) Solitary: Showing none of the three featured mentioned above (most insects)
- b) Subsocial: The adults care for their own young for some period of time (cockroaches)
- c) Communal: Insects use the same composite nest without cooperation in brood care (Digger bees)
- d) Quasisocial: Use the same nest and also show cooperative brood care (Euglossine bees)
- e) Semisocial: In addition to the features in quasisocial, also has a worker caste (Halictid bees)
- f) Eusocial: In addition to the features of semisocial, there is overlap in generations (Honey bees)

Eusociality was thought to be extremely rare throughout the animal kingdom, and it was only seen in Hymenoptera (ants, bees, and wasps) and Isoptera (flies) in insects (termites). However, this has recently expanded to a few additional groups: infertile soldiers in gall aphids (Homoptera) would sacrifice their life for their clone sisters who can reproduce, making them eusocial because some soldiers do not reproduce while others do. This is likewise the case with gall-forming social thrips (Thysanoptera). Eusociality was only found in non-insects twice: in a mammal and a marine animal. Naked mole rats live in Africa's complex underground tunnel systems, and while animals in the same nest are closely related, only one female (the queen) reproduces, despite the fact that workers, who are normally sterile, can ovulate when removed from the nest, presumably due to the queen's lack of inhibition.

Evolution of Eusociality: What are the possibilities for eusociality? Darwin believed that sterile workers in a bee colony, which are unable to transmit their genes, provide a unique challenge to his theory of natural selection in his 1859 book '*Origin of Species.*' This is due to the fact that natural selection relies on the transmission of 'traits' that provide individuals with selected benefits, and these traits must be determined genetically (so they are heritable). How can workers pass on their 'helpful attributes/traits' to the next generation if they are sterile?

Genetic Explanations: This conundrum perplexed biologists until William Hamilton (1964) devised an intriguing explanation for how a feature might be inherited without being passed down via the generations. Hamilton coined the term 'inclusive fitness,' which basically means that someone can be reproductively fit even if they have no direct progeny. While traditional fitness solely considers how many children a person has, inclusive fitness considers all people who share the person's genes (or animal). For example, I should share around 50% of my genes with my full brother, so if I choose not to marry and have children, but instead help my brother raise four children, I will have two children. The term 'inclusive fitness' refers to the inclusion of anyone else's fitness. Although workers do not reproduce, if they share DNA with their mother (the queen) in order to raise additional sisters (future queens), their genes will be passed down to future generations as well.

In fact, in honey bees and other hymenoptera, sisterhood is more common than in other species. This is due to the haplo-diploidy sex determination: drones emerge from unfertilized eggs and only have one copy of chromosomes (haploid) from their mother (no father), whereas females are fertilized and have two copies of chromosomes (diploid). Because haploid drones lack the complementary copy of genes required for gene exchange, all sperm generated by a single drone are identical. If the queen marries a drone, all of her daughters will share 50% of the father's genes and 25% of the mother's DNA. As a result, the coefficient of relatedness among the children is 0.75. In a diploid organism, this is substantially higher than the 0.5 for sister-sister (such as humans). Because of their heightened relatedness, workers who share the same father and mother are referred to as 'super-sisters.' Kin selection is the hypothesis that one can pass genes down via one's family and improve one's fitness.

Because super-sisters share 75% of their genes, Hamilton hypothesized that it is really a better deal to be a worker, because a new queen would get 75% of her genes by common ancestry with her, whereas the queen only passed 50% of her genes to the new queen. In this respect, the inclusive fitness of the sterile worker sisters is higher than that of the fertile mother. Because half-sisters (workers who have the same mother but are fathered by different males) are only connected to one another by 0.25, the honey bee queen actually mates with more than one male (drone), in some circumstances as many as more than 30 drones. Similar to other diploid species, the average relatedness among the workers in such a colony is close to the average between 0.75 and 0.25, which is 0.5.

Relationship		Relatedness (r)	
• Mother	daughter	1/2	
• Mother	son	1/2	
• Father	daughter	1	
• Father	son	0	
• Daughter	mother	1/2	
• Son	mother	1	
• Brother	sister	1/2	
• Brother	brother	0	
• Sister	sister	1/4	
• Sister	brother	1/4	

Fig. 4.1 Average Relatedness

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However, it is easy to see how eusociality can evolve more quickly in groups where individuals are closely related, either because of haplodiploidy or because of mating systems. Animals within a group are highly linked in both termites and naked mole rats, possibly due to inbreeding. However, it is known that some males in naked mole rats relocate to different nests to perform periodic outcrossing, which may be necessary to lessen the expense of inbreeding. Because the mother can reproduce asexually, all colony members are clones in aphids (parthenogenesis).

Social Behaviour in Primates

The term 'society' refers to a group of individuals of the same species who work together in ways other than sexual and parental conduct. Mothers, daughters, sisters, aunts, and nieces make up the group. Dispersion among males is more common than dispersion among females. Many mammals have complex social structures. High body size, large brain capacity, open habitats, and diurnal behaviour are all linked to social behaviour in mammals. Survival and fitness, cooperative predator avoidance, ready access to mates, kin selection, and thermoregulatory benefits are all thought to be enhanced by sociality. However, there are drawbacks, including as competition for food, mates, and space, increased visibility to predators, and the spread of disease and parasites.

Social Structure: The majority of primates, including humans, live in huge social groupings. Semi-terrestrial species, such as baboons, benefit from being in a large community since predatory cats, dogs, and hyenas are less likely to attack them. It also aids in the preservation of limited food supplies. When the diet is fruit, this is especially true for nonhuman primates. Because there is minimal competition for their food, leaf-eaters like langurs prefer to establish smaller social groups. The few night primate species are usually small, solitary hunters. The majority of nonhuman primate societies are more or less closed to contact with other non-human primate communities. They are usually confined to specific environments and only rarely migrate outside of their natural range. This hostility from other armies prevents large groups of people from forming, which might lead to a rapid depletion of local resources. In most cases, communities shun one other and are hostile to outsiders. As a result, social connections between members of different troops are uncommon, particularly among women. Chimpanzees are an exception to this rule. When chimps from different populations meet, they often have an exciting, pleasant interaction that lasts several hours before some of the older females swap groups. They appear to be looking for new partners.

Contact between groups of the same species in some forest-dwelling primates takes the shape of a specific territorial defence behaviour. Rather than avoiding each other, groups congregate around their common territorial line and demonstrate aggressive behaviour. For this reason, howler monkeys and gibbons all make extremely loud vocalizations. This is a ritualized, largely harmless kind of aggression used to terrify individuals of the surrounding community. All of these animals have tiny home ranges that allow them to see and be attracted to the food supplies of neighbouring territories.

Non-human Primate Social Group Composition: While there is a lot of variety in the composition of social groups among monkeys, there is very little variation

within each species. In fact, the majority of nonhuman primate species follow only one of the following general patterns:

Single Female and Her Offspring: The group pattern of a single female and her progeny is uncommon in primates but typical in other animals. They do, however, come together with females for mating on occasion. Males of these species typically have vast territories that overlap multiple female territories.

Monogamous Family Group: Monogamous families are made up of an adult man and female, as well as their children. When the children reach adulthood, they form their own nuclear families. While this is the most common group pattern in humans, it is uncommon in nonhuman primates. It can be found in small Asian apes as well as some New World monkeys. For gibbons and monkeys, monogamous family groups are the most typical pattern.

Polyandrous Family Group: Monogamous and polyandrous family groups exist among the smallest New World monkeys. They usually begin with a monogamous couple. A second adult guy may eventually join the household to help with kid rearing. Both adult males have a chance to mate with the adult female if this happens. Nonhuman primates rarely exhibit this polyandrous mating style.

One-Male-Several-Female Group: Polygynous mating patterns are found in one-male-several-female groups. That is, a single man mates with multiple females on a regular basis. Polygyny is not a promiscuous mating tendency in general. The male and his female partners, on the other hand, constitute a separate mating and child-rearing group. Baboons, langurs, howler monkeys, and gorillas all have this pattern.

It would be a mistake to believe that males dominate nonhuman primate communities with one male and multiple females. Females govern the social group to a significant extent. Despite the fact that males are larger, stronger, and more aggressive, females outnumber males. Mothers, sisters, and aunts work together to keep other unrelated females at bay. They also choose their mutual partner as a group from among a variety of eligible suitors who pass through their territory. The male that is picked is usually one who is not abusive to them and is prepared to work with them to defend their area. It's possible that your relationship with a certain male will be short-lived. The community's steady core is a group of connected females. This is a far cry from the stereotype of masculine dominance.

When predator pressure is a problem, one-male-several-female groups may take on a new shape. Baboon populations in open grasslands are substantially larger, frequently containing several polygynous families. Males are the dominant, dominating members of such many one-male-several-female group cultures. Adult males not only 'herd' their sexually mature females, but they also keep the group in order and guard it from predators. Gorillas, on the other hand, rarely have to worry about predators. As a result, their societies are dominated by a single adult male, his mates, and their young ones. When males attain maturity, the dominant silverback male usually drives them away. Exiled male eventually form their own one-male, multiple-female groupings.

