

# Glossary in Evolutionary Biology

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This list contains terms, which a student in evolutionary biology should know. The terms denoted with an \* are for an advanced level (Courses in evolutionary and quantitative genetics). This Glossary has been compiled with the help of the following books:

- J.R. Krebs & N.B. Davies; *An Introduction to Behavioural Ecology*. 3. Ed., Blackwell UK. 1993.
- S.C. Stearns & R.F. Hoekstra; *Evolution: An Introduction*. Oxford University Press. 2005.
- D.A. Roff; *The Evolution of life histories*. Chapman & Hall. 1992.

**Adaptation:** A state that evolved because it improved reproductive performance, to which survival contributes. Also the process that produces that state.

**Adaptive evolution:** The process of change in a population driven by variation in reproductive success that is correlated with heritable variation in a trait.

**\*Additive genetic variance:** The part of total genetic variance that can be modelled by allelic effects whose influence on the phenotype in heterozygotes is additive (Additive means that the phenotype of the heterozygote is halfway between the phenotype of the two homozygotes). This part of genetic variance determines the response to selection by quantitative traits.

**Aging (=Ageing):** (See Senescence).

**Allele:** One of the different homologous forms of a single gene; at the molecular level, a different DNA sequence at the same place in the chromosome.

**Allele frequency:** Proportion the copies of a given allele among all alleles at the locus of interest.

**Allometry:** Relationship between the size of two organisms or their parts. E.g. larger organisms produce larger offspring. Allometry is important because many life history traits scale with body size.

**Allopatric:** Species are allopatric if they occur in non-overlapping geographically regions.

**\*Allopolyploidy:** An increase in the number of chromosomes involving hybridization followed by chromosome doubling. The offspring then contain chromosomes from both parental species.

**Altruism:** Behaviour that benefits others at a cost to oneself.

**Ancestral:** Originating prior in evolution to the derived state.

**Anisogamy:** Having gametes of different sizes, large eggs and small sperm.

**Annual:** Organism with a 1-year life-span. (Compare Univoltine, Perennial, Multivoltine).

**Antagonistic pleiotropy:** Phenomenon in which a gene has a positive effect on one component of fitness but a negative effect on another.

**Apomixis:** A form of clonal propagation in which progeny genetically identical to the mother are formed without genetic recombination.

**Apomorphic:** Derived, relative to an ancestral, or plesiomorphic, state.

**Autopolyploidy:** Doubling of one's own entire chromosome set. May lead to new tetraploid species.

**Autosome:** A chromosome not involved in sex determination.

**\* Bed hedging:** Life history patterns that reduce variance in fitness. The proverb "Don't put all eggs in one basket" describes a bed-hedging strategy.

**Biennial:** Organism that lives for 2 years, breeding in the second year.

**\*Bootstrapping:** A statistical method to estimate our confidence in a pattern. One takes random samples of the original data (with replacement to get a data set of the same size) and repeats the calculations with the new, artificial data sets many times. The patterns that do not change, or only rarely change, receive our confidence. The bootstrap value is the proportion of times a pattern is repeated in a bootstrapping procedure.

**Breeding true:** Displaying the same character state in the offspring as in the parents, an indication that the trait is genetically determined and that the parents are genetically similar.

**\* Broad-sense heritability:** The proportion of total phenotypic variation that can be ascribed to all the genetic differences among individuals in a population. For example, the amount of variation caused by differences among individuals in the population. For example, the amount of variation caused by differences among full-sib families.

**\*Canalization:** The limitation of phenotypic variation by developmental mechanisms. It can be demonstrated by disturbing developmental control to reveal the underlying genetic variability that had been canalized.

**Clade:** A branch of the evolutionary tree containing all the species descended from a single common ancestor. A clade is always monophyletic.

**Cladogenetic:** Evolutionary change occurring during speciation events. Usually applied to fossils.

**\*Cline:** A spatial gradient in trait values or gene frequencies.

**Clone:** A group of genetically identical individuals. Clones are the result of asexually reproduction. Bacteria, viruses, but also some metazoan, such as aphids, rotifera and cladocera (water fleas) can reproduce clonally.

