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# 1 Evolutionary Thinking

## Introduction (Lecture)

- ▷ Essential questions of evolutionary biology:
  - Why do organisms look so different?
  - Why develop elaborate sexual traits?
  - Why do organisms senesce?
- ▷ Evolution is mainly an historical science and thus must rely on other methods of reconstructing the past or making inferences about evolutionary forces.
- ▷ **Proximate**: a question about a mechanistic cause; provides an immediate explanation about **how** a mechanistic cause functions.
- ▷ **Ultimate**: **why**, or the reason, a trait or organism is the way it is; an evolutionary explanation.
- ▷ Example of proximate vs ultimate in Galapagos finches:
  - Proximate: developmental growth factor is increased/decreased in some birds.
  - Ultimate: different habits are selected on breaks that maximize food gathering ability.
- ▷ Evolutionary biology's approach to answering questions:
  - **Empirical data**: **observation** studies, experiments; the *comparative method*.
  - **Theory**: **predictions** that use models and mathematical reasoning which can be **tested** with empirical data.
- ▷ Overview of the components of evolution by natural selection:
  - Genetic variation exists, via mutations.
  - Mutations are heritable.
  - There is an advantage to survival and/or reproduction from the mutation.
  - Individuals with the advantage in survival/reproduction are selected for.

## 10 Studying Adaptation

### Hypothesis Testing: Oxpeckers Reconsidered

- ▷ **Adaption:** a trait, or a suite of traits, that increases the fitness of its possessor.
- ▷ No hypothesis for the adaptive value of a trait should be accepted simply because of its plausibility.
- ▷ Oxpeckers and impalas traditionally were thought to have a mutually beneficial existence; oxpeckers ate ticks and impalas provided a safe environment.
- ▷ Experiments on cattle were done to test whether this observation was true:
  - Results show red-billed oxpeckers have no effect tick loads of cattle.
  - Red-billed oxpeckers maintained open wounds, even enlarging existing wounds to feed on the cattle's blood.
  - Red-billed oxpeckers removed hosts' earwax; whether this is good or bad is unclear.
  - Even these results must remain in question, as cattle are not the native host for the birds.
- ▷ Other important points to remember:
  - Differences among populations or species are not always adaptive.
  - Not every trait is adaptive.
  - Not every adaptation is perfect, often the adaptation just happened to work well enough or by chance better than other adaptations.

### Experimental Design

- ▷ Defining and testing effective control groups is critical.
- ▷ Treatments of controls and experimental measures must be handled as close to exactly alike as possible.
- ▷ Randomization is a key technique for equalizing miscellaneous effects and a tool to avoid bias.
- ▷ Reproduction is essential in order to help remove potential outlier effects.
  - Allows for greater understanding of precision, accuracy, and variation by providing more data for statistical tests.

## 4 Evolutionary Trees

### How to Read an Evolutionary Tree

- ▷ **Phylogeny**: aka evolutionary tree or phylogenetic tree, is a diagram showing the history of divergence and evolutionary change. Essentially, it's the **genealogical relationships** of organisms based on descent with modification.
  - **Taxa**: the units you are analyzing, e.g. certain species or DNA sequences.
    - **Character**: a feature or trait present among the taxa of interest, e.g. teeth of mammals or nucleotides of DNA sequences.
      - *Character state(s)*: an **alternative condition** of a character, which are able to evolve one to another, e.g. pointed/flat teeth of mammals.
    - **Ancestral character**: a trait that was **possessed by the common ancestor**.
    - **Derived character**: a trait the was **not possessed by the common ancestor** and instead **evolved** in at least one of the descendants.
      - **Synapomorphy**: derived character state shared by **two or more** taxa and used to define a clade of taxa.
      - **Autapomorphy**: derived character state in only **one** taxon.
    - **Outgroup**: a taxon or taxa that are used to root the phylogeny or determine ancestral character states.
    - **Ingroup**: the set of taxa that are the focus of the phylogeny.
  - **Nodes**: points at which the tree splits; represents mutations, speciation events, or **character changes**.
  - **Anagenesis**: descent with modification, but **no speciation**.
  - **Cladogenesis**: **speciation**, origin of clades.
    - **Clade**: also known as a **monophyletic group**, an ancestor and **all** of its descendants.
    - **Paraphyletic group**: a group of organisms consisting of an ancestor and **some** of its descendants.
  - **Sister**: a taxa or clade that are most closely related to each other; they **share the most recent** common ancestor.
- ▷ **Homology**: similarity due to common descent; **continuity** of a trait, character, or character state through time.
  - *Homologous trait*: found in a taxa that inherited the trait from a common ancestor.

- ▷ **Homoplasy:** or analogous, similarity in the characters or traits in different taxa due to convergent evolution, parallelism, or reversal, but **not due to common descent**.
  - **Convergent evolution:** similar traits due to selective forces and **not shared ancestry**.
    - **Parallelism:** convergent evolution in **recently diverged** taxa.
  - **Reversal:** derived traits or character states that revert to the ancestral form.

## Inferring Phylogenetic Trees

- ▷ **Parsimony:** relationships that require the **smallest number of character changes** are most likely to be correct.
  - Based on shared and **derived** traits(synapomorphies).
  - Reconstruction using parsimony:
    1. Code characters.
    2. Make up a taxon×character matrix.
    3. Search for synapomorphies, and the shortest tree.
      - Outgroups can help polarize (ancestral vs derived) the characters.
  - **Treelength:** a measure of evolutionary change using parsimony.
    - Shortest tree length produces most parsimonious tree.
    - Length determined by number of synapomorphies.
    - Homoplasious characters increase tree length.
- ▷ **Distance Methods:** converts a sequence alignment to genetic distances between pairs of sequences.
  - Branch length is proportional to genetic differences.
- ▷ **Maximum likelihood:** a method of estimating the parameters of a probability distribution by **maximizing a likelihood function**.
  - One of the more dominant means of statistical inference.
  - **Likelihood:** measure of goodness of fit of a statistical model to a sample of data for given values of the unknown parameters.
  - $P(D|H)$ ; probability(P), Data(D), Hypothesis(H)
  - **Bayesian:** uses the likelihood function to create a quantity called the *posterior probability* of trees using a model of evolution based on prior probabilities in order to produce the most likely tree.

- **Bootstrapping:** creating a value that indicates how many times out of 100 (normally) that the same branch was observed when repeating the phylogenetic reconstruction on re-sampled (pseudoreplicated) set of data.

## 6 Mechanisms of Evolutionary Change

### Hardy-Weinberg Equilibrium

- ▷ **Population:** a group of interbreeding individuals and their offspring.
- ▷ **Gene pool:** the set of all genes, or genetic information, in any population.
- ▷ **Genotypic frequency:** number of individuals with