Multimale-Multifemale Group: The multimale-multifemale group is the most common social group type among semi-terrestrial primates. There are no stable

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heterosexual ties in this system, as both males and females have a variety of mates. Baboons, macaques, and some monkeys are known for this behaviour. Both males and females in these groups usually maintain a dominance structure. Each person is ranked in relation to other people of the same gender in the community. Because everyone knows who they must defer to and who must be submissive to them ahead of time, this tends to decrease major conflict within the group. The rank of one's mother determines one's position in the dominance hierarchy among rhesus macaques. Primatologists refer to the top-ranking individuals as the alpha male and alpha female. Everyone else in the community looks up to them. A woman's position in the hierarchy follows her throughout her life. Most young adult male rhesus macaques, on the other hand, leave their original community and eventually join others in search of mates. They return to the bottom of the male dominance hierarchy when they do so. Alpha guys mate more frequently than others. This gives the social organization the appearance of a one-male-several-female group on the surface. Younger females, on the other hand, frequently sneak away to mate with males lower in the dominance hierarchy. The group of female relatives is the stable core of rhesus macaque societies. They live their entire lives in their natal village and work together to defend it against other females.

Fission-Fusion Society: A fission-fusion society is one in which the size and composition of the social group fluctuates throughout the year as a result of various actions and conditions. Chimpanzees have a social pattern similar to this. Individuals move in and out of communities on a regular basis. Adult males will occasionally go off on their own to forage or form a hunting party with a few other guys. Females switch from one group to the next on a regular basis. This happens a lot when females are in estrus and looking for a partner. As a result, foraging and sleeping groups reorganise on a regular basis. Male chimps constitute the community's reasonably solid core, as they rarely join other groups.

Check Your Progress

- 6. Define kin selection.
- 7. What is social organization in animals?
- 8. What is inclusive fitness?
- 9. What is reciprocal altruism.
- 10. What is herding in mammals?

4.4 **REPRODUCTIVE BEHAVIOUR**

All of the events and activities that are directly involved in the process by which an organism develops at least one replacement of itself are referred to as reproductive behaviour in animals. In evolutionary terms, an individual's purpose in reproducing is not to perpetuate the population or the species; rather, it is to maximize the representation of its own genetic features in the next generation relative to other members of the population. Although it is easier mechanically for an organism to divide into two or more individuals, the primary form of reproductive behaviour for this purpose is sexual rather than asexual. Even many species that do exactly

this and this does not include all so-called primitive forms intersperse their typical asexual pattern with sexual reproduction every now and then.

4.4.1 **Reproductive Strategies**

Although every organism strives to survive, individual survival is insufficient to ensure the species' existence. Individuals are need to reproduce. Because reproduction requires extra energy, it appears that species that are best fitted to capture energy from the environment are also the ones most likely to leave a large number of progeny. Survival of the fittest aids in the survival of animals and plants that are powerful and well-adapted to their surroundings.

Two techniques for leaving living offspring have been uncovered by scientists. These are known as the r-strategy and the k-strategy. Some creatures, such as animals and plants, utilize one method or the other: some appear to favour one over the other, while others appear to fall somewhere in the middle. To help you remember which method is which, the R stands for Rapid. R-selected parents have a lot of children, but they don't look after them. We see that r-selected creatures have a lot of kids, but most of them never grow up. r-selected creatures, such as frogs, are a good example. Frogs lay a lot of eggs and then leave them to hatch into tadpoles in the water. Dragonfly larvae, fish, and fishing birds eat some of the eggs, and many of the small tadpoles are also devoured. Many animals await the tadpoles' transformation into frogs on the shore, including foxes, snakes, cats, and other small predators. If one frog out of a hundred survives to become a parent, that is quite remarkable. Frogs, on the other hand, continue to reproduce because they lay so many eggs.

Elephants are an example of an animal that has been chosen by K animals. Female elephants have infants every three years or so, and each time they only have one. The entire group looks after and protects the children throughout their childhood and youth. Elephants can thrive in stable habitats by reproducing at a rate that keeps their numbers close to constant. Elephants do not need to generate numerous elephant offspring because they secure the survival of a large majority of their young.

Reproductive Strategies				
r-selected	k-selected			
mature rapidly	mature slowly			
short-lived: most die before they reproduce	tend to live long lives: low juvenile mortality rate			
have many offspring: tend to reproduce more	have few offspring at a time			
invest little in individual youngsters	care for their young one			
most pest species are r-selected	most endangered species are k-selected			
population not regulated by density: boom and bust population figures	population stabilizes near carrying capacity			
opportunistic- invade new areas	maintain number in stable ecosystems			

Table 4.1 Reproductive Strateg	gies
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4.4.2 Mating Systems

Mating is one of the most significant animal activities. It is the union of an adult male and a female in order to generate offspring. Adults who succeed in enticing a mate are more likely to produce offspring. Animals with traits that aid in attracting a partner and producing progeny are more fit. The features will grow increasingly widespread in the population as the genes that encode these traits are passed down to the following generation.

Monogamy: Male and female defend a territory against solitary individuals, both range together, mate as a pair, and often live as a pair, e.g. lemurs, monkeys, and gibbons - may have two females or two males, with one not breeding. Males and females in monogamous species pair up for the breeding season. Individuals may form lifelong bonds in various instances.

Polyandry: Mate with more than one male - the smaller animals (females) need more help raising offspring and thus get more paternal care (carrying the infants and supplementing their food).

Polygyny: Howler monkeys, leaf monkeys, and gorillas, for example, face pressure to increase group size in order to defend resources when one male mates with more than one female. Males in polygynous species have several female companions during a breeding season. In some circumstances, a male may have authority over a huge number of females, whereas in others, a male may engage in sequential polygyny, in which he meets with multiple females. Multimale polygyny occurs when the number of females increase and one male is unable to keep other males out, as in howler monkeys, capuchins, baboons, macaques, and leaf monkeys.

There are various subcategories of polygynous and polyandrous mating systems that are classified according to whether they are resource-based or not. A man protects a resource that might support numerous females in a resourcebased polygynous mating system. Females gather in regions with the sole aim of picking a partner in a non-resource driven mating system like a lek. Males congregate and exhibit in these areas in order to acquire access to females.

Lek Paradox: Females end up settling on a male's territory or depositing eggs on a male's territory as a result of the quality of his territory in the evolution of a resource-based mating system. Females approach and select from among the available males. The lek's dilemma is that they normally only mate with one guy. Many females, on the other hand, form a line and mate with a single male. The real conundrum is why other males bother to come to the lek at all if only one male would be copulated. These males would be better off looking for females because they would at least obtain one or two copulations and would not wind up as enormous losers. Many species form leks - fish, insects, birds. It is nearly a winner take all form of mating. There are big winners and big losers.

4.4.3 Courtship

Courtship in animals is a complicated set of behaviours that lead to mating. This conduct sends a message to each possible mate that the other isn't a threat. It also informs each animal that the other's species, gender, and physical characteristics are suited for mating. The majority of pre-mating practices are ritualistic. They are

made up of a set of species-specific fixed action patterns. Each predetermined action causes the partner to respond in kind, with one action encouraging the next. Courtship allows one or both sexes to choose a mate from a pool of potential partners. The females are usually the ones that make the decisions. Males exhibit in a lek, a small communal space where females choose a mate from the displaying males, in some bird species. Males compete for mates in general, and females choose the highest-quality guy available. Courtship has the potential to attract predators rather than mates.

Several basic factors influence a female's choice of mate:

- If a woman is responsible for the care of her children, she chooses a man who capable and feasible. In birds like the common tern, for example, the female chooses a good fish catcher. Male birds display fish to female birds during courtship and may even feed them to her. This indicates his ability to provide for his children. Furthermore, females prefer males who provide resources such as food or shelter, which aid a mating couple in producing more viable offspring.
- Males of the long-jawed long-horned beetle, which lives in Arizona's desert, compete for saguaro cactus fruit. In exchange for access to the fruit, the females mate. Large mandibles enable a male to beat other males, seize control of the fruit, and therefore attract females. Another key component in mate selection is genetic fitness.

In creatures that lack parental care, kids rely on traits inherited from their parents to survive. Energetic displays and a dazzling look during courtship suggest robust health. Immunities are passed down from parents who are active and attractive, to their children. The intensity of secondary sex features, such as colourful plumage and long tails in birds, may influence attractiveness. Another advantage is that babies with inherited beautiful characteristics are more attractive to mates.

4.4.4 Sexual Selection

Charles Darwin created the theory of sexual selection, which posits that the frequency of features can rise or fall based on the beauty of the bearer. Today, biologists distinguish between 'male to male combat' (in which males usually fight), 'mate choice' (in which females usually choose male mates), and 'mate compulsion' (forced mating).

Qualities chosen for 'male combat' are referred to as 'weapons,' while traits chosen for 'mate choice' are referred to as 'ornaments.' Internally fertilizing animals such as mammals and birds have recently received a lot of attention for cryptic female choice, a phenomena in which a female may simply dispose of a male's sperm without his knowing. In male-to-male warfare, sperm competition is the equivalent. The exact effect of sexual selection is determined by the sex ratio, which is normally skewed toward the 'limiting' sex (typically females). Intrasexual competition includes male-to-male conflict, whereas intersexual competition includes mate choice and mate compulsion.

