

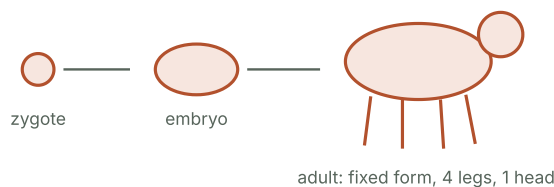
Population Attributes & Growth

Unitary and modular organisms, group attributes of a population, life and fecundity tables, survivorship, age and sex structure, dispersal, dispersion, and exponential and logistic growth. Each topic has a diagram; numerical topics have a worked example.

01 Unitary and modular populations

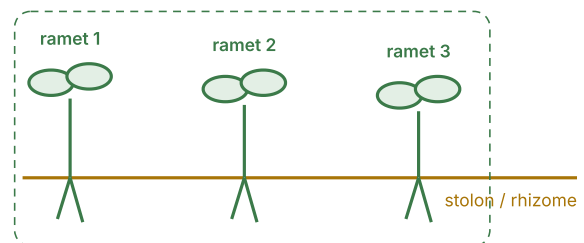
A **population** is a group of individuals of one species living in the same area at the same time and capable of interbreeding. What counts as an "individual" depends on how the organism is built (Harper, 1977; Begon et al.).

Unitary organism



Body plan is determinate; 1 zygote = 1 countable individual

Modular organism (one genet, many ramets)



Repeated modules; all ramets share one genotype (1 genet)

A unitary animal develops into one fixed form. A modular plant keeps adding modules (shoots, leaves, ramets) through vegetative growth, so the "individual" can be counted two ways.

Unitary organisms

- Form is **determinate**: fixed number of legs, eyes, segments
- Development from zygote follows a predictable programme
- Easy to count: one zygote = one individual
- Examples: most animals — mammals, birds, insects, fish

Modular organisms

- Form is **indeterminate**: zygote produces a module that repeats itself
- **Genet**: the genetic individual from one zygote. **Ramet**: a physiologically independent unit of a genet
- Population can be counted as genets or ramets; module number often matters more ecologically
- Examples: plants (trees, grasses, strawberry), corals, sponges, hydroids, bryozoans

What makes an organism unitary

In a unitary organism the zygote develops through a fixed, predictable sequence of stages (embryo, larva or juvenile, adult) into a body whose basic form is laid down in the genes. A dog always has four legs and one heart; an insect always has six legs and three body regions. Growth stops, or nearly stops, once adult size is reached. Because form is fixed, every individual is clearly separate and one zygote always gives exactly one individual, so counting the population is straightforward.

What makes an organism modular

In a modular organism the zygote develops into a basic unit of construction, the **module**, which then produces more modules like itself. In a flowering plant the module is the **phytomer**: a leaf, its axillary bud and the internode of stem. Each bud can grow into a new shoot carrying more phytomers. In a coral the module is the polyp; in a bryozoan it is the zooid. Growth is **indeterminate**: the organism keeps adding modules for as long as conditions allow, so its final shape and size depend heavily on the environment. Two oak trees of the same age can look completely different.

Genets and ramets

The **genet** is everything derived from one zygote; it is the genetic individual. Many modular organisms spread by vegetative growth (runners, rhizomes, root suckers, budding), and the connections between parts may later break. Each physically separate and physiologically independent piece is a **ramet**. A strawberry plant with runners, a bamboo clump, a stand of water hyacinth or a quaking aspen grove can be one genet made of hundreds or thousands of ramets.

Why the difference matters ecologically

- **Size, not age, predicts fate.** In modular organisms the number of modules decides how many seeds or gametes are made and how likely the organism is to survive; age is a poor predictor.
- **Partial death is common.** A grazer eating leaves kills modules, not the genet. Unitary animals rarely survive losing a large part of the body.
- **Two levels of population.** Harper described a plant as a "population of modules". Ecologists can study the birth and death of leaves or shoots within one individual as well as the birth and death of whole individuals.
- **Mostly sessile.** Modular organisms are usually fixed to one spot; they "move" by growing, and they disperse as seeds, spores or larvae.
- **Ageing differs.** Many genets show little senescence because old modules are continually replaced by new ones; some clones are thousands of years old.

FEATURE	UNITARY	MODULAR
Body form	Determinate, genetically fixed	Indeterminate, shaped by environment
Growth	Stops at adult size	Continues by adding modules
Counting unit	Individual	Genet, ramet or module
Predicts fecundity	Age	Size (number of modules)
Partial predation	Usually fatal	Usually survived
Mobility	Mostly mobile	Mostly sessile
Examples	Mammals, birds, insects, fish	Plants, corals, sponges, hydroids, bryozoans, fungi

02 Unique and group attributes of a population

An individual organism is born, ages and dies. A population does not: it has statistical properties that exist only at the group level. Odum called these **group attributes**; they are unique to the population because no single individual can possess them.

INDIVIDUAL ATTRIBUTE	CORRESPONDING POPULATION (GROUP) ATTRIBUTE	MEASURED AS
Is present in an area	Density	individuals per unit area or volume
Is born	Natality (birth rate)	births per individual per unit time
Dies	Mortality (death rate)	deaths per individual per unit time
Has an age	Age distribution / age ratio	proportion in each age class
Is male or female	Sex ratio	males : females
Moves	Dispersal and dispersion	immigration, emigration; spatial pattern
Grows	Growth form, biotic potential (r), carrying capacity (K)	change in N over time

$$N(t+1) = N(t) + B - D + I - E \quad (B \text{ births, } D \text{ deaths, } I \text{ immigrants, } E \text{ emigrants})$$

Why these attributes are "unique" to the group

A single deer can be born or die, but it cannot have a birth *rate*, a density or a sex ratio. These quantities only exist when many individuals are considered together, so they are called **group** (or **emergent**) attributes. Odum listed them as the characteristics unique to the population level of organization. They are statistical: they are averages, ratios or distributions calculated over all members.