**\*Coalescence:** A process occurring during the calculation of how long ago two alleles shared a common ancestor: the branches of a genealogy coalesce as one works back in time.

**\*Codon bias:** Synonymous codons do not occur with equal frequency.

**Coevolution:** Evolutionary changes in one thing – genes, sexes, and species – induce evolutionary changes in another, which in turn induce further evolutionary changes in the first, and so forth.

**\*Colinearity:** A property of homeobox genes: they have the same sequence along the chromosome as the segments of the body whose development they control.

**Comparative analysis:** The relations of two or more traits among higher taxa (e.g. species, genera, families) are analyzed with proper control for phylogeny and covariates such as body weight.

**Conflict:** Evolutionary conflict arises when two genes that interact with each other have different transmission patterns and therefore different evolutionary interests. Conflict arises, because the genes have only partially overlapping interests.

**Conjugation:** A form of mating in which two bacteria build a tube between them through which both plasmids and chromosomal DNA can be exchanged. Bacteria can be induced to conjugate by transposons and plasmids, which thereby achieve horizontal transmission.

**Conserved function:** A property of paralogous genes with high DNA sequence homology that code for proteins with similar function in distantly related organisms.

**Convergence:** Two species resemble each other not because they shared common ancestors but because evolution has adapted them to similar ecological conditions.

**Cyclical parthenogenesis:** A life cycle typical of aphids, rotifers, cladocerans, and some beetles, in which a series of asexual generations is interrupted by a sexual generation. The offspring of the sexual generation are often adapted to resist extreme conditions and to disperse.

**Deme:** A local,  $\pm$  randomly mating population, connected with other such populations by gene flow. A set of demes makes a metapopulation. Often used in the same context as population.

**\*Density-dependent selection:** Selection that favours different trait values at different population densities. In contrast, under density-independent selection the same trait value is favoured under all densities.

**Derived:** Defined relative to ancestral: originating later in evolution than the ancestral state.

**Dioecy:** Having separate sexes; individuals are either males or females; used for plants. (See gonochorism.)

**Diplontic life cycle:** A life cycle in which diploid somatic adults produce haploid gametes by meiosis that fuse to form diploid zygotes that develop into somatic adults.

**Directional selection:** Selection that always acts in a given direction; for example, always to increase the value of a trait, or always to decrease it.

**Disruptive selection:** Selection that favours the extremes and eliminates the middle of a frequency distribution of trait values; for example, increasing the frequency of small and large individuals and reducing the frequency of medium-sized individuals.

**Divergence:** Related species no longer resemble each other because evolution has adapted them to different ecological conditions.

**Dominance / Dominant allele:** In diploids an allele is dominant if it, but not the recessive homolog, is expressed in the phenotype of heterozygotes.

**Downstream gene:** A gene under the control of a regulatory gene; the genes downstream from a regulatory gene constitute a regulatory pathway.

**Duplication:** Copying of a DNA sequence without loss of the original and increasing the size of the genome by inserting the copied sequence elsewhere. Duplication is important in the evolution of genomes.

**Ectotherm:** Organism that does not generate its own internal temperature: invertebrates, reptiles and amphibians. (Plants might also be so classified.)

**\*Effective population size:** The size  $N_e$  of an ideal population that would experience the same amount of genetic drift as a real population of size  $N$ . This defines effective population size for drift; there are other definitions for unequal family sizes, subdivided populations, differences in male versus female reproductive success, and variable population sizes.

**Endotherm:** Organism that generates its own internal temperature: mammals and birds. Some fish (e.g. tuna) and insects (e.g. bumble bees) have mechanisms that give them some degree of endothermy. (See also Ectotherm).

**\*Epigenetic inheritance:** Somatic inheritance of the differentiated state of the cell through cycles of cell division.

**Epistasis:** Name given to the phenomenon in which the effect of two or more non allelic genes in combination is not the sum of their separate effects.

**ESS Evolutionarily stable strategy:** A strategy, which, if adopted by individuals in a population, prevents the invasion into the population of a mutant adopting an alternate strategy.

**Eukaryote:** An organism with a cell nucleus surrounded by a nuclear membrane, usually with organelles, such as mitochondria and chloroplasts, that have their own circular DNA genome. Eukaryotes include the protists (single celled eukaryotes), fungi, plants, and animals.