Females frequently prefer to mate with males who have external ornaments¹ - morphological traits that are exaggerated. These could evolve as a result of an Various Aspects of Animal Behaviour

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arbitrary female preference for a particular component of male morphology being amplified by genetic drift, eventually leading to selection for males with the proper adornment. The sexy son hypothesis is what it's called. Genes that enable males to produce enormous decorations, on the other hand, may simply display stronger illness resistance or a more efficient metabolism, both of which are beneficial to females. The good genes hypothesis is the name for this concept.

An organism's success is determined not just by the number of offspring left behind, but also by the quality or likelihood of success of those offspring: reproductive fitness. Sexual selection, also known as interspecies selection, is the expansion of organisms' ability to distinguish themselves at the species level.

Males are more excited than females in almost all species, and 'the female, with the rarest of exceptions, is less eager than the male, she is coy' (shy/reserved). In his book '*The Descent of Man and Selection in Relation to Sex*,' Darwin wrote these remarks 140 years ago. He theorized that females choose mates who are 'vigorous and well-armed,' similar to how a male might improve the breed of his game-cocks by selecting those birds who are triumphant in the cock-pit.'

Males, who can generate a large number of kids with little effort, distribute their genes most efficiently by mating frequently. Female reproductive production is regulated significantly more by the metabolic costs of generating eggs or kids, therefore partner quality rather than mate number serves a female's interests.'

Male aim to fertilize as many females as possible, while females look for males with the greatest genes. As in the case of peacocks, genetically superior males differentiate themselves as the winners of male-male competitions, as well as having the most expensive and exquisite ornaments. The 'sexual-selection theory' is made up of these male and female profiles, as well as the 'cheap sperm/expensive egg' explanation.

More sex is usually better for males, according to sexual-selection theory. Males who mate whenever the opportunity arises, and when possible, create their own opportunities, will have more offspring. This trend appears to be followed by mammals. About 90% of mammalian species are polygynous, with one male caring for many females. Monogamy, on the other hand, is not only possible, but also common.

90% of bird species are economically monogamous, meaning that the male and female birds work together to raise the eggs in their nest. Some of those eggs are often sired by surrounding males, while females lay some eggs in neighbouring nests, resulting in a distribution of parental ties in neighbourhoods. As a result, economic monogamy in birds frequently occurs without reproductive monogamy. Males contribute to parental care in monogamous mammals by creating a den, burrow, or lodge, protecting the family's feeding territory, feeding his partner, and so on. Although not as common as in birds, mammalian monogamy does happen. Most wild canines, as well as 15 percent of primates, are faithful to a single mating partner. Monogamy too contradicts sexual selection.

Sexual selection considers mating to be only for the sake of conception. However, the purpose of mating is frequently not to produce children; rather, it fulfils a societal function. To be solely for conception, mating occurs far too frequently in relation to the quantity of children produced. As with our closest living relatives, sex closeness strengthens adult relationships, reduces social conflicts, and keeps groups together. Strong social ties let men and females work together to protect and rear their young.

4.4.5 Sperm Competition

'Competition between sperms of two or more males for the fertilisation of an ovum' is the definition of sperm competition. Sperm competition is frequently described as having lottery tickets; the more tickets a man has, the better his chances of winning (i.e., fathering babies) (i.e., the more sperm he inseminates a female with). However, sperm are expensive to make, and the energy could be better spent elsewhere, such as defending a territory against other males; this is known as strategy.

Sperm competition may lead to evolutionary changes such as enlarged testes to produce more sperm. Because such adaptations are costly, animals with little sperm competition invest instead in mate competition. Other ways to compete for sperm include enhancing the sperm itself or the materials used to package it (spermatophore). In primates relative size of testes compared to body mass against the mating system and it reveals that promiscuous chimpanzees have larger testes compared to polygynous gorillas.

Some experts have even speculated that sperm competition may result in the 'fittest' sperm reaching the egg. The sperm may swim freely and must reach the egg before it dies. The highest-quality sperm may also carry high-quality genes to the egg. As a result, a female who engages in many matings may be setting up a sperm competition in which the best sperm from a variety of guys compete for the prize. The female not only has children with potentially greater genetic quality, but she also has kids with a wide range of characteristics.

4.4.6 Parental Care

Parental care has several significant advantages, therefore it's puzzling why it's not more widespread in the animal kingdom. An organism that provides a boost to its progeny would have a significant advantage over one that does not. When eggs are laid in organisms that do not have parental care, more energy is provided to the eggs. This solely material provisioning is extremely beneficial to the children. In most cases, bigger is better. As a result, the ideas presented below apply equally to animals with and without parental care.

Lack's Hypotheses: Parental care or provisioning, according to David Lack, is a somewhat expensive enterprise. There is a cost of reproduction, which sets a limit on how much an animal can do to care for its progeny. Lack has devised an experimental method for determining whether such reproduction costs exist in birds. Lack experimented with clutch size, reasoning that the mother bird would work harder to fledge the extra young, and that the additional cost of parental care would contribute to increased mortality in the next breeding season. Researchers have documented such reproductive costs since Lack's time. They also discovered that energy constraint could present itself as a decline in fitness in other ways than just survival costs. In tests with several species, the researchers Various Aspects of Animal Behaviour

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discovered that they had no significant effect on the parents' survival. Rather, they found that the size of fledglings or the number of fledglings that survived was reduced in nests that received extra eggs compared to control nests. Fledgling size or perhaps fledging survival was enhanced in nests where eggs were removed.

The second finding shows that there is a trade-off between a bird's ability to create a large number of high-quality offspring and its ability to produce a large number of low-quality offspring. Elephants in Africa have overlapping promiscuity. Over sixty percent of mammalian species use this method. The ultimate strategy for males, food supplies on a home range are not defendable, predation hazards are low, and males can randomly mate and without the duty of future parental care are some of the reasons overlap promiscuity is so widespread. Females must be able to raise babies without the assistance of a father for this technique to succeed. Females benefit from promiscuity because they can care for their young alone, it reduces the chance of inbreeding, and they receive good genes from successful males as well as resource gifts from competing males.

Aside from the nutritional investment in the egg, the least level of parental care is none. Additional investment occurs in the form of protecting the eggs and young, giving additional nutrients, and social information transmission. The essential balance, which can be described as a game, is whether more reproduction will be obtained by creating more offspring or by caring for the existing progeny. For most animals, however, evolutionary history has heavily influenced this game; species that generate highly reliant offspring do not have a range of potentially viable options, including abandoning neonates.

Even if evolution has already overcome many of the challenges, birds and mammals have long struggled with the balance between now and future reproduction. These disagreements revolve around topics such as weaning, juvenile dispersal, and the balance between the benefits of communal foraging and the expenses of feeding a larger social group.

In most cases, the female is the primary caregiver when there is significant parental care. Male partners may stay with the female to ensure paternity, especially if there are no other opportunities to mate, and the male presence may extend to assisting with the defence of the young and collecting food. Most biologists consider this asymmetry of parental involvement to be a result of disparities in gametic investment. Before depositing an egg or giving birth, many terrestrial and some aquatic species carry the growing zygote inside. This allows the man plenty of time to leave the female and look for other partners. Because her mate has abandoned her, the female is 'stuck' with parental care after laying the eggs or giving birth. In exceptional cases, such as seahorses and midwife toads, males are the primary caregivers. These are interesting examples of how evolution can be driven to unusual solutions.

For the first three to five years of their lives, African elephant calves rely on their moms. Young male elephants' interaction behaviours were compared to those of young female elephants. Female elephants remain with their birth family for the rest of their lives, while male elephants remain with the group until they reach puberty, which occurs between the ages of nine and fifteen. Feeding, relaxing, and travelling are all common calf activities.

As for calves at this age, more time is necessary for nursing, so both males and females spend less time travelling and sleeping. In comparison to females, male spend more time suckling and playing. Weaning takes up to four years and is commonly completed following the birth of a new sibling. Milk is the principal source of sustenance for young calves for the first two years of their lives. Playing, which includes chasing, mounting, rolling, trunk wrestling, and sparring, is the most common interaction amongst adolescent elephants. After the first year of life, the rate of play decreases considerably, especially among family members. Pokes, shoves, slaps, chases, and threats are occasionally witnessed in aggressive contacts; the incidence of competitive interactions increases with age, particularly among males. The mean distance between child and mother grows regularly as calves of both sexes get older, however male calves tend to be more independent of their mothers. Male calves engage with their mothers at a steady rate, whereas female calves interact with their mothers at a slower rate as they get older. This research provides evidence that the generation and maintenance of behavioural sex differences among juvenile elephants develops as a consequence of, and to reinforce, divergent adult social organization.