The full list (after Odum)

- **Density** — how many individuals per unit space
- **Natality** and **mortality** — rates of addition and loss
- **Age distribution** — proportions of young, breeding and old individuals
- **Sex ratio** — proportions of males and females
- **Biotic potential** — the maximum rate of increase ($r_{\max}$) under ideal conditions
- **Growth form** — the shape of the curve of N against time (J or S)
- **Dispersal** — movement in and out; **dispersion** — spatial pattern
- **Genetic attributes** — gene frequencies, adaptiveness, reproductive fitness

Four primary processes

Only four processes change population size: **births** and **immigration** add individuals; **deaths** and **emigration** remove them. Every other attribute acts through these four. In a closed population (an island, a culture flask) there is no immigration or emigration, so only births and deaths matter.

Environmental resistance and regulation

The gap between the biotic potential and the growth actually achieved is called **environmental resistance**: shortage of food, space, mates, plus predation, disease and bad weather. Factors that limit a population are of two kinds:

- **Density-dependent factors** act more strongly as density rises: competition for food, predation, parasitism, disease, accumulation of wastes. They tend to regulate a population near K.
- **Density-independent factors** affect a fixed proportion regardless of density: floods, frost, fire, drought. They cause fluctuations but cannot by themselves hold a population at a steady level.

03 Population density

Types of density

- **Crude density**: number (or biomass) per *total* area, e.g. 200 deer per 100 km² of forest
- **Ecological (specific) density**: number per area of *usable habitat*, e.g. fish per m³ of pond water actually occupied
- **Absolute density**: actual count per unit area. **Relative density**: index such as catch per trap-night or calls heard per hour

Methods of estimation

- **Total count**: census of large or conspicuous animals
- **Quadrat method**: count in sample plots, scale to whole area (plants, sessile animals)
- **Mark–release–recapture**: mobile animals
- **Indirect indices**: pug marks, faecal pellets, nests, call counts

Lincoln–Petersen index: $N = (M \times n) / m$

WORKED NUMERICAL

50 fish are caught, tagged and released ($M = 50$). A week later 40 fish are caught ($n = 40$), of which 10 carry tags ($m = 10$).

$N = (50 \times 40) / 10 = \mathbf{200 \text{ fish}}$. If the pond is 0.5 ha, density = $200 / 0.5 = \mathbf{400 \text{ fish per ha}}$.

Assumptions: closed population, marks not lost, marked and unmarked equally catchable, marked animals mix randomly.

Why density is the central attribute

Density determines how strongly individuals compete, how easily they find mates, how fast disease spreads and how attractive the population is to predators. Most of the other attributes (natality, mortality, dispersal) change with density, so it is usually the first thing an ecologist measures.

Units

Small, numerous organisms are counted per unit area or volume (plankton per litre, earthworms per m²). Large animals are expressed per km² or per hectare. Where individuals differ greatly in size, as in trees or fish, **biomass density** (kg per hectare) or cover is more meaningful than number, because one large tree is not ecologically equal to one seedling.

Crude vs ecological density, explained

A lake of 10 hectares holding 1000 fish has a crude density of 100 fish per hectare. If the fish only live in the 2 hectares of shallow, weedy margins, their ecological density is 500 per hectare. Ecological density reflects the crowding that the animals actually experience, so it is the better measure for questions of competition and resource use.

The quadrat method in steps

- Choose quadrat size suited to the organism (1 m² for herbs, 10 × 10 m for shrubs, 20 × 20 m for trees).
- Place quadrats randomly or along a transect; count individuals in each.
- **Density** = total individuals / (number of quadrats × quadrat area).
- **Frequency** (%) = quadrats in which species occurs / total quadrats × 100 — indicates how widely spread a species is.
- **Abundance** = total individuals / number of quadrats in which the species occurred — indicates how crowded it is where present.

Mark–release–recapture logic

If marked animals mix freely, the proportion of marked animals in the second sample (m/n) should equal the proportion of marked animals in the whole population (M/N). Rearranging $m/n = M/N$ gives $N = Mn/m$. The estimate fails if marks fall off, if marked animals become trap-shy or trap-happy, or if births, deaths or migration happen between samples.

Other relative methods

When absolute counts are impossible, ecologists use indices that rise and fall with density: catch per unit effort in fisheries, number of pug marks per km in tiger surveys, faecal pellet groups for deer, calls per hour for frogs and birds, or percentage of plant cover.

04 Natality and mortality

Natality (birth rate)

- Ability of a population to increase through reproduction (birth, hatching, germination, fission)
- **Maximum (absolute, physiological) natality**: theoretical maximum under ideal conditions; constant for a species
- **Ecological (realized) natality**: actual births under real field conditions; varies with density, food, climate
- **Crude birth rate** $b = \Delta N_n / (N \cdot \Delta t)$
- **Age-specific natality** m_x : offspring per female of age x

Mortality (death rate)

- Number of deaths in a population per unit time
- **Minimum (physiological) mortality**: deaths from old age alone under ideal conditions
- **Ecological (realized) mortality**: actual deaths from predation, disease, starvation, climate
- **Crude death rate** $d = \Delta N_d / (N \cdot \Delta t)$
- **Physiological longevity**: maximum lifespan possible.
Ecological longevity: average lifespan actually achieved

Per-capita growth rate: $r = b - d$ ($r > 0$ growing, $r = 0$ stable, $r < 0$ declining)

WORKED NUMERICAL

A population of 2000 rabbits has 600 births and 400 deaths in a year. $b = 600/2000 = 0.30 \text{ yr}^{-1}$; $d = 400/2000 = 0.20 \text{ yr}^{-1}$; $r = 0.30 - 0.20 = \mathbf{0.10 \text{ yr}^{-1}}$ (10% growth per year). Crude birth rate in human terms = 300 per 1000.