**Eusociality:** A social system with non-reproductive workers. For example ants and termites.

**Evolution:** The process during which the genetic composition of a population changes. Changes can result from selection, genetic drift, mutation or migration. Small evolutionary events are often called microevolution.

**Evolutionarily stable strategy:** See ESS.

**\*Exon:** The part of a eukaryotic gene whose DNA sequence is preserved in post-transcriptional splicing and is represented in the spliced mRNA and in the resulting amino acid sequence of the protein product. Exons occur in eukaryotes but not in prokaryotes.

**Expected lifetime fecundity:** See  $R_0$ .

**Fitness:** Relative lifetime reproductive success, which includes the probability of surviving to reproduce. In certain situations, other measures are more appropriate. Important modifications to this definition: inclusion of the effects of age-specific reproduction, and of fluctuations of density dependence. (See also Inclusive fitness).

**Fixation:** If an allele at a polymorphic locus goes to fixation it reached a frequency of 100%. This means that it replaced all other allelic variants.

**\*Fixation probability:** The probability that a new mutation will reach fixation.

**\*Fixation time:** The time that it takes new mutations that get fixed to reach fixation, in generations.

**Founder effect:** Changes in gene frequencies that occur in a population founded with a small sample of a larger population.

**\*Frequency-dependent selection:** A mode of natural selection in which either rare types (negative frequency-dependent selection) or common types (positive frequency-dependent selection) are favoured.

**Game theory:** In evolutionary biology, a method of analysis based on the principle that several individuals compete for some "prize" that can be equated to fitness.

**Gene:** In population genetics used loosely to describe any information contained in the DNA, not necessarily coding for a protein.

**Genealogy:** A tree describing the history of a single gene, as opposed to a phylogeny, which uses information from many genes or traits to reconstruct the history of a set of species.

**Gene flow:** Genes flow from one population to another when organisms born in one place, migrate and have offspring in another place that survive to reproduce there.

**Gene frequency:** The frequency of an allele in a population. If there are 100 individuals in a population of diploid individuals, and we consider one locus (one gene) that is present in two forms (two alleles),  $A$  and  $a$ , then if 20 of the individuals carry two copies of  $A$  (they are  $AA$  homozygotes), 60 of the individuals are  $Aa$  heterozygotes, and the remaining 20 individuals are  $aa$  homozygotes, then the gene frequencies are calculated as the number of each allele divided by the total number, in this case,  $(40+60)/200=0.50$  for both alleles.

**\*Gene substitution:** The process by which a new mutation becomes fixed in a population.

**Genetic bottleneck:** A temporary reduction in population size, that causes alleles are being lost and others are fixed. (See also Founder effect).

**\*Genetic diversity:** The probability that two homologous alleles chosen at random from a population differ.

**Genetic drift:** Random change in allele frequencies due to chance factors. Variation in genes is not correlated with variation in reproductive success.

**\*Genetic imprinting:** Genes marked by DNA methylation in the germ line of parents; some are marked in mothers, others in fathers. Methylated genes are not expressed in the early development of the offspring.

**Genetic locus:** A particular defined site of a chromosome. At a given locus there can be several or many alleles, i.e., alternative versions of the gene.

**Genomic conflict:** (See Conflict).

**Genotype:** In evolutionary biology, the information stored in the genes of one individual; in population genetics, the diploid combination of alleles at one locus present in an adult prior to meiosis. (Compare Phenotype).

**Genotype frequency:** The proportion of individuals in the population that carry a given genotype at the locus or loci of interest.

**\*Gonochorism:** Having separate sexes; individuals are either males or females, not both; used for animals. (See Diecy).

**Group selection:** Selection acting on groups rather than individuals. Thus evolution is seen to involve the differential survival of groups rather than individuals. Usually considered to be of minor importance for evolution.

**Haplontic life cycle:** A life cycle in which haploid adults produce haploid gametes by mitosis; the diploid zygotes immediately undergo meiosis to produce haploid individuals.

\* **Hard selection:** Selection favouring individuals with particular characteristics; both density- and frequency-independent. (see Soft Selection.)

**Hemimetabolous:** Insects showing incomplete metamorphosis, there being no obvious resting stage; examples are grasshoppers, aphids, and bugs. (See Holometabolous.)