Calves and older female siblings, as well as family members, might interact because of the strong genetic and social links that exist among family groups. Young calves are frequently cared for by animals other than their mothers, who provide protection, interaction, and help. Allomothering aids in the preservation of matriarchal civilizations and improves calf survival. Live calves are fully reliant on their mothers for survival throughout the first three months of their lives. Calves learn to feed independently after the age of two, therefore allomothering has the greatest impact between the ages of three and twenty-four months. Calves are rarely located more than two metres from a family member until they are completely weaned around the age of five. Touching, welcoming, playing, stroking, consoling, and suckling were some of the ways young elephants interacted.

Aggression rates between calves and young adult males were higher than the rate of aggression between allomothers and calves. If a calf vocalizes distress, an immediate response by a family member is observed. Nearly all interactions between calves and allomothers (including occasional interactions from unrelated females) are helpful, affectionate, and positive. Known siblings cared for claves more often than distantly related females. Calves of young, inexperienced mothers needed more assistance from allomothers than experienced mothers.

4.5 BIOLOGICAL RHYTHMS

Any cyclic shift in the level of a body chemical or function is referred to as a biological rhythm. It refers to a cyclic pattern of physiological changes or changes in activity in living creatures that is most typically synced with daily, monthly, or annual environmental changes. Internal (endogenous) - governed by the internal biological clock, for example, the body temperature cycle; or external (exogenous) - controlled by synchronizing internal cycles with external stimuli, for example, sleep/wakefulness and day/night. These stimuli are known as zeitgebers, which means 'time givers' in German. These stimuli include environmental time cues such

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as sunlight, food, noise, or social interaction. Zeitgebers help to reset the biological clock to a 24-hour day.

Types of Rhythms

In both vertebrate and invertebrate species, a vast range of biological rhythms have been observed, and these rhythms are often classified by the length of a single cycle. Circadian rhythms, for example, are daily rhythms that last around 24 hours and mimic the geophysical cycles of day and night. The most obvious example of a circadian rhythm is the alternating pattern of activity followed by periods of rest (sleep) found in most vertebrate animals. Biological cycles, on the other hand, do not have to be 24 hours long. Ultradian rhythms occur more frequently than every 24 hours. Many hormones (e.g., cortisol) and enzymatic processes, for example, have rhythms that last only a few hours. Infradian rhythms, on the other hand, are rhythms that last longer than 24 hours but less than a year. This type of rhythm can be found in reproductive endocrine activity cycles, such as menstruation cycles in humans and estrous cycles in nonhuman animals. Finally, some animals have circannual rhythms that last for about a year and persist in the absence of external effects. Yearly cycles in breeding activity and reproductive endocrinology are typical in circannual rhythms. Some birds and rodents, for example, have yearly oscillations in gonadal mass and changes in reproductive hormones (e.g., testosterone, oestrogen), and these swings remain even when the animals are kept in laboratory conditions. Seasonal rhythms, which also resemble a year, are closely related to circannual rhythms. Seasonal rhythms, on the other hand, are formed in reaction to environmental signals and do not endure in the absence of these indications, unlike real circannual rhythms. Although many kinds of biological rhythms have been identified, the majority of research within the field of chronobiology has focused on circadian and circannual/seasonal rhythms.

4.5.1 Circadian And Circannual Rhythms

Let us first discuss circadian rhythm:

Circadian Rhythm

Circadian is derived from the Latin words circa (meaning 'around') and diem (meaning 'day'). A circadian clock is found in the suprachiasmatic nuclei of humans (and other mammals) (SCN). In the hypothalamus, the SCN is located. It's a little clump of roughly 10,000 nerve cells. A biological clock is the internal mechanism that causes and maintains such a rhythmic phenomena even in the absence of an apparent outside trigger. When an animal that functions according to such a clock is rapidly translocated to a geographic point where the environmental cycle is no longer synchronous with the animal's cycle, the clock continues for a time to function synchronously with the original environmental cycle.

The sleep/wakefulness cycle, body temperature, hormone secretion patterns, blood pressure, digestive secretions, and awareness levels are all examples of physiological and behavioural rhythms. Morning and evening circadian rhythms are two types of circadian rhythms that have been studied extensively. The circadian pacemaker and the behavioural attribute of morningness vs. eveningness have a clear link. Evening individuals prefer to wake up between 9 a.m. and 11 a.m. and

retire between 11 p.m. and 3 a.m., whereas morning folks awaken between 5 a.m. and 7 a.m. and go to bed between 9 p.m. and 11 p.m. Majority of people falls somewhere between the two types of circadian rhythms. Evidence has shown that morning types have more rigid circadian cycles evening types who display more flexibility in adjusting to new schedules.

Circadian Rhythm and Animal Behaviour

The physiological activities of an organism are controlled by a circadian rhythm, which lasts about 24 hours. The French scientist Jean Jacques d'Ortous de marian was the first to describe this pattern in the movement of plant leaves. Animals' resting and feeding patterns, brain wave activity, hormone synthesis, and other biological functions related to the daily cycle are all affected by circadian rhythms. Light is converted into nerve impulses in the retina of the eye, which are then transmitted to the hypothalamus nuclei of the central nervous system. The hypothalamic suprachiasmatic nuclei (SCNs) are the main generators of circadian rhythms and a component of the entrainment system that synchronises the animal with its surroundings, particularly illumination conditions. The wavelength, intensity, timing, and duration of the illumination stimulus all influence the circadian system. These endogenous biological rhythms help us anticipate periodic changes in the environment, which is crucial for adaptive behaviour.

Importance of circadian rhythm in animals

Animals, including humans, have circadian rhythmicity in their sleeping and feeding patterns. Core body temperature, brain wave activity, hormone production, cell regeneration, and other biological activities all have distinct rhythms. Furthermore, photoperiodism, or an organism's physiological response to the length of day or night, is critical for both plants and animals, and the circadian system is involved in day length measurement and interpretation. Many species' existence depends on accurate forecasting of seasonal weather conditions, food availability, and predator activity.

Circannual Rhythms

Circadian rhythms, or daily cycles, are partly a response to light or dark cycles, whereas circannual cycles are partly a response to variations in the relative length of daylight hours. Bird migrations, reproductive activities, and animal hibernation are all part of it. The circannual clock is a system that regulates biological seasonality. Certain activities, such as reproductive maturation and behaviour, occur in many species (even when kept in constant conditions in the laboratory) with a predictable rhythm whose duration is near to (typically a little shorter than) 365 days. In mice, for example, deletion of the SCN does not eradicate circannual rhythms, implying that the circannual clock is a distinct system from the circadian clock and is located elsewhere in the animal's brain or body. Circumannual rhythms' physiology is poorly understood. The durations of free-running circannual rhythms are too far apart from 365 days to be realistic on their own. They must be entrained to the calendar year in the same way as circadian rhythms must be entrained to the day/night cycle. Temperature cycles, noise, social cues, and other factors can all influence circadian rhythms, but light is by far the most powerful. What about cyclical patterns? A variety of environmental cues act as main triggers for annual physiological

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changes, depending on the geographic region. Rain (e.g., monsoon), temperature, and social cues can all influence reproductive maturation and behaviour, hibernation, and migration. These signals are referred to as 'proximal cues' because they have a direct impact on the commencement of annual biological events. The proximal cues, on the other hand, can only act if the organism is already 'prepared' for them. Plants and animals may follow free-running circannual cycles in nearly constant settings, such as at the poles and at the equator. Elephant seals, for example, have a ten-month breeding season that occurs in a different month each year. Bird migrations are noticeably rhythmic events. They usually occur at specific seasons and times of day, and are thus representations of a roughly yearly (circannual) as well as a roughly diurnal (circadian) rhythmicity. Both of these rhythms represent basic environmental adaptations and function as biological clocks to cope with annual and daily variations in external environments. Many bird species, such as warblers, migrate exclusively at night. When kept in cages provided with an appropriate arrangement of perches, the birds' locomotor activity can be measured by means of microswitches mounted underneath the perches. With this widely used experimental method, it has been shown that locomotor activity in summer and winter is restricted to daytime, i.e., it occurs exclusively in the light portion of the light:dark (L:D) cycle. In autumn and spring, however, the seasons corresponding to natural migratory activity, the birds exhibit additional locomotor activity at night. . The cycle is frequently accompanied by migratory fattening (indicated by an increase in body mass) and is followed by a moult in the winter and a reproductive activity period in the summer. Under such steady conditions, the time of the rhythm is typically longer or shorter than 12 months, attesting to its endogenous circannual nature. Endogenous daily (circadian) and annual (circannual) rhythms function as biological clocks in migratory birds, allowing them to maintain their temporal orientation. In both autumn and spring, circannual rhythms are important for the start of migration. This function of timing migrations is especially crucial for birds that spend the majority of their time in the winters close to the equator where the environment is too constant. Circadian signals cause changes in the circadian system in typically day-active but nocturnally migrating birds, resulting in the establishment of nocturnal activity. Although the exact nature of these signals is unknown, there is evidence that changes in the daily cycle of melatonin secretion by the pineal gland are linked to the waxing and waning of nocturnal activity, and may even be directly implicated. These alterations in melatonin pattern are likely to affect the circadian system's overall synchronization qualities to Zeitgebers, allowing circadian rhythms to adjust to new surroundings more quickly following long journeys.