IN DETAIL

Natality in detail

Natality is the population's inherent ability to increase. It includes every way new individuals appear: birth in mammals, hatching in birds and reptiles, germination in plants, and fission or budding in microorganisms. **Maximum natality** is the theoretical upper limit for the species when no ecological factor is limiting; it is set by physiology, such as the number of eggs an ovary can produce. **Ecological natality** is always lower and changes with food, climate, density and the age structure of the population.

Factors that affect natality

- **Age at first reproduction** — breeding earlier raises r far more than producing extra offspring later
- **Clutch or litter size** and number of breeding events per year
- **Semelparity vs iteroparity** — breeding once and dying (Pacific salmon, bamboo, annual plants) or breeding repeatedly (humans, most birds)
- **Proportion of females** and of individuals in the reproductive age class
- **Food supply and body condition** — well-fed females lay more eggs
- **Density** — crowding lowers natality in many species (density-dependent)

Mortality in detail

Mortality is the loss of individuals by death. **Minimum mortality** is the theoretical loss under ideal conditions, when individuals die only of old age at their physiological lifespan.

Ecological mortality is the real loss in nature from predators, parasites, disease, starvation, accidents and harsh weather. Ecologists often express mortality as its complement, **survival rate** $= 1 - \text{mortality rate}$, because survival is what the population "keeps".

Longevity

Physiological longevity is the maximum lifespan an individual can reach under optimal conditions (e.g. about 120 years for humans). **Ecological longevity** is the average lifespan individuals actually reach in a particular environment. The difference between them is a measure of how much ecological mortality the population suffers.

Expressing rates

Rates can be **crude** (per whole population: births per 1000 people per year) or **specific** (per age group, sex or other category). Specific rates are more informative because a population full of young adults will have a high crude birth rate even if each woman has few children. In demography, the crude birth and death rates are given per 1000 per year; the difference gives the natural rate of increase.

05 Life tables

A life table is an age-by-age summary of survival and death in a population. It was developed by actuaries for insurance and introduced to ecology by Raymond Pearl (1921) and Deevey (1947).

Cohort (dynamic, horizontal) life table

Follows one **cohort**, a group born at the same time, from birth until the last one dies. Accurate, but practical only for short-lived or sessile organisms (annual plants, barnacles, insects).

Static (time-specific, vertical) life table

Records the age structure of a population at **one point in time**, or ages at death (e.g. Murie's Dall sheep skulls). Assumes a stable age distribution. Used for long-lived animals.

COLUMN	MEANING	FORMULA
x	age class	—
n _x	number alive at start of age x	observed
l _x	proportion of original cohort surviving to age x (survivorship)	n _x / n ₀
d _x	number dying between x and x+1	n _x - n _{x+1}
q _x	age-specific mortality rate	d _x / n _x
L _x	average number alive during the interval	(n _x + n _{x+1}) / 2
T _x	total individual-time units lived from age x onward	Σ L _x from x to the end
e _x	life expectancy: further time an individual of age x is expected to live	T _x / n _x

WORKED NUMERICAL · HYPOTHETICAL COHORT OF 1000 INSECTS (AGE IN WEEKS)

X	N _x	L _x	D _x	Q _x	L _x	T _x	E _x
0	1000	1.000	600	0.600	700	1290	1.29
1	400	0.400	160	0.400	320	590	1.48
2	240	0.240	120	0.500	180	270	1.13
3	120	0.120	90	0.750	75	90	0.75
4	30	0.030	30	1.000	15	15	0.50
5	0	0	—	—	0	0	—

Check: $e_1 = 590/400 = 1.48$ weeks is higher than $e_0 = 1.29$. Surviving the very high first-week mortality ($q_0 = 0.6$) raises an individual's remaining life expectancy — a common exam point.

Why ecologists use life tables

A life table shows *when* in life individuals die. That tells us which stage is most vulnerable, how long an average individual will live, and which stage to protect in conservation or to target in pest control. Combined with a fecundity schedule it predicts whether the population will grow or shrink.

Constructing a cohort life table

- Mark or follow a group of individuals born at the same time (n_0).
- Choose suitable age intervals (days for insects, years for mammals).
- Count the survivors at the start of each interval (n_x) until all have died.
- Calculate the other columns from n_x using the formulas above.

Constructing a static life table

Count individuals of each age class present at one time, or determine the age at death of individuals found dead. The classic example is Adolph Murie's collection of 608 Dall sheep skulls from Mount McKinley (Denali), aged by horn rings; Deevey (1947) used it to build a life table. The static method assumes that birth and death rates have been constant for a long time, so that today's age structure reflects survival through each age.

Reading the columns

- l_x always falls from 1; plotting it gives the survivorship curve.
- d_x shows in absolute numbers when deaths peak; the d_x column must sum to n_0 .
- q_x shows the risk of dying for those still alive; it is the best column for comparing how dangerous each age is.
- e_x summarizes everything ahead of an individual; it can rise after a dangerous early stage, as in the worked example.

k-values and key-factor analysis

Varley and Gradwell introduced the killing power $k_x = \log_{10} n_x - \log_{10} n_{x+1}$. Unlike q_x , k-values can be added: total mortality $K = \sum k_x$. Tracking k-values over several years shows which stage's mortality varies most with total mortality; that stage contains the **key factor** driving population change (e.g. winter disappearance in the winter moth).

Uses

Life insurance premiums, human demography, fisheries and wildlife harvest quotas, identifying the vulnerable stage of an endangered species, timing pest-control measures, and comparing survival between habitats or sexes.

06 Fecundity tables

A fecundity (fertility) schedule adds m_x , the average number of **female** offspring produced per female of age x . Combined with l_x it tells us whether the population will grow.

$$R_0 = \sum l_x m_x \quad | \quad T = \sum x \cdot l_x m_x / R_0 \quad | \quad r \approx \ln R_0 / T$$

R_0 NET REPRODUCTIVE RATE

Average female offspring per female over her lifetime. $R_0 > 1$ growing; $= 1$ stable; < 1 declining.