\* **Heritability:** Measure of the proportion of phenotypic variance attributable to genetic effects. (Heritability in the *broad sense* refers to all genetic sources. Heritability in the *narrow sense* refers only to the additive portion of genetic variance.)

**Heterogametic:** For organisms with chromosomal sex determination, the sex having two different sex chromosomes is heterogametic. Males are XY in most mammals, but in birds the females are the heterogametic sex.

**Heterosis:** The phenomenon in which the heterozygote has a higher fitness than either homozygote.

**Heterozygosity:** The proportion of a population that is heterozygous at a locus; also the average proportion of loci heterozygous per individual.

**Heterozygotic advantage:** See Heterosis.

\* **Hitch-hiking:** Changes in the frequencies of alleles that are linked to alleles on other loci, which change in frequency due to selection.

**Holometabolous:** Insects showing a complete metamorphosis; that is, having a pupal stage; examples are beetles, butterflies, and flies. (See also Hemimetabolous.)

**Homeobox:** A 180 base-pair sequence in important regulatory genes that codes for a protein segment that binds to DNA as a key part of a transcription factor.

**Homogametic:** The sex having two similar sex chromosomes; for organisms with chromosomal sex determination; females are XX in humans.

**Homology:** Identity of one trait in two or more species by descent from a common ancestor.

**Homoplasy:** Similarity for any reason other than common ancestry. The commonest cause of homoplasy in morphological traits is probably convergence; in DNA sequences, simple mutation.

**Inbreeding:** The mating of related organisms. Leads to increased homozygosity and to inbreeding depression.

**Inbreeding depression:** The reduction in the survival or reproduction of offspring of related parents caused by homozygote deleterious recessive genes that were present in the parents as heterozygotes.

**Inclusive fitness:** That fraction of fitness accruing to an individual by virtue of interactions with related individuals. (See also Kin Selection).

**Individual selection:** Selection generated by variation in the reproductive success of individual organisms, affecting all their genes and traits. Individual selection comes about through differential survival and reproduction of individuals rather than groups. (Compare Group Selection).

**Induced responses:** A change in a phenotype that occurs in response to a specific environmental signal (= cue) and that improves survival and/or reproduction. Without the signal, the change does not take place. (See also Phenotypic plasticity).

**Infanticide:** The killing of an offspring by its parent.

**Instar:** Growth in insects and crustaceans is accomplished by molting; development can, therefore, be divided into a series of discrete stages, called instars.

**Intrinsic rate of increase,  $r$ :** A measure of population growth. It is the instantaneous rate of increase of a population or genotype. It is used as a measure of fitness. (See also  $r$ ) (= Malthusian parameter).

**Intron:** A sequence within a gene that is removed after transcription and before translation by gene splicing; its DNA sequence is not represented in the RNA sequence of the spliced mRNA or the amino acid sequence of the resulting protein; introns occur in eukaryotes but not prokaryotes.

**Isogamy:** Mating partners have gametes of the same size. (Compare Anisogamy)

**Iteroparity:** Repeated breeding. (Compare Semelparity)

**Iteroparous:** Having several discrete reproductive events per lifetime.

**Kin selection:** Adaptive evolution of genes caused by relatedness; an allele causing an individual to act to benefit its relatives will increase in frequency if that allele is also found in the relatives and if the benefit to the relatives more than compensates the cost to the individual.

\* **K-selection:** Selection acting on the density-dependent fitness parameter,  $K$ . (Compare  $r$ -selection). This concept is not used anymore in evolutionary biology.

**Lek:** A traditional display site where males gather to defend mating territories and females come to mate. The word is derived from the Swedish word for sports field or display.

**Lineage-specific developmental mechanisms:** Developmental mechanisms found within all organisms of one lineage but not in other lineages, responsible for the morphology that characterizes the lineage. They limit the genetic variation that can be expressed in the lineage.

**Macroevolution:** The pattern of evolution at and above the species level, including most of fossil history and much of systematics.

**Malthusian parameter:** (See  $r$  and Intrinsic rate of increase)

**Mating types:** Sets of potential mating partners. Mating can occur between partners of different type but not with partners of the same type.