4.5.2 Orientation and Navigation

The position of the animal in relation to gravity or a resource is referred to as orientation. This is the stance that the animal assumes in order to gain access to the resource. The purpose of the membranous labyrinth in vertebrates and the statocyst in invertebrates is to preserve upright posture against gravity.

When an animal tries to approach an object, such as food or water, object orientation occurs. The movement of aquatic animals upwards in a pond or lake is known as strato-orientation. It's termed zonal orientation when animals try to travel

from grassland to woods, deserts, or mountains. Long-distance migratory animals usually have a topographical or geographical direction. Migrants often return to breed in the exact locality where they were hatched or born. This journey homewards, particularly that of birds, may cover thousands of miles.

Animals' ability to orient themselves geographically has been proved in homing tests. Animals are taken from a certain location (typically the nest), transported over various distances, and their speed and degree of success in returning are measured. After being transferred 800 kilometres (500 miles), starlings have returned to their nests; swallows have returned over 1,800 kilometres (1,100 miles). In 12 1/2 days, a Manx shearwater (Puffinus puffinus) flew from Massachusetts to Britain, covering 4,900 kilometres (3,050 miles). After being released on Whidbey Island, Washington, Laysan albatrosses (Diomedea immutabilis) returned to Midway Island in the Pacific, covering 5,100 kilometres (3,200 miles) in 10.1 days. Experiments with certain fish and mammals have revealed a comparable ability to homing.

Both random and focused searches have been recorded in birds and fish, indicating that homing animals employ recognized landmarks. Homing experiments with gannets viewed from the air have shown that after being released, the birds explore the area and pause, as if looking for landmarks. Topographical (for example, mountain systems, river systems, and coastlines) to ecological (for example, vegetation zones) to climatic landmarks are all examples of landmarks (e.g., air masses differing in temperature and humidity, prevailing winds). Fishes may use comparable hints to orient themselves in the same way humans do. Passive drifting is crucial in the migrations of larvae and juvenile fishes like eels, cod, herring, and plaice, as well as adult fishes like herring and cod that are passive after spawning. Because they drift with the current, their movements are consistent from year to year.

Navigation in birds

During migration, birds employ a variety of techniques to navigate. Many people utilise celestial navigation, or menotaxis, which is a means of aligning the body to the arc of the sun, the phases of the moon, or the pattern of stars in a specific season. Because they can detect the UV light that the sun generates, hummingbirds and pigeons can estimate the position of the sun even on overcast days.

Experiments in planetarium on night migrant birds, such as white throated warblers and indigo buntings reveal that they orient themselves by the position of stars in the night sky. Some birds are sensitive to coriolis force that arises by deflection of winds in the northern hemisphere by earth's rotation.

Some diurnal birds orient themselves on the migration route using topographical landmarks such as mountains, river valleys, and forests. Ocean waves produce infrasound, or low-frequency sounds, which some people can sense. Many birds, particularly seabirds, use scents to locate their destinations. Many birds have instincts, internal compasses, or biological clocks that guide them along the migration path. Young birds' intrinsic ability to navigate allows them to follow the migratory route precisely without any prior training or experience. Some birds such as oil birds of South America and Himalayan cave swift possess echolocation and can be guided by it. Various Aspects of Animal Behaviour

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Because of the presence of magnetite in their head and neck muscles, some birds, such as pigeons, are sensitive to changes in the earth's magnetic field. W.T. Keeton wore miniature bar magnets on the backs of pigeons in the early 1970s. Pigeons with non-magnetic bars found their way home when released in unfamiliar locales, while those with bar magnets became disoriented.

In a 2007 German scientists found tiny iron oxide crystals in the skin lining of the upper beak of pigeons, which might be of help to the birds to sense the earth's magnetic field and assist them to identify their geographical position. Cryptochromes, which change their chemistry in the presence of a magnetic field, were also detected in the retinas of migratory birds' eyes. The chemicals might then alter light-sensing cells in the retina, causing them to generate images in response to the magnetic field, which could aid the bird's navigation during flight.

Infrasound travels far further than regular sound and is produced by a variety of natural phenomena such as ocean waves, surf, winds, storms, earthquakes, and other geological events. Birds are said to be able to hear infrasounds that humans cannot, and hence have this additional navigational aptitude.

Other Animals

Birds use directional orientation techniques that are comparable to those employed by other animals. Various crustaceans, particularly the sand flea, *Talitrus saltator* have been seen to be oriented to the Sun. The Sun is used by a variety of insects, including bees and certain beetles (families Scarabaeidae, Tenebrionidae, and Carabidae), to plot their journey with amazing accuracy.

Fish can also use celestial bearings; salmon, for example, are said to use the Sun. Experiments with the parrot fish (Scarus) revealed a Sun compass reaction that could also be seen in other species. Because of the qualities of light beams travelling through water, it is considerably more difficult to locate the Sun in water than in air. Experiments reveal that fishes use topographical signals to identify their range, particularly their spawning areas. In this case, visual bearings are quite important. Chemical substances could potentially supply information.

Mammals employ visible markers for orientation, at least within short distances. Scented trails are presumably useful within a restricted area proportionate to the size of the animal; olfaction is vital in mammals' lives. Some mammals, on the other hand, migrate over great distances and can return home after being transported far from home; bats, for example, have travelled 265 kilometres (165 miles) back to their homes. While random exploration plays a role in these motions, it's also possible that real navigation is engaged in some of them.

4.5.3 Migration of Fishes and Birds

Mammals use visible cues to help them navigate, at least over short distances. Scented trails are likely to be effective within a limited area corresponding to the animal's size; olfaction is critical in mammals' existence. Some mammals, on the other hand, migrate long distances and can return home after being separated from their families; bats, for example, have travelled 265 kilometres (165 miles) back to their homes. While random exploration may be at work in some of these motions, it's also plausible that true navigation is at work.

Bird Migration

Early Ideas

Birds have been known to disappear from particular places for parts of the year for ages. However, it was not realized for a long time that this was because they merely flew somewhere else far away. Small birds, such as swallows, were once thought to hibernate in the mud at the pond's bottom throughout the winter. Another theory was that certain geese (which migrated to the Arctic during the summer) were the same species as a barnacle. Goose barnacles and Barnacle geese are common names derived from this mythology. Although these ideas now seem bizarre, they begin to make sense when you realize that they date back to times when the world was believed to be both flat and much smaller than we know it to be today.

Determinants of migration

- i. Seasonally, the timing of migration is influenced by internal 'clocks' that are influenced by day length and perhaps also weather. This topic was discussed in the last lecture.
- ii. The weather has a big influence on the exact timing of migratory movements on shorter time periods. When the conditions are favourable for flying in the direction they need to go, birds tend to move (e.g., when they have a tailwind, when air turbulence is low, when it is not raining).
- iii. During the night, many birds migrate. This could be due to a number of factors.
 (1) Because there are less thermals (updrafts) created by warming of the Earth's surface, the atmosphere is more stable at night than during the day. (2) The air temperature is cooler, which may make thermoregulation simpler; keep in mind that flight generates a lot of heat, which birds must dissipate. (3) The risk of predation may be lower at night than during the day.
- iv. But some species do migrate by day. In particular, large soaring birds such as hawks, storks and pelicans move during the daytime. These birds use thermals to help them travel.

Kinds of Migration

The different kinds of migration are:

a. Latitudinal Migration

- i. Most people think of migration as a north-south movement and this is perhaps the most common pattern. There are, however, various other types of migration.
- ii. North-south migration makes sense in North America because it reflects changes in temperature patterns and because the majority of geographical landforms that influence migration (mountain ranges, significant rivers) travel in this direction. (Migrants in Europe, on the other hand, are more eastwest split.)
- iii. Although the basic pattern is north-south, not all birds fly north in the same direction they fly south. Many birds follow an elliptical course that allows

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them to take advantage of prevailing winds and favourable feeding chances throughout the year. As a result, many birds migrate north across the heart of North America in the spring, then return south by an easterly path in the fall.

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| b. Elevational Migration

- i. Another common form of migration occurs up and down the slopes of mountains.
- ii. Just like latitudinal movements, these migrations occur because birds that breed at high elevations need to leave in winter to avoid harsh conditions.

c. Molt Migration

- i. Some birds move to a specific area to molt, then continue on their migration to somewhere else to spend the winter.
- **ii.** Certain waterbirds, in particular, are well known for making these movements. The behaviour is most common in species that become flightless while molting their flight feathers. These birds typically move to large lakes or bays where there is abundant food (to provide energy to grow feathers) and where they can easily stay far from shore (and predators).

d. Seabird Movements

- i. Although some seabirds especially those that nest near the poles do make north-south movements, many take less obvious routes during migration, e.g., travelling east-west across the oceans.
- ii. The reason for these differences is that food availability in the oceans is not as dependent on climate as it is on land. Instead oceanography plays a big role in determining where food is most abundant.

e. Irruptive Movements

- i. In some species the degree of migratory movement (the distances traveled, the proportion of the population that moves, etc.) can vary hugely from year to year.
- ii. These species are usually those that have food supplies that fluctuate widely from year to year and include many northern or montane species (e.g., various finches, some owls). In an 'irruption' year, these birds can be very common far south of their typical winter range.

