

Glossary accompanying the lecture: “Evolutionary Biology”

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This list contains terms, which participants of the lecture “Evolutionary biology” should know. 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.
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Adaptation: A state that evolved because it improved reproductive performance, to which survival contributes. As well as 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.

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: The proportion of the copies of one allele among all alleles at the locus of interest.

Allometry: Relationship between the size of two organisms or a specific part. 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.

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

Ancestral: Originating prior in evolution to the derived state.

Anisogamy: Anisogametic species have gametes of different sizes: large eggs and small sperm (in plants pollen). Females produce the large gametes. Isogametic species have gametes of equal size.

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

Antagonistic pleiotropy: 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 the progeny (offspring) is genetically identical to the mother. They are formed without genetic recombination.

Apomorphic: Describes a derived character found in a group of organisms (taxon).

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

Autosome: A chromosome not involved in sex determination.

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

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

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.

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

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.

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 partial overlapping interests, for example gene in mitochondria (maternal transmission) and genes in the nucleus.

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 asexually reproducing generations is interrupted by a sexually reproducing generation. The offspring of the sexual generation are often adapted to resist extreme conditions and to disperse.

Deme: A local more or less randomly mating population, which is connected with other such populations by gene flow. Sets of demes make a metapopulation. Deme is often used in the same context as population.

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

Dioecy: Having separate sexes; individuals are either male or female. Dioecy is used for plants. Gonochorism is the equivalent term in animals.

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

Directional selection: Selection that acts in a given direction. E.g. always increasing the value of a trait, or always decreasing it.

Disruptive selection: Selection that favours the extremes and eliminates the middle of a frequency distribution of trait values. E.g. increasing the frequency of small and large individuals and reducing the frequency of medium-sized individuals.

Divergence: Related species no longer resemble each other (they are diverged) 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, which are downstream from a regulatory gene, constitute a regulatory pathway.

Duplication: Copying of a DNA sequence without the loss of the original. This process increases the size of the genome by inserting the copied sequence elsewhere. Duplication is important in the evolution of genomes.

Ectotherm: Organisms that do not generate their own internal temperature: invertebrates, reptiles and amphibians. (Plants might also be so classified.)

Endotherm: Organisms that generate their own internal temperature: mammals and birds. Some fish (e.g. tuna) and insects (e.g. bumble bees) have mechanisms that give them some endothermic properties. (See Ectotherm).

Epistasis: The phenomenon in which the effect of two or more non-allelic genes in combination are 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, which 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. E.g. 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.

Expected lifetime fecundity: See R_0 .

Fitness: The relative ability for reproductive success during the lifetime of an organism. It includes the probability of surviving to reproduce. In certain situations other measurements 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 in this population.

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

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 This is 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 which survive to reproduce there.

Gene frequency: The frequency of an allele in a population. E.g. 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 . 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. The gene frequencies are then calculated as the number of each allele divided by the total number. In this case it is $(40+60)/200=0.50$ for both alleles.

Genetic bottleneck: A temporary reduction in population size, in which certain alleles are lost and others are fixed. (See also Founder effect).

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

Genetic locus: A particular defined site of a chromosome. At a given locus there can be one to 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 to 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.

Hemimetabolous: Insects showing incomplete metamorphosis without having an 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: Used for organisms with chromosomal sex determination. The sexes having two different sex chromosomes are 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 given locus and the average proportion of heterozygous loci per individual.

Heterozygotic advantage: See Heterosis.

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

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

Homology: The identity of one trait in two or more species that descended from a common ancestor.

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

Inbreeding: The mating of related individuals. Leads to increased homozygosis and to inbreeding depression (low fitness of the offspring).

Inbreeding depression: The reduction in the survival and or reproductive ability of offspring from related parents. Deleterious homozygote recessive genes that were present in the parents as heterozygotes cause inbreed depression.

Inclusive fitness: That fraction of fitness accruing to an individual by 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 of the same individual. (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 beneficial to 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.

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 in 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.

Locus: The position of a given gene on a chromosome.

Macroevolution: The pattern of evolution at the species level and above. It includes fossil history and 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: Reductive 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. It is a form of genomic conflict. The driver gene is called a segregation distorter.

Mendelian segregation: 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. With Mendelian segregation, alleles of diploid organisms have a 50% chance to be present in sexual offspring.

Metapopulation: A set of populations make a metapopulation. The populations are connected by gene flow.

Microevolution: The process of evolution within populations, including adaptive and neutral evolution. The smallest micro-evolutionary events are changes in gene frequency. Microevolution is caused by selection, genetic drift, gene flow and mutation.

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 are produced. They are used in the cytoplasm for energy release and biosynthesis. Most eukaryotes (organisms with a cell nucleus) have mitochondria.

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

Monocy: Individuals reproduce both as males and as females, also called hermaphrodites. Monocy is used only for plants, hermaphrodites more typically is used for animals.

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

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.

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 fitness. The new states are equally fit as the old ones.

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

Null model: An assumption that no real difference exist between two populations. 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 while their offspring are already reproductive.

Paraphyly: A group that does not contain all species, which descended from the most recent common ancestor of its members. Examples include reptiles (strictly speaking birds should be included here) and crustacean (insects are derived from crustaceans).

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: An organism that lives for several years. (See Multivoltine, Annual, Univoltine)

Phage: A virus that infects bacteria (also bacteriophage).

Phenology: The sequence of events in life history.

Phenotype: The phenotypic expression of a genotype. The functional properties of an organism or a 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 local adaptation and speciation.

Phenotypic plasticity: Phenotypic variation expressed through 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 deduce the location of ancestors.

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

Pleiotropy: One gene affecting two or more traits.

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

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

Polymorphism: The existence of several morphs within a species or a population. Frequently used in biology to refer to genetic polymorphism. Can also describe the presence of more than one allele at a given locus in a population. The pattern of polymorphisms in a population is caused by 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, which are classified into other groups. It is considered to be a misclassification. The former phylum “Vermes” was such a misclassification, including all worm-like animals.

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 research question being asked, the organism being studied and will often be arbitrary. The genetic information carried by all members of a population is its gene pool. A set of populations makes a metapopulation.

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

Prokaryotes: Organisms that lack a nucleus and organelles such as mitochondria or chloroplasts. Prokaryotes include the Eubacteria and the Archea. The other big group of organisms are the Eukaryotes.

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.

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 as well as response to selection. Example for quantitative traits are morphological and life-history traits.

R_0 : The net reproductive rate or expected lifetime fecundity. It takes survival and fecundity (fertility) 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 in 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 .)

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: It describes how the development maps the genotype and the phenotype as a function of the environment. Populations and families can be described as having a mean reaction norm.

Recessive allele: An allele is recessive if it does not affect 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 acting as an information copier as well as 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 an organism at a certain age to the future lifetime reproductive success.

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.

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

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

Semelparity: Breeding once and then dying, sometimes called "big bang" reproduction. (E.g. Salmon)

Senescence: Decline in function as a result of aging. Mostly defined as an increase in the mortality rate with increasing age class.

Sex allocation: The allocation of reproductive efforts to male versus female function in hermaphrodites, as well as 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, meaning the ability to choose or compete with other individuals of the same sex for a mating partner.

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. The splitting of one species into two new separate species through acquisition of reproductive isolating mechanism.

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

Stasis: A long period without evolutionary change.

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

Sympatry: Species occurring in the same geographic area and habitat.

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

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

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.)