**Meiosis:** Reduction division of diploid germ cells to yield haploid gametes.

**Meiotic drive:** Distortion of the fairness of meiosis by nuclear genes to increase their representation in the gametes at the expense of other alleles. Form of genomic conflict.

**Mendelian lottery:** A particular allele will or will not be represented in the offspring because of the segregation of alleles at meiosis and the random chance that any particular gamete will form a zygote.

**Metapopulation:** A set of population (=demes) makes a metapopulation. The populations are connected by gene flow.

\***Method of independent contrasts:** A comparative method that controls for the fact that character states in related organisms are not statistically independent because of shared ancestors. The basic idea is that *differences* between one pair of species are independent of *differences* between another pair of species even if both pairs are related.

**Microevolution:** The process of evolution within populations, including adaptive and neutral evolution. The smallest microevolutionary events are changes in gene frequency.

**Migration:** The movement of an organism from one habitat to another. It may or may not involve a return.

**Mitochondria:** Intracellular organelles with their own genomes, derived from bacterial ancestors. The energy factories of the cell where ATP and the intermediate products of the Krebs cycle, used in the cytoplasm for energy release and biosynthesis, are made.

**Molecular clock:** The approximately constant rate of nucleotide or amino acid substitutions for particular genes and classes of genes within particular lineages.

**Monecy:** Individuals reproduce both as males and as females; hermaphrodites; used for plants.

**Monophyletic:** All species in a monophyletic group are descended from a common ancestor, and all species descended from that ancestor are in that group.

**\*Multigene family:** Sets of multiple copies of genes derived by duplication from a common ancestor gene and retaining the same function.

**Multilevel evolution:** Adaptive evolution occurring simultaneously at several levels of a biological hierarchy, e.g. nuclear and cytoplasmic genes.

**Multivoltine:** A phenology comprising several generations per year. (See Annual, Univoltine, Perennial.)

**Mutation:** Any change in the nucleic acid sequence of an organism, either a point mutation, a deletion, an insertion, or a chromosomal rearrangement. Mutations may be beneficial, detrimental or neutral in their effect.

**\*Narrow-sense heritability:** The fraction of total phenotypic variance in a trait that is accounted for by additive genetic variance. It is a measure for the potential response to selection.

**Natural selection:** Variation in reproductive success associated with genetic variation.

**Neonate:** Newborn, juvenile.

**Net reproductive rate:** See  $R_0$ .

**Neutral:** Variation in state is not correlated with variation in reproductive success: states are equally fit.

**Neutral evolution:** The change and occasional fixation of alleles caused by the drift of alleles not correlated with reproductive success.

**\*Nucleotide diversity:** The average number of nucleotide differences per site between randomly chosen pairs of sequences.

**Null model:** A model of no effect. It is used in statistic as the base line against which a hypothesis is tested.

**Overdominance:** Phenomenon in which the character of the heterozygote is expressed more markedly in the phenotype than in that of either homozygote.

**Overlapping generations:** Population structure in which parents may still reproduce when their offspring are already reproductive.

**Paraphyly:** A group does not contain all species descended from the most recent common ancestor of its members.

**\*Parsimony:** A criterion used in cladistic tree-building: the best tree has the fewest changes in character states and the least homoplasy.

**Parthenogenesis:** Asexual reproduction from an egg cell that may or may not involved recombination, depending on the mechanism. In most cases the daughters are exact genetic copies of the mother.

**Perennial:** Organism that lives vor several years. (See Multivoltine, Annual, Univoltine.)

**Phage:** A virus that infects bacteria.

**Phenology:** The sequence of events in life history.

**Phenotype:** The phenotypic expression of a genotype. The material organism, or some part of it, as opposed to the information in the genotype that provides the blueprint (Compare Genotype).

**Phenotypic differentiation:** The differentiation of phenotypes in separated gene pools during and after speciation.

**Phenotypic plasticity:** Phenotypic variation expressed by a single genotype in different environments.

**Phylogenetic trait analysis:** A comparative method in which one constructs a phylogenetic tree, plots character states (traits) on the tree, and infers transitions in character states from their position on the tree. Geographical locations of taxa can be plotted onto the tree to infer the location of ancestors.