The advantages of migration are:

Advantages

- i. Enables birds to take advantage of good feeding conditions.
- ii. Provides nesting opportunities that would not be available if the bird stayed on its wintering grounds (e.g., seabirds).
- iii. Allows birds to avoid climate extremes.
- iv. Reduces competition with other species during the breeding season.
- v. May also allow birds to avoid parasites.

Disadvantages

- i) Very high energy costs.
- ii) High risk associated with long flights, often over harsh terrain or through poorly known areas (especially for young birds).

Biological Capabilities Required for Migration

The following are the capabilities required for migrations:

Physiological

- i) Prior to migration, birds store fat and use it as fuel. Fat is a good fuel because it produces more energy per gram than carbohydrate or protein, it produces a lot of water as a metabolic by-product (which is useful for avoiding dehydration), it can be mobilised at low temperatures, and it can be easily stored in the bird's body without interfering with the bird's aerodynamic shape.
- ii) Prior to migration, certain birds undergo a substantial restructuring of their internal organs, reducing the size of some body parts to permit the growth of other parts. During migrating, for example, some shorebirds shrink their digestive systems.

Neurological

Birds also need to have an amazing ability to find their way around in order to migrate thousands of miles, often returning to exactly the same place year after year.

Note: Migration makes it exceedingly difficult to conserve rare and declining bird populations, because effective conservation can require protection of multiple sites, often 1000s of miles apart.

Fishes Migration

In ecology, migration is the vast movement of animals from one location to another, having different purposes depending on the sorts of species.

Fish migratory behaviour is a common occurrence. Their voyage is mostly for the purposes of feeding and breeding.

Types of Fish Migration on The Basis Of Needs

- **a.** Alimentary or Feeding Migration: Migration for search of feeding ground. It occur when food resources get exhausted.
- b. Gametic or Spwaning Migration: It occur during breeding season in search for the suitable spawning ground.
- c. Climatic or Seasonal Migration: Migration in search for suitable climatic condition.
- d. **Osmo-Regulatory Migration**: Migration for water and electrolytes balance from sea to fresh water and vice-versa.
- e. **Juvenile Migration:** It is larval migration from spawning ground to the feeding habitats of their parent.

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Movement of Fishes during the Migration

- **a. Drifting movement:** It is a passive movement of fish along with water currents.
- b. **Dispersal movement:** It is a random locomotory movement of fish from a uniform habitat to diverse direction.
- c. **Swimming movement:** It is an orientated movement of fish either toward or away from the source of stimulus.
- d. **Denatant and Contranatant movement:** It is an active swimming movement. Denatant movement is swimming with the water current while contrantant movement is swimming against water current.

Types of Fish Migration

The migration of some fishes is a regular journey and is truly an innate animal behaviour. Fish migrations are classified into following types:

1. Diadromous Migration

- It is the migration of fish between sea and fresh water.
- As we know, most of the fishes are restricted to either fresh water or sea water. Changes in habitat may cause osmotic imbalance in those fishes. However some fishes regularly migrate between sea and fresh water and have perfect osmotic balance, they are the true migratory fish. This migration is of two types-

i. Anadromous migration

- It is the migration of marine fishes from sea to fresh water for spawning.
- Fishes spend most of their life living and feeding in sea.
- They only migrate during breeding season to the river for spawning ground.
- Eg. Salmon, Hilsa, Lamprey, etc.
- Salmon migrate for breeding during winter from sea to river. While migrating, some physiological changes occur:
 - o stops feeding during journey
 - o changes colour from silver to dull reddish brown
 - o gonads mature

They choose a good spawning spot and build a saucer-shaped nest in which the female deposits her eggs and the male smelts them. Alevins, or juvenile larvae, developed from the egg. When alveins return to the water, they evolve into parr and ultimately into adults.

ii. Catadronous migration

- It is the migration of fresh water fishes from river to sea during breeding season for spawning. Eg. Eel (*Anguilla spp.*)
- Both European eel (*Anguilla anguilla or Anguilla vulgaris*) and the American eel (*Anguilla rostrata*) migrate from the continental rivers to

Sargasso Sea off Bermuda in south Atlantic for spawning, crossing Atlantic Ocean.

- Before and during migration some physiological changes occur in their bodies:
 - o deposit large amount of fat in their bodies which serves as reserve food during the journey
 - o Colour changes from yellow to metallic silvery grey.
 - o Digestive tract shrinks and stops feeding
 - o Eyes get enlarged and vision sharpens. Other sensory organs also become sensitive.
 - o Skin serves respiratory organ.
 - o Gonads get matured and enlarged.

The lay eggs in suitable spawning ground and are fertilized by males. After spawning they die. The larva hatch out and develop into young ell and finally return to river.

2. Potamodromous Migration

• It is fresh water migration of fresh from one habitat to another for feeding or spawning. Eg.- Carps, catfish, etc.

3. Oceanodromous Migration:

• It is the migration of fish within sea in search of suitable feeding and spawning ground. Eg.- Clupea, Thummus, Tuna, etc.

4. Latitudinal Migration

- It is the migration of fish from north to south and vice-versa.
- It is a climatic migration.
- Eg.- Sword fish migrate north in spring and south in autumn.

5. Vertical Migration

• It is a daily migration of fish from deep to the surface and vice-versa for food, protection and spawning. Eg. Sward fish usually move vertically downward to greater depth for food.

6. Shoreward Migration

• It is the migration of fish from water to land. However it is a temporary migration. Eg. Eel migrate from one pond to another pond via moist meadow grass.

Significance of Fish Migration

- To find suitable feeding and spawning ground
- For protection from predators
- Survive from extreme climatic conditions
- Increases genetic diversity
- It is an adaptation characteristic for survival and existences

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4.6 LEARNING AND MEMORY

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Animal learning, the alternation of behaviour as a result of individual experience. When an organism can perceive and change its behaviour, it is said to be learned. It appears self-evident that animals can learn. The cat that runs to its food dish when the cupboard door opens; the rat that solves a maze in the laboratory; the bird that learns its species' song—all of these and many other instances show that animals can learn. However, what does it mean to suggest that animals can learn? To put it another way, what is learning? This is a tough question to answer, and some theorists argue that there is no such thing as a single, all-encompassing definition of learning. Furthermore, a little moment of reflection reveals the existence of various types of learning. Learning number concepts, for example, appears to be somewhat different from learning the relationship between the sound of a cupboard door and the receipt of food.

Learning

Learning is a process that occurs as a result of experience and manifests itself in an individual's behaviour. Genes control learning ability, but learned processes throughout an individual's lifespan are not genetically transferable. Learned habits are more flexible than natural behaviours. Many learnt behaviours can be changed to accommodate changing circumstances. When roads are wet or icy, for example, drivers may need to adjust their driving style (a learned behaviour) or risk losing control of their vehicle. Learned behaviours are more adaptable than innate behaviours because they can be modified as the environment changes. More intelligent species often have a higher share of learnt behaviours rather than natural ones.

The General Nature of Learning

Many animals appear to follow regular and seemingly unchanging patterns throughout their lifetimes. The life cycle of many solitary insect species, for example, consists of the following unchanging events: females lay their eggs on a specific plant or captured prey; newly hatched larvae immediately begin eating and then follow a standard developmental stage sequence; adults recognize appropriate mates using a set of fixed signs and perform a fixed sequence of mating responses. Generation every generation, the same unchanging sequence is repeated. And, of course, it's a resounding success. Because such reactions were and continue to be adaptive, the same collection of stimuli always elicits the same set of responses. There is no need for an animal's behaviour to alter if the conditions do not change. Many areas of mammalian behaviour exhibit a similar fixity. When a dog's foot is pricked, a young child's hand is burned; when an object is brought swiftly near their eyes, both people and rabbits blink; and young infants of virtually all mammalian species sucking is prompted by contact with the lips.

When the same answer is always acceptable in a given situation, there's no reason for an animal to have to learn what to do in that situation. The world, however, is not always that stable. The food supply that was abundant yesterday may be depleted today, and the foraging animal that returns to the same location

every day would starve to death. Furthermore, a specific food supply may be reduced temporarily but will be refilled if left long enough; the successful forager must remember where the supply was and when it was last visited. To put it another way, conditions can vary, and the same response may not always be appropriate for the same stimuli.

Types of Learning

Learning has been classified differently by various scientists. Thorpe's (1963) classification is most widely used:

- 1. Flexible Habituation, Conditioning, Trail and Error, cognition
- 2. Restricted-Imprinting

4.6.1 Conditioning

Conditioned behaviours are the result of associative learning, which takes two forms: classical conditioning and operant conditioning.