T GENERATION TIME

Mean age at which females give birth.

R INTRINSIC RATE OF INCREASE

Per-capita growth rate per unit time (approximate formula).

X	L_x	M_x	$L_x M_x$	$X \cdot L_x M_x$
0	1.000	0	0	0
1	0.400	2	0.80	0.80
2	0.240	3	0.72	1.44
3	0.120	3	0.36	1.08
4	0.030	1	0.03	0.12
Σ			$R_0 = 1.91$	3.44

WORKED NUMERICAL • SAME INSECT COHORT

$R_0 = 1.91 \rightarrow$ each female replaces herself almost twice: the population is **growing**.

$T = 3.44 / 1.91 = \mathbf{1.80 \text{ weeks}}$. $r \approx \ln(1.91) / 1.80 = 0.647 / 1.80 = \mathbf{0.36 \text{ per week}}$.

IN DETAIL

From life table to fecundity schedule

A life table only describes deaths. To predict population change we also need births, recorded age by age as m_x . Only females and female offspring are usually counted, because females limit reproduction in most species. Putting l_x and m_x together gives a **life-and-fecundity table**.

Why multiply l_x by m_x

m_x is the output of a female who is alive at age x , but not every newborn female reaches age x . $l_x m_x$ is therefore the expected daughters produced at age x *per newborn female*, allowing for the chance she dies first. Summing across ages gives R_0 , the expected lifetime daughters per newborn female.

Related measures

- **Gross reproductive rate** $GRR = \sum m_x$: offspring a female would produce if she survived to the maximum age. It ignores mortality and always exceeds R_0 .
- **Net reproductive rate** $R_0 = \sum l_x m_x$: replacement per generation.
- **Generation time** $T = \sum x \cdot l_x m_x / R_0$: average age of mothers at the birth of their daughters.
- **Intrinsic rate** $r \approx \ln R_0 / T$; exact value from the **Euler–Lotka equation** $\sum e^{-rx} l_x m_x = 1$.

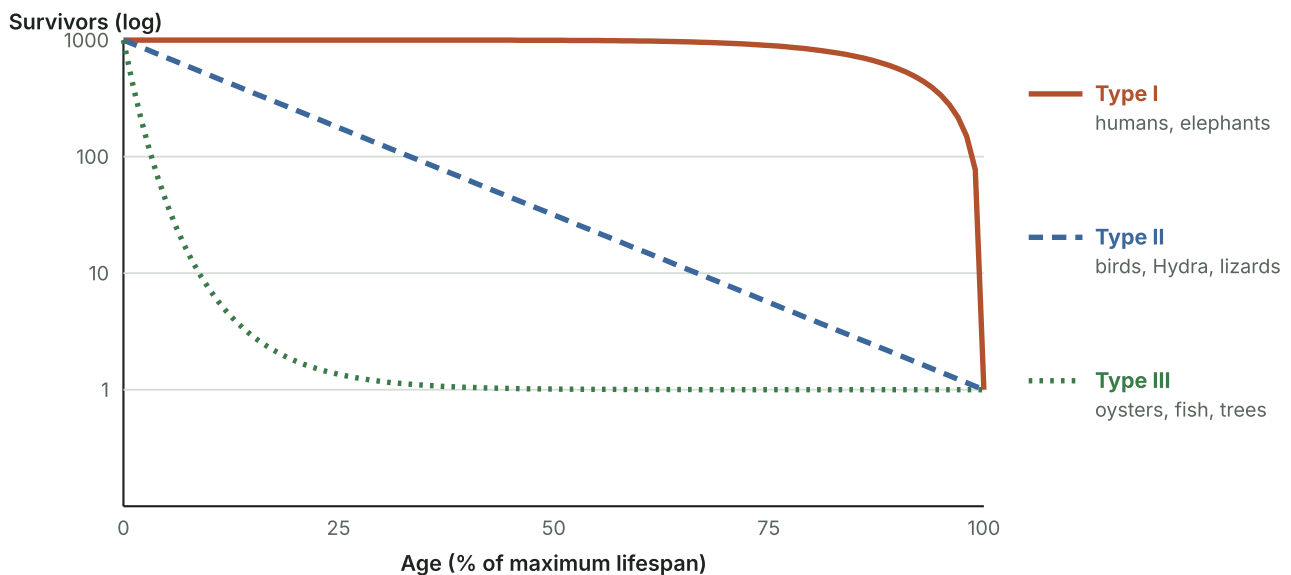
- **Finite rate of increase** $\lambda = e^r$: factor by which the population multiplies each time unit ($\lambda > 1$ growth).
- **Reproductive value** v_x (Fisher): expected future offspring of an individual of age x . It is usually highest just as breeding begins, which is why harvesting young breeding females harms a population most.

Interpreting R_0 and T together

Two populations with the same R_0 grow at different speeds if their generation times differ: shortening T has a large effect on r . This is why early maturity is favoured in disturbed habitats and why insect pests can explode so quickly.

07 Survivorship curves

Plotting l_x (usually as log number of survivors out of 1000) against age gives a survivorship curve. Pearl (1928) and Deevey (1947) described three idealized types. The log scale matters: a straight line means a **constant** proportion dies at every age.



Idealized curves, starting with 1000 newborns. Most real populations fall between these shapes, and some change type with life stage.

Type I · convex

Low mortality through most of life; deaths concentrate in old age. Few offspring, high parental care.

HUMANS IN DEVELOPED COUNTRIES, LARGE MAMMALS, DALL SHEEP

Type II · diagonal

Constant **proportion** dies at each age (constant q_x), giving a straight line on a log scale.

MANY BIRDS, HYDRA, LIZARDS, RODENTS

Type III · concave

Very heavy juvenile mortality; the few survivors live long. Huge numbers of offspring, no parental care.