**Phylogeny:** The history of a group of taxa described as an evolutionary tree with a common ancestor as the base and descendent taxa as branch tips.

**Pleiotropy:** One gene has effects on two or more traits.

**Plesiomorphic:** Ancestral, relative to a derived, or apomorphic, state.

**Point mutation:** A change in single DNA nucleotide, e.g. adenine mutates to thymine, or an insertion or deletion of a single nucleotide.

**Polymorphism:** Strictly, the existence of several morphs within a species or a population: frequently used in biology to refer to a genetic polymorphism. Also the presence of more than one allele at a given locus in a population. The pattern of polymorphisms in a population is its genetic variation.

**Polyphenism:** A form of induced response in which the phenotypes are discrete.

**Polyphyly:** A group is polyphyletic if its species are descended from several ancestors that are also ancestors of species classified into other groups.

**Polyploidization:** A doubling of the complete chromosome set.

**Population:** The individuals of a given species living within a given area and thus potentially capable of mating with each other (if they are of opposite sexes). In practice the definition depends on the question and organism and will often be arbitrary. The genetic information carried by all members of a population is its gene pool. A set of population makes a metapopulation.

**Population genetics:** The discipline that studies changes in frequencies of alleles in populations and variation across populations. Issues include mutation, selection, inbreeding, assortative mating, gene flow, and drift.

**\* Power (Statistical power):** The probability of rejection of the null hypothesis when it is in fact false ( $= 1 - \beta$ , where  $\beta$  is the probability of a type II error).

**Prokaryotes:** Organisms that lack a nucleus and organelles such as mitochondria or chloroplasts. Prokaryotes include the Eubacteria and the Archaea.

**\*Protandry:** Individuals are born as males, reproduce as males, then change sex and reproduce as females. In plants, individuals express male function prior to female function, producing pollen before being pollinated.

**\*Protogyny:** Individuals are born as female, reproduce as females, then change sex and reproduce as males. In plants, individuals express female function prior to male function, being pollinated before producing pollen.

**Proximate causation:** The mechanical determination of traits during the lifetime of an organism, including biochemistry, development, and physiology.

**Pseudogene:** A non functional copy of a gene; it is not expressed.

**\*Punctuated equilibrium:** A pattern seen in many but not all lineages in the fossil record, in which a long period of stasis is broken by a short period of rapid change. In some cases the rapid change is associated with speciation.

**Punctuation:** A short period of rapid change breaking a long period of stasis in the fossil record.

**Quantitative genetics:** The discipline that studies changes in traits in populations when many genes affect one trait. Common themes are heritability, genetic variance and covariance, response to selection.

**$R_0$ :** The net reproductive rate or expected lifetime fecundity. It takes survival and fecundity into account. It is a measure of fitness when the population is stationary (i.e. not changing in size) or for species with non-overlapping generations).



**$r$**  : The instantaneous rate of increase of a population or genotype. It is used as a measure of fitness. (Note: The greek symbol for lambda is often used to define the finite rate of increase =  $e^r$  ).

\*  **$r$ -selection**: Selection acting on the measure of fitness  $r$  , contrasted with selection acting on the density-dependent measure,  $K$ . (compare  $K$ -selection) This concept is not used anymore in evolutionary biology.

**Random**: A word with many meanings. In evolution mutations are random with respect to the needs of the organism in which they occur. They are not distributed at random along the DNA sequence (some parts of genomes are more mutable than others) and they are not always random with respect to environmental conditions (in bacteria and fungi environmental stimuli can increase the mutation rate).

**Reaction norm**: A property of genotype: how development maps the genotype into the phenotype as a function of the environment. Usually given for one genotype and one environmental factor. Populations and families can be described as having mean reaction norms.

**Recessive allele**: An allele is recessive if it is not expressed in the phenotype in the heterozygous diploid state.

**Regulatory gene**: A gene that turns another gene, or group of genes, on or off. Small changes in regulatory genes cause large changes in phenotypes.

**Replicator**: The organism in its role as information copier, the mechanism that copies the DNA sequence of the parent and passes it to the offspring.

**Reproductive effort**: Energy that is devoted to reproduction. There are several ways in which this may be defined.

**Reproductive value**: The expected contribution of organisms in that stage of life to the future lifetime reproductive success.