Classical conditioning is the process of forming mental associations between stimuli to learn emotional and reflexive reactions. A dog, for example, can learn to fear a veterinarian facility by doing the following: If the dog has never visited the clinic before, the clinic's stimuli (such as its appearance, scent, and sound) should be neutral or meaningless. However, after being restrained by technicians and injected with a needle, the dog may associate the look, smell, and sound of the vet clinic with physical restraint and the pain of the injection, so the next time it is taken in for a procedure, the clinic stimuli will no longer be neutral, eliciting the same fear as physical restraint and injection. The dog learns a relationship between two events, or stimuli, via classical conditioning (also known as Pavlovian conditioning Fig 4.2). One of these stimuli is a 'neutral' or insignificant stimulation that a dog would typically ignore. Because it may only generate strong behaviour as a result of conditioning, this stimulus is known as the Conditioned Stimulus, or CS. The other stimulus is a biologically significant stimulus, such as food, to which a dog normally pays close attention. Because it can elicit powerful behavioural reactions without any conditioning, this stimulus is known as the unconditioned stimulus, or US.



Fig 4.2 Structure of Classical Conditioning

Ivan Pavlov, a Russian scientist, taught dogs to salivate in response to the ringing of a bell in a classic example. Pavlov achieved this by repeatedly introducing a bell (CS) and food (US) in close proximity in time. The typical reaction of a naive dog

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to the ringing of a little bell is for it to twitch its ears or look in the direction of the noise. A morsel of food, on the other hand, can lead the dog to exhibit powerful behaviours such as enthusiasm, salivation, digging and pawing, chewing, and eating. The Unconditioned Response, or UR, is a powerful response triggered by exposure to a US. The CS and the US get correlated in the dog's 'mind' through classical conditioning, so that behaviour that is naturally activated by the US (the UR) also becomes triggered to some degree by the CS. This taught reaction is called the Conditioned Response, or CR, when a CS develops the potential to activate behaviour that is ordinarily induced by a US. As a result, Pavlov's dog ultimately learned that the bell meant food and began salivating in response to it (CR).

4.6.2 Habituation

Habituation is vital for modifying an animal's behaviour to its surroundings, and it may be found in all kinds of creatures, from weevils to whales. Animals learn to save energy and time by not responding to a stimulus that is irrelevant to them. 'It is the progressive fading of a reaction when a stimulus that elicits that response is presented repeatedly, or it is the decrease in probability of a response occurring when a stimulus that elicits that response is provided repeatedly.' If a neutral stimulus - that is, a stimulus that has neither noxious nor beneficial consequences, is repeatedly delivered to an organism, it's response to the stimulus tends to decrease gradually. By habituation, animals learn 'What not to do.'

For example,

- A spider relaxes in its web. The experimenter vibrates a location on its web, simulating the signal used to trap an insect. The spider dashes out to explore the cause of the vibration; however, nothing is discovered, and the spider returns to its original position in the web's centre. The spider no longer rushes out to investigate after being exposed to the same neutral stimulus numerous times; instead, it remains in the web's centre. It becomes accustomed to that stimuli.
- When a snail crawling across a sheet of glass is tapped, it retracts inside its shell. It reappears after a little interval and continues to move. The snail retracts again after a second tap, but it reappears swiftly. Frequent tapping on the glass eventually causes no response from the snail, and it continues to move. This is referred to as habituation.
- If you create a strange noise in front of the family dog, it will react by rotating its head and ears towards the source of the noise. If the stimulus is provided repeatedly and the dog does not experience anything nice or unpleasant, the dog will eventually stop responding.

Almost all animals are able to learn not to respond to repeated stimuli which have proved to be harmless.

The terms 'habituation' and 'fatigue' are not interchangeable. It has been suggested that habituation is linked to a change in the Central Nervous System. Fatigue, on the other hand, is caused by an accumulation of lactic acid in the muscles. A tired animal will not respond to a stimulus, no matter how different it is, whereas a habituated animal would respond even if the stimulus is changed. Second, a fatigued animal will respond to the identical stimulus after a rest, whereas a habituated animal will remain unresponsive to the stimulus even if it is repeated every 24 hours. The difference between fatigue and habituation is that fatigue is a momentary change in human physiology and habituation is a permanent alteration in the Central Nervous System.

Animals learn in a variety of ways, one of which is habituation. Animals learn to reduce the frequency of a behaviour in response to a recurrent stimulus in this sort of learning. When a conduct does not result in a benefit or reward, this is called a non-beneficial or non-rewarding activity. Habituation has been observed in almost every animal species. It is adaptive because it is a waste of energy to respond to a stimulus when there is no benefit or reward. The behaviour of certain species of little songbirds when confronted with a stuffed owl or other 'predator' is an example of habituation. When the birds see a stuffed owl in their cage, they react as if it were a genuine predator. They appear to be terrified and attempt to flee. The birds become less responsive as the plush owl remains in the cage without moving. They grow accustomed to the stuffed owl's presence. Coyotes invading human neighbourhoods is another example of habituation. They've become accustomed to humans in these areas and are no longer scared to approach.

4.6.3 Insight Learning

The application of previous experiences and reasoning to solve difficulties is known as insight learning. In contrast to operant conditioning, insight learning involves no trial and error. An animal, on the other hand, uses previous experience to work through a solution to a problem. The answer frequently appears as a flash of understanding. Insight learning necessitates a high level of intelligence. Apes (chimps, gorillas, and orangutans), crows, and humans are among the creatures most likely to learn this manner.

Examples of Insight Learning

- Chimpanzees are the apes that are found in the wild 'fishing' for termites. The animals insert a 'tool' in a termite mound hole, such as a twig, and the termites crawl onto the twig. The chimp then pulls the twig out of the hole and consumes the termites. Chimpanzees can also utilize leaves to absorb liquids and pebbles to shatter nuts. They've even been seen using their teeth to sharpen twigs and use them as spears to kill small animals for sustenance. Gorillas may use tools to solve problems as well. For example, they have been observed using small branches as walking sticks and as measuring sticks to test the depth of water before wading through it.
- Orangutans use small sticks to get at edible seeds inside prickly fruits without being pricked. They may also use leaves to make rain-hats and roofs over their sleeping nests.
- Crows and kindred birds are known for their intellect and have huge brains in comparison to their body size. Insight learning is also used to address difficulties. A crow, for example, was seen laying nuts on a major street's crossing, where automobiles would drive over them and crack the shells. The crow entered the street once the traffic light turned red to retrieve the

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nutmeats. Crows have also been seen collaborating to devour trashcan food waste. Some of the birds ate the scraps inside the can while others propped up the lid. The crows then traded places so that everyone got a chance to eat.

• Humans (*Homo sapiens*) has larger brains (for their body size) and is smarter than any other species. Humans are also known for their tremendous ability to solve problems using insight learning, which includes everything from learning to start a fire to landing a man on the moon. Consider difficulties you've previously solved. Perhaps you figured out how to utilize a new computer software using logic and previous expertise with existing programmes. You may have also utilized logic and prior knowledge to solve math problems or progress through a video game level.

4.6.4 Association Learning

Ivan Pavlov (1849-1936), a Russian physiologist, was studying the digestive system of dogs in the early twentieth century when he noticed an intriguing behavioural phenomenon: the dogs began to salivate when the lab technicians who normally fed them entered the room, even though the dogs had not yet been fed. Pavlov noticed the dogs were salivating because they knew they were about to be fed; the dogs had learned to correlate the technicians' entry in the room with the food that would soon follow. Pavlov and his team of researchers began researching this mechanism in greater depth. He conducted a series of studies in which dogs were exposed to a sound just before getting food in a series of trials. He meticulously adjusted the sound's commencement and the timing of the food's delivery, as well as the amount of salivation produced by the dogs. The dogs first salivated just when they saw or smelled the meal, but after many pairings of the sound and the food, they began to salivate whenever they heard the sound. The animals had developed a link between the sound and the food that would follow. Pavlov identified classical conditioning as a fundamental associative learning method.

Classical conditioning refers to learning that occurs when a neutral stimulus (e.g., a tone) becomes associated with a stimulus (e.g., food) that naturally produces a behaviour. After the association is learned, the previously neutral stimulus is sufficient to produce the behaviour.

As you can see in Fig 4.3, '4-Panel Image of Whistle and Dog,' psychologists use specific terms to identify the stimuli and the responses in classical conditioning. The **unconditioned stimulus (US)** is something (such as food) that triggers a naturally occurring response, and the **unconditioned response (UR)** is the naturally occurring response (such as salivation) that follows the unconditioned stimulus. The **conditioned stimulus (CS)** is a neutral stimulus that, after being repeatedly presented prior to the unconditioned stimulus, evokes a similar response as the unconditioned stimulus. In Pavlov's experiment, the sound of the tone served as the conditioned stimulus that, after learning, produced the **conditioned response (CR)**, which is the acquired response to the formerly neutral stimulus.

Note: UR and the CR are the same behaviour — in this case salivation — but they are given different names because they are produced by different stimuli (the US and the CS, respectively).

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Fig. 4.3 Pavlov's Experiment on Classical Conditioning

Conditioning is advantageous to organisms in terms of evolution since it helps them to create expectancies that help them prepare for both good and unpleasant situations. Consider what happens if an animal scents a new meal, consumes it, and then becomes ill. If the animal can associate the smell (CS) with the food (US), it will rapidly learn that eating the food results in a negative outcome and will avoid eating it in the future.