OYSTERS, MOST FISH, MANY PLANTS AND INSECTS

IN DETAIL

How the curve is drawn

Survivorship is plotted as the number surviving out of 1000 born ($1000 \cdot l_x$) on a **logarithmic** y-axis against age. Age is often expressed as a percentage of maximum lifespan so that species with very different lifespans can be compared on one graph. The log scale is used because it shows the *rate* of mortality: the steeper the slope at any point, the higher the proportion dying at that age.

Type I — convex (late loss)

Almost all individuals survive through youth and middle age; mortality rises sharply near the maximum lifespan. These species produce few offspring and invest heavily in each through parental care, so the young are well protected. Examples: humans in developed countries, elephants, Dall sheep, many large mammals, and annual plants grown in good conditions.

Type II — diagonal (constant loss)

The probability of dying is about the same at all ages, so the log curve is a straight line. Death is often caused by factors that strike randomly with respect to age, such as predation. Examples: many songbirds, Hydra, lizards, small rodents, and seed banks of some plants.

Type III — concave (early loss)

Mortality is enormous among eggs, larvae or seedlings, then falls sharply; the few survivors may live a long time. These species produce huge numbers of small offspring with no parental care. Examples: oysters and other marine invertebrates with planktonic larvae, most bony fish, forest trees, many insects. An oyster may release millions of eggs per season.

Variations

- **Stair-step curves** in insects with complete metamorphosis: mortality is concentrated at moults and pupation, with flat stretches in between.
- **Changing type over history**: human populations moved from nearly Type II/III (high infant mortality) to Type I as medicine and nutrition improved.
- **Sex differences**: males of many mammals have steeper curves than females.

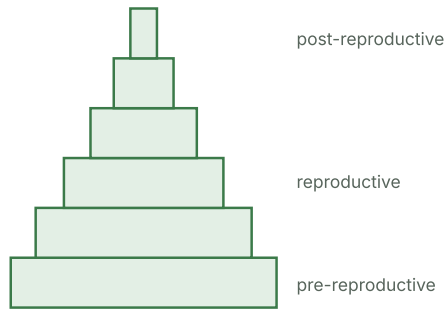
Link to life-history strategy

Type I is typical of K-selected species (few, large, well-cared-for offspring), and Type III of r-selected species (many small offspring). Type II lies between.

08 Age ratio and age pyramids

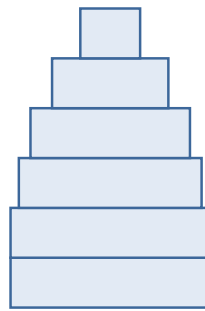
Bodenheimer (1938) divided a population into three ecological ages: **pre-reproductive**, **reproductive** and **post-reproductive**. The ratio among them predicts the future of the population and is shown as an age pyramid.

Expanding (triangular)



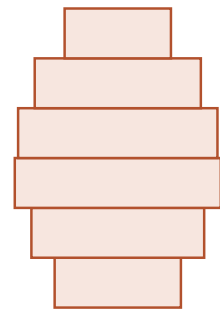
Many young, high birth rate
e.g. India 1970s, Nigeria

Stable (bell-shaped)



Young $\approx$ reproductive
e.g. USA, France

Declining (urn-shaped)



Few young, ageing population
e.g. Japan, Italy

Bars from bottom to top: youngest to oldest age classes. Width is the proportion of the population in that class.

Why age ratio matters

- A large pre-reproductive base means future growth even if birth rate falls (population momentum)
- Fisheries and wildlife: a population of mostly old fish is overharvested at young ages
- Lotka: a population with constant b and d reaches a **stable age distribution**

Age ratio index

Commonly expressed as the ratio of young to adults, e.g. fawns per 100 does in deer management. A falling young:adult ratio signals poor recruitment.

The three ecological ages

The relative length of each age differs widely among species. A mayfly spends one to three years as a nymph (pre-reproductive) and a day or less as a reproductive adult. Seventeen-year cicadas spend 17 years underground. Many birds become reproductive within a year and remain so until death. Humans have long pre-reproductive and post-reproductive periods. The post-reproductive class contributes nothing to growth but still uses resources.

How animals are aged

Field ecologists determine age from growth rings in fish scales and otoliths (ear stones), annual rings in tree trunks, horn rings in sheep and goats, tooth wear and tooth cementum layers in mammals, plumage in birds, and body size in many invertebrates.

Reading an age pyramid

- **Expanding (triangular):** broad base of young, narrow top. High birth rate, high death rate, short life expectancy. The population will keep growing because large young cohorts are about to enter the reproductive class.
- **Stable (bell-shaped):** pre-reproductive and reproductive classes roughly equal. Birth and death rates are balanced, so numbers change little.
- **Declining (urn-shaped):** narrow base, broad middle and top. Birth rate below replacement; the population is ageing and will shrink.

Stable and stationary age distributions

Lotka showed mathematically that if age-specific birth and death rates stay constant, the population settles into a **stable age distribution**: the proportion in each age class stays the same while total numbers rise or fall at a constant rate r . If, in addition, $r = 0$, the distribution is called **stationary**. A sudden event (war, epidemic, baby boom) disturbs this, and the effect travels up the pyramid for decades.

Applications

Wildlife managers use young-to-adult ratios to judge breeding success. In fisheries, catches made up of mostly young fish warn of overfishing. Planners use human pyramids to forecast school, job and pension needs. Pest outbreaks are predicted when large numbers of young insects are present.

09 Sex ratio

The ratio of males to females in a population, usually written as males per 100 females (Indian census: females per 1000 males).

Primary sex ratio

At fertilization (conception). Close to 1:1 in XY systems.

Secondary sex ratio

At birth or hatching. Human $\approx$ 105 males : 100 females.

Tertiary sex ratio

Among sexually mature adults. Shaped by sex-different mortality; in humans it shifts toward females in old age.

Fisher's principle (1930)

If one sex becomes rare, parents producing that sex gain more grandchildren, so selection pushes the ratio back toward 1:1 investment in sons and daughters.

Exceptions

- **Local mate competition** (Hamilton, 1967): fig wasps and parasitoids produce female-biased broods when brothers compete for the same mates
- **Haplodiploidy** (bees, ants): queen controls sex by fertilizing eggs or not
- **Temperature-dependent sex determination**: turtles, crocodiles
- **Polygynous mammals** (deer, seals): adult ratio female-biased due to male mortality

IN DETAIL

How sex is determined

- **Chromosomal**: XX/XY (mammals, *Drosophila*) or ZZ/ZW (birds, butterflies), giving a primary ratio near 1:1
- **Haplodiploidy**: unfertilized eggs become males, fertilized become females (bees, ants, wasps)
- **Environmental**: incubation temperature in turtles and crocodiles; in *Bonellia* the larva becomes male if it settles on a female
- **Sequential hermaphroditism**: clownfish change from male to female, wrasses from female to male

Why ratios change between primary and tertiary

Even if the primary ratio is 1:1, males and females may die at different rates as embryos, juveniles and adults. In most mammals, males die more often: they fight, take more risks, grow larger and are more vulnerable to disease. The tertiary (adult) ratio is therefore commonly female-biased. In humans the secondary ratio is about 105 boys to 100 girls, but by old age women outnumber men.

Fisher's principle explained

Every offspring has exactly one father and one mother. If males are scarce, each male fathers on average more offspring than each female mothers, so parents that produce sons gain more grandchildren. That advantage spreads genes for producing sons until the ratio returns to equality. The same argument works in reverse if females are scarce. The stable outcome is equal *investment* in the two sexes, which gives a 1:1 ratio when sons and daughters cost the same.

Ecological importance

- In monogamous species, a skewed ratio leaves the excess sex unable to breed, reducing natality.
- In polygynous species (deer, elephant seals), one male mates with many females, so harvesting some males hardly affects births — the basis of male-only hunting quotas.
- A skewed ratio lowers **effective population size**: $N_e = 4N_mN_f / (N_m + N_f)$. With 10 males and 90 females, $N_e = 4 \times 10 \times 90 / 100 = 36$, not 100, so genetic diversity is lost faster.
- In India, the Census 2011 child and overall sex ratios drew attention to sex-selective practices; the overall figure was 943 females per 1000 males.

10 Dispersal and dispersion

The two words sound alike but mean different things. **Dispersal** is *movement* of individuals into or out of a population. **Dispersion** is the *spatial pattern* of individuals within the habitat at a given time.

Emigration

One-way movement **out** of a population.
Lowers N; often triggered by crowding.

Immigration

One-way movement **into** a population.
Raises N and brings new genes.

Migration

Periodic **two-way** movement, departure and return (Siberian crane to Bharatpur, salmon, monarch butterflies).

Importance of dispersal

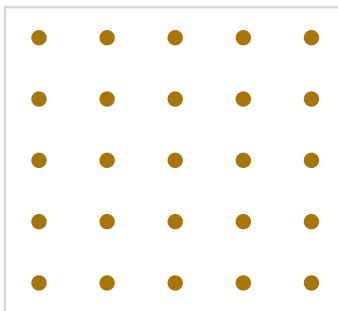
- Colonizes new habitats and recolonizes after local extinction (metapopulations)
- Reduces crowding, competition and inbreeding; maintains gene flow
- Modes: active (walking, flying, swimming) or passive (wind, water, animals — seeds, spores, larvae)

Random



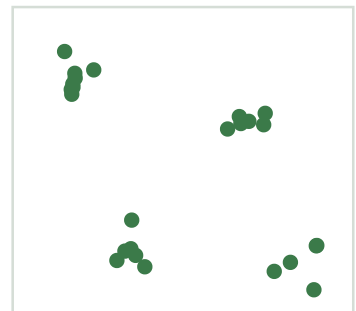
$$s^2/\bar{x} \approx 1$$

Uniform (regular)



$$s^2/\bar{x} < 1$$

Clumped (aggregated)



$$s^2/\bar{x} > 1$$

Each panel holds 25 individuals. The variance-to-mean ratio of quadrat counts ($s^2/\bar{x}$) identifies the pattern.

Random

Position of one individual has no effect on another. Uniform environment, no strong interaction. Rare in nature.

FLOUR BEETLES IN FLOUR,
SOME FOREST TREES

Uniform

Individuals evenly spaced because of competition or territoriality.

CREOSOTE BUSHES
(ALLELOPATHY), NESTING
PENGUINS, CROP FIELDS

Clumped

Most common pattern. Patchy resources, social grouping, limited seed dispersal. Allee (1931): moderate aggregation can raise survival.

HERDS, SCHOOLS OF FISH,
PLANTS AROUND WATER

WORKED NUMERICAL · VARIANCE-TO-MEAN RATIO

Ten quadrats give counts 0, 0, 6, 1, 0, 9, 0, 0, 4, 0. Mean $\bar{x} = 20/10 = 2.0$.

$\Sigma x^2 = 36 + 1 + 81 + 16 = 134$. $\Sigma (x - \bar{x})^2 = 134 - 10(2.0)^2 = 94$. Sample variance $s^2 = 94/9 = 10.44$.

$s^2/\bar{x} = 10.44 / 2.0 = 5.22 > 1 \rightarrow$ the distribution is **clumped**.

Dispersal in detail

Dispersal is the movement of individuals away from their place of birth or from one breeding site to another. **Natal dispersal** is movement from birthplace to first breeding site; **breeding dispersal** is movement between successive breeding sites. In many birds females disperse farther; in many mammals males do, which reduces inbreeding.

Causes of dispersal

- Crowding and competition for food, mates or territories (density-dependent emigration)
- Avoiding inbreeding with relatives
- Escaping deteriorating habitat (drying ponds, seasonal food loss)
- Seasonal cycles driving migration

Modes

Active dispersal uses the organism's own movement. **Passive** dispersal relies on external agents: wind (dandelion seeds, spiders ballooning), water (coconut, mangrove propagules, marine larvae), animals (burrs on fur, fruits eaten by birds) and humans (weeds, invasive species). Barriers such as mountains, rivers and roads limit dispersal and isolate populations.

Consequences

Dispersal links separate local populations into a **metapopulation**, in which local extinctions are offset by recolonization. It spreads genes (gene flow), slows genetic divergence between populations and lets species track changing climates.

Dispersion: why the three patterns arise

- **Random:** the environment is uniform and individuals neither attract nor repel each other. This is uncommon because habitats are rarely uniform.
- **Uniform:** individuals push each other apart through competition for a scarce resource (roots for water in deserts), chemical inhibition (allelopathy) or territorial behaviour (nesting seabirds keeping pecking distance).
- **Clumped:** the most common pattern. Resources occur in patches, offspring stay near parents (vegetative reproduction, heavy seeds), or animals group for protection, hunting or mating.

Allee's principle

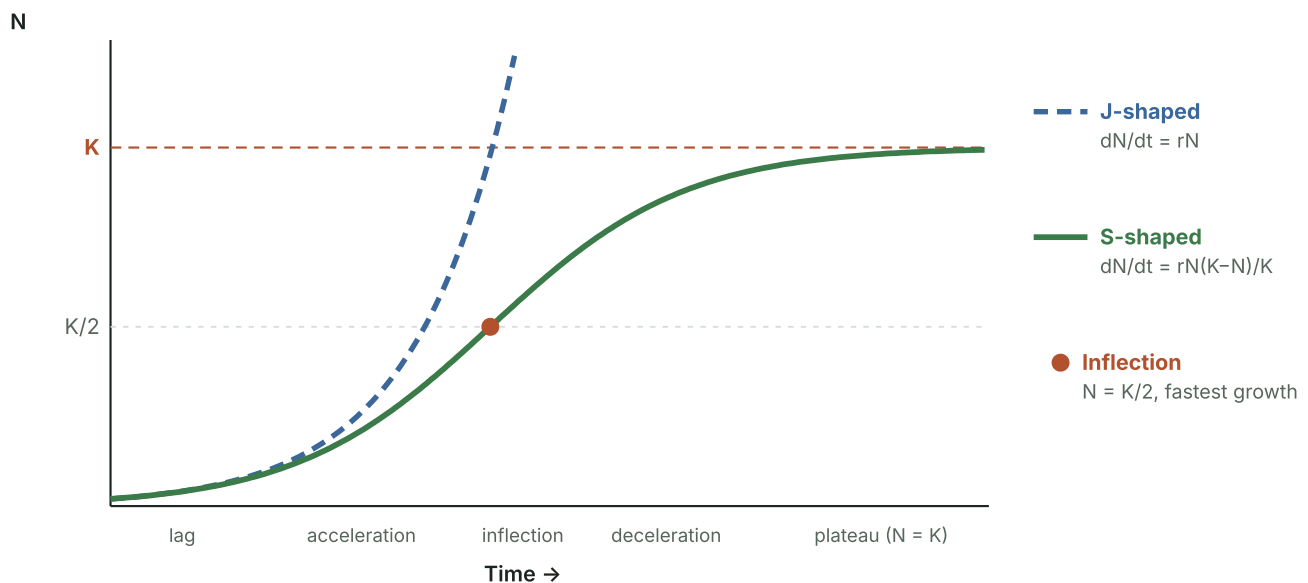
Allee showed that both undercrowding and overcrowding can be harmful. Moderate aggregation can increase survival through group defence, easier mate finding, cooperative feeding and modified microclimate (huddling penguins). Below a threshold density, growth rate may even fall — the **Allee effect**, important for rare species.

Measuring dispersion

Besides the variance-to-mean ratio, the **Clark–Evans nearest-neighbour index** R = observed mean distance to nearest neighbour / expected mean distance for a random pattern is used. $R = 1$ random, $R < 1$ clumped (minimum 0), $R > 1$ uniform (maximum 2.15 for a perfect hexagonal pattern).

11 Population growth: equations and patterns

Odum recognized two basic growth forms: the **J-shaped** (exponential) curve and the **S-shaped** (sigmoid, logistic) curve.



Both curves start at the same N_0 with the same r . The gap between them is environmental resistance.

Exponential (J-shaped) growth

$$dN/dt = rN \rightarrow N_t = N_0 e^{rt}$$

- Unlimited resources; r is the **biotic potential** ($r_{\max}$)
- Doubling time $t_d = \ln 2 / r \approx 0.693 / r$
- Ends abruptly in a crash when resources run out or the season ends: algal blooms, insects in spring, lemmings

Logistic (S-shaped) growth

$$dN/dt = rN (K - N) / K$$

$$N_t = K / (1 + a e^{-rt}), \quad a = (K - N_0) / N_0$$

- Verhulst (1838); rediscovered by Pearl & Reed (1920)
- $(K - N)/K$ = unused carrying capacity; growth slows as $N \rightarrow K$
- Maximum growth rate $rK/4$ occurs at $N = K/2$ — basis of maximum sustainable yield in fisheries

Phases of the logistic curve

- **Lag phase**: few individuals, adjusting to environment; slow growth
- **Acceleration (log) phase**: near-exponential growth while N is small
- **Inflection point** at $K/2$: growth rate is at its maximum
- **Deceleration phase**: environmental resistance (food, space, waste) increases
- **Plateau / equilibrium**: N fluctuates around K , births $\approx$ deaths

WORKED NUMERICALS

(a) $r = 0.5$ per day, $K = 1000$, $N = 200$: $dN/dt = 0.5 \times 200 \times (1000 - 200)/1000 = \mathbf{80 \text{ individuals per day}}$.

(b) Maximum possible growth rate for the same population: at $N = K/2 = 500$, $dN/dt = rK/4 = 0.5 \times 1000 / 4 = \mathbf{125 \text{ per day}}$.

(c) Exponential: $N_0 = 100$, $r = 0.1$ per day, after 10 days $N = 100e^{1} = \mathbf{272}$. Doubling time = $0.693/0.1 = \mathbf{6.9 \text{ days}}$.

Overshoot & oscillation

With a time lag in response to density, N overshoots K and oscillates around it (damped or stable cycles), e.g. Nicholson's blowflies.

Irruption & crash

J-shaped growth followed by sudden collapse: reindeer on St. Matthew Island rose to ~6000 then crashed to 42.

r- and K-selection

MacArthur & Wilson (1967): r-strategists (high r , small, many offspring, Type III) vs K-strategists (near K , large, few offspring, Type I).

Exponential growth explained

If resources are unlimited and r stays constant, each individual adds offspring at the same per-capita rate no matter how many others there are. The number added per unit time is then proportional to N , so the bigger the population, the faster it grows. The curve starts slowly and then shoots upward like the letter J. This happens when a species colonizes a new, empty habitat or when limits are briefly removed. It cannot continue for long: sooner or later resources run out, and the population usually crashes rather than levelling off.

Deriving the logistic equation

Verhulst added a brake to the exponential equation. Suppose the environment can support at most K individuals. When N is small, nearly all of K is unused and growth is almost exponential. As N rises, the fraction of capacity still free, $(K - N)/K$, falls toward zero. Multiplying the exponential rate by this fraction gives:

$$dN/dt = rN \times (K - N)/K = rN(1 - N/K)$$

The per-capita growth rate is now $r(1 - N/K)$, which falls in a straight line as N rises: it equals r when N is near 0 and zero when $N = K$. Integrating gives $N_t = K / (1 + a e^{-rt})$, with $a = (K - N_0)/N_0$.

Why the maximum growth rate is at $K/2$

$dN/dt = rN - rN^2/K$. Differentiating with respect to N and setting it to zero: $r - 2rN/K = 0$, so $N = K/2$. Substituting gives the maximum growth rate $rK/4$. At low N there are too few breeders; near K there is too little free capacity; halfway is the best balance.

Assumptions of the logistic model

- K is constant (stable environment)
- Every individual has the same effect on growth; no age, sex or size structure
- Density affects growth instantly, with no time lag
- No immigration or emigration; population is closed

Experimental evidence

Pearl (1927) fitted the logistic to Carlson's data for yeast cells in culture, which levelled off near 665 units. Gause's *Paramecium* cultures and laboratory populations of flour beetles and *Drosophila* also follow S-shaped curves. Sheep introduced into Tasmania grew rapidly in the early 1800s and then fluctuated around a ceiling of about 1.7 million.

Limitations

Real populations have time lags (gestation, maturation), so they often overshoot K and oscillate. K changes with seasons and years. Natural populations also have age structure and are influenced by predators and immigration. The logistic is a useful first approximation, not an exact law.

Other growth patterns

- **Damped oscillation:** N overshoots K and swings back and forth with decreasing amplitude until it settles.
- **Stable limit cycles:** long time lags cause regular boom-bust cycles (Nicholson's blowflies).

- **Population cycles:** regular multi-year cycles in nature, e.g. the ~10-year snowshoe hare–lynx cycle in Canada.
- **Irruptions:** sudden outbreaks, as in locust swarms or algal blooms, followed by crashes.
- **Discrete growth:** species breeding in one season per year are modelled as $N_{t+1} = \lambda N_t$ instead of a continuous equation.

FEATURE	R - SELECTED	K - SELECTED
Environment	Unpredictable, disturbed	Stable, predictable
Population size	Fluctuates, often below K	Near K
Body size	Small	Large
Maturity	Early	Late
Offspring	Many, small, little care	Few, large, much care
Lifespan	Short	Long
Survivorship	Type III	Type I
Examples	Insects, weeds, bacteria	Elephants, whales, humans, trees

Q End-semester question set

Long answer

- Q1** Distinguish between unitary and modular organisms. Explain genet and ramet with examples, and discuss the problem of counting modular populations. 10 marks
- Q2** What is a life table? Distinguish between cohort and static life tables. Construct a life table from given n_x data and compute l_x , d_x , q_x and e_x . 10 marks
- Q3** Derive the logistic growth equation. Draw the sigmoid curve, explain its phases, and show that growth rate is maximal at $N = K/2$. 10 marks
- Q4** Describe the three types of survivorship curves with examples. How are they related to r- and K-selection? 10 marks

Short answer

- Q1** Crude density vs ecological density. 3 marks
- Q2** Maximum natality vs ecological natality. 3 marks
- Q3** Dispersal vs dispersion. 3 marks

Q4 Draw and interpret expanding, stable and declining age pyramids. 5 marks

Q5 Primary, secondary and tertiary sex ratio; state Fisher's principle. 5 marks

Q6 Define R_0 , generation time and intrinsic rate of increase. 5 marks

Numericals

Q1 In a lake 120 fish are marked. A later sample of 150 contains 30 marked fish. Estimate population size. (Ans: 600) 3 marks

Q2 Quadrat counts: 2, 3, 2, 1, 2, 3, 2, 1. Find $s^2/\bar{x}$ and the dispersion pattern. (Ans: $\bar{x} = 2.0$, $s^2 = 0.571$, ratio 0.29 $\rightarrow$ uniform) 5 marks

Q3 $r = 0.2 \text{ yr}^{-1}$, $K = 5000$. Find dN/dt at $N = 1000$ and the maximum growth rate. (Ans: 160 yr^{-1} ; 250 yr^{-1} at $N = 2500$) 5 marks

Q4 Given $l_x = 1, 0.5, 0.2, 0.05$ and $m_x = 0, 4, 5, 2$ for $x = 0-3$, find R_0 and T . (Ans: $R_0 = 3.1$; $T = 4.3/3.1 = 1.39$) 5 marks

Notes based on standard texts (Odum, Begon et al., Krebs). The life-table cohort and quadrat counts are hypothetical teaching data.