**Residual reproductive value**: The remaining contribution to lifetime reproductive success after the current activity has made its contribution.

**Satellite males**: Males that take up station in the vicinity of a calling or displaying male. The satellite male may attempt to intercept incoming females or to replace the displaying male when it leaves.

\***Secondary reinforcement**: The reinforcement of prezygotic barriers to hybridization after secondary contact between isolated populations.

**Segregation distortion**: Deviation from the Mendelian ratios that give equal chances to homologous alleles in meiosis; unfair ratios can be caused by nuclear genes that interfere with meiosis or with the products of meiosis to improve their own chances at the expense of their homolog. (=Meiotic drive)

\* **Selection differential**: Difference between the mean value of the population and the mean value of the parents that give rise to the subsequent generation.

**Selection response**: The difference between the mean of the parental population and the offspring mean after selection.

**Semelparity**: Breeding once and dying; sometimes called "big bang" reproduction.

**Senescence**: Decline in function as a result of aging. For example increase in mortality rate with increasing age class.

\* **Sensitivity analysis**: Analysis of the reaction of a model to variation in one or more of its component parameters or functions.

**Sex allocation**: The allocation of reproductive effort to male versus female function in hermaphrodites and to male versus female offspring in species with separate sexes.

**Sex ratio**: The ratio of females to males. Usually this is 1:1 in sexual species, but under certain conditions sex ratios can be strongly female biased.

**Sexual dimorphism**: Males and females have different phenotypes.

**Sexual selection:** The component of natural selection that is associated with success in mating.

**Siblicide:** The killing of one offspring by its sibling.

**Sibling species:** Species that are reproductively isolated but cannot be distinguished easily.

**Soft selection:** Also called rank-order selection. Selection that favours a particular number or percentage of the population regardless of their absolute characteristics: frequency- and density-dependent. (See Hard Selection.)

**Species:** Either a set of organisms that could share grandchildren (the biological species concept), or the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (the phylogenetic species concept).

**Speciation:** Species formation. Split of one species into two.

**Stabilizing selection:** Selection that eliminates the extremes of distribution and favours the centre.

**Stasis:** A long period without evolutionary change. (See also Punctuation).

**Strategy:** The terms *strategy* and *tactic* have frequently been applied to alternative methods of maximizing fitness: thus, for example, semelparity and iteroparity may be called strategies (or tactics). The two terms are, strictly not synonyms and apply specifically to warfare, not biology. In a life history context they are usually regarded as synonymous.

**Sympatry:** Occurring in the same geographic area.

**Synapomorphy:** A shared, derived character state indicating that two species belong to the same group.

**Synergism:** A non additive interaction between two or more factors, e.g. two genes.

**Synonymous mutation:** A point mutation (change in a single nucleotide) that does not change the amino acid for which the DNA triplet codes.

**Trade-off:** A change in one trait that increases fitness causes a change in the other trait that decreases fitness. The two traits are fitness components. A trade-off is often seen in form of a negative correlation between two fitness components, e.g. egg size (larger eggs have better survival) and egg number.

**\*Transcription factor:** A gene product that binds to DNA at a specific site and regulates the expression of genes downstream from that site.

**\*Transduction:** A virus that infects bacteria picks up some bacterial DNA from one host and transfers in to the next host, which may incorporate the DNA if it survives the infection.

**\*Transformation:** Bacteria take up DNA from the medium and incorporate it into their circular chromosome.

**\*Truncation selection:** Artificial selection in which only individuals with a value of a trait above (ore below) some threshold are allowed to breed.

**\*Type I error:** Rejection of a statistical null hypothesis when it is, in fact, true.

**\*Type II error:** Failure to reject the statistical null hypothesis when it is, in fact, false.

**Ultimate causation:** The evolutionary determination of the state of a trait at the level of population or lineage through adaptive evolution or drift.

**Univoltine:** Phenology with a single generation per year.

**Viviparity:** Giving birth to live young.

**Wild type:** A term used in classical genetics to designate the standard genotype in the population from which mutations formed deviations. (Modern molecular data have destroyed the concept by revealing so much variation that the concept has become less meaningful.)