4.6.5 Reasoning

The most advanced form of learning is commonly recognized as insight learning. Animals solve issues too rapidly to have gone through a trial-and-error process, therefore insight responses are those emerging from a rapid appreciation of relationships. The animal appears to reach a conclusion through reasoning (described as 'the ability to spontaneously combine two or more independent or isolated experiences to generate a new experience that is effective for achieving a desired purpose'). The capacity of an animal to create diversions in a maze is a frequent experimental approach used to test for reasoning. Shepard discovered that after rats had figured out a maze, they swiftly took advantage of newly discovered shortcuts (created by removing partitions, so that what was previously a blind alley became a quicker route to the goal box). Another probable example of reasoning is chimpanzees getting bananas high up in their cage by stacking boxes on top of each other or putting lengths of stick together.

4.6.6 Cognitive Skills

Mate selection, foraging, and a variety of other behaviours are influenced by cognitive processes like as perception, learning, memory, and decision making.

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Although there are as many definitions of animal cognition as there are researchers, most scientists agree that animal cognition, like its human counterpart, essentially involves the processing of information: how a subject receives data from the world it inhabits (including data from other animals) through its species-specific perceptual system (auditory, visual, olfactory, gustatory, somato-sensory). The behaviour of primates has piqued people's interest. However, intelligent behaviour has been recorded in large and small mammals, birds, fish, ants, bees, and other animals. Animals in the lab manipulate levers, pull strings, dig for food, swim through water mazes, avoid electric current, and select colours and patterns. They solve problems to find an escape route, reach hanging bananas, remove termites from a hole with a stick, and cross water with a wooden log, demonstrating higher mental abilities such as 'insight,' which is the ability to notice and understand situations, and 'reasoning,' which is the ability to combine spontaneously two or more separate experiences to formulate a new activity that is effective for achieving goals. These have been observed in mammals, with the majority occurring in nonhuman primates. Humans, of course, have the best development. As a result, these words are more closely associated with psychology than with ethology. Humans, other primates, and some non-primate animals are capable of sophisticated learning that does not fit under the heading of classical or operant conditioning.

Problem-Solving in Chimpanzees

Wolfgang Kohler, a German scientist, was one of the first to study problem-solving in chimpanzees. He discovered that chimps were capable of abstract reasoning and could think their way through alternative problem solutions, visualizing the outcome of a solution even before implementing it. Kohler, for example, put a banana in the chimps' cage that was too high for them to reach in one experiment. Faced with this predicament, some of the chimps placed the boxes one on top of the other, climbed on top of them, and obtained the banana after a few failed starts and frustration. This response indicates that they were able to visualize the outcome of stacking the boxes before actually doing so.

Check Your Progress

- 11. What is habituation?
- 12. Why do animals use reproductive strategies?
- 13. Define migration.
- 14. What is circannual rhythm?
- 15. Give one example of circadian rhythm.
- 16. What is cognition?

4.7 ANSWERS TO CHECK YOUR PROGRESS

1. Territoriality is the behaviour by which an animal lays claim to and defends an area against others of its species, and occasionally members of other species as well.
- 2. The two most common types are Batesian mimicry and Mullerian mimicry.
- 3. Habitat selection is an active behavioural process by an animal and each species searches for features within an environment that are directly or indirectly associated with the resources that an animal would need to reproduce, survive, and persist.
- 4. The competitive exclusion principle says that two species can't coexist if they occupy exactly the same niche (competing for identical resources).
- 5. Homing is the inherent ability of an animal to navigate towards an original location through unfamiliar areas. This location may be either a home territory, or a breeding spot.
- 6. Kin selection occurs when an animal engages in self-sacrificial behaviour that benefits the genetic fitness of its relatives.
- 7. The interactions that occur between two or more individual animals, usually of the same species, when they form simple aggregations, cooperate in sexual or parental behaviour, engage in disputes over territory and access to mates, or simply communicate across space is known as social organization.
- 8. Inclusive fitness is the number of offspring equivalents that an individual rears, rescues or otherwise supports through its behaviour (regardless of who begets them).
- 9. Reciprocal altruism is one solution to the evolutionary paradox of one individual making sacrifice for another unrelated individual. If individuals interact repeatedly, altruism can be favoured as long as the altruist receives a reciprocal benefit that is greater than its initial cost.
- 10. Herding is the act of bringing individual animals together into a group (herd), maintaining the group, and moving the group from place to place—or any combination of those.
- 11. Habituation is a simple learned behaviour in which an animal gradually stops responding to a repeated stimulus. Imprinting is a specialized form of learning that occurs during a brief period in young animals—e.g., ducks imprinting on their mother.
- 12. The reproductive strategies of males and females are related to the characteristics of their respective gametes: while sperm cells are abundant, 'cheap' and easy to replace, ovules are scarce and more costly to obtain; this leads males and females to carry out different reproductive strategies.
- 13. Migration, in ethology, the regular, usually seasonal, movement of all or part of an animal population to and from a given area. Example: birds, hoofed animals.
- 14. Circannual rhythms have evolved as genetically programmed adaptive timing mechanisms to allow organisms use favorable seasons to reproduce and grow, and survive through unfavorable seasons.
- 15. The sleep-wake cycle is one of the most common examples of circadian rhythm.

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16. Cognition is defined as the mental action or process of acquiring knowledge and understanding through thought, experience, and the senses.

4.8 SUMMARY

- The primary behavioural categories among animals are related to reproduction, sustenance, development and survival which involve intraand inter-species competition as well as the influence of the abiotic and biotic environment.
- Habitat selection refers to the strategies used by organisms to choose among patches or habitats that differ in one or more variables, such as food availability or predation risk, that influence its fitness.
- The majority of animals are at risk of being eaten. Because it's difficult to pass on your genes after you've died, the prospect of predation puts organisms under intense selective pressure, resulting in a variety of behavioural methods that help them survive. An organism must be able to recognize predatory dangers and apply appropriate methods to evade discovery by predators in order to avoid becoming dinner. If avoidance fails, animals can employ behaviours that deter predators from attacking them, as well as methods that boost their odds of surviving an assault if one does occur.
- Territoriality involves the collective behaviour of organisms, how they use space to communicate ownership/occupancy of areas and possessions.
- Animal social behaviour refers to the set of interactions that occur when two or more individual animals, usually of the same species, create basic aggregations, cooperate in sexual or parental activity, participate in territorial and mate access disputes, or simply communicate across space.
- Reproductive behaviour refers to any activity geared toward the development of at least one replacement of oneself in a group of animals. The most prevalent way of reproduction is when a female's egg is fertilized by a male's sperm. Genetic variety is produced as a result of the unique combination of genes, which contributes to a species' adaptability. To avoid predators and egg and sperm waste, the processes of approach, identification, and copulation are well developed. The majority of single-celled creatures, as well as some more complex organisms, reproduce asexually.
- The suprachiasmatic nucleus, a brain internal clock, is responsible for biological cycles (SCN). It's found in the hypothalamus. The pituitary gland and the autonomic nervous system are managed by the brain in this area. Throughout the day, the SCN sends signals to regulate the activity of organisms in the body.
- Learning helps the animals to alter their behaviour on the basis of experience and memory helps them to store and retrieve the past information at the conscious and sub-conscious level.

4.9 KEY TERMS

- **Courtship**: It refers to the behaviour by which different species select their partners for reproduction. Usually, the male starts the courtship, and the female chooses to either mate or reject the male based on his 'performance'.
- **Dispersal:** It refers to the factor that allows animals to avoid competition, avoid inbreeding, to colonize new habitats and animals disperse by leaving their natal area and finding new territories or home ranges.
- **Parental Care:** Parental care refers to a behavioural and evolutionary strategy adopted by some animals, involving a parental investment being made to the evolutionary fitness of offspring.
- Sexual Selection: It refers to the theory of sexual selection postulates that the evolution of certain conspicuous physical traits—such as pronounced coloration, increased size, or striking adornments—in animals may grant the possessors of these traits greater success in obtaining mates.
- **Biological Rhythm:** It refers to the periodic biological fluctuation in an organism that corresponds to, and is in response to, periodic environmental change.

4.10 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

- 1. What is the difference between operant and classical conditioning?
- 2. What types of functions are controlled through the biological clock?
- 3. What are the various reproductive strategies in animals?
- 4. Write down some examples of social behaviour in animals.
- 5. What does habitat selection depend on?
- 6. What is territoriality and its importance?
- 7. What is an example of insight learning in animals?

Long-Answer Questions

- 1. Describe the way Pavlov's early work in classical conditioning influenced the understanding of learning.
- 2. Review the concepts of classical conditioning, including Unconditioned Stimulus (US), Conditioned Stimulus (CS), Unconditioned Response (UR), and Conditioned Response (CR).
- 3. Discuss the types of behaviours and adaptations that increase the reproductive success of animals.
- 4. Explain the concept of social organization in insects.

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- 5. Explain the biological and emotional causes of aggression in animals.
- 6. What would happen if parental care did not exist in animals? Explain.
- 7. Describe some examples of learned behaviours in animals.

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4.11 FURTHER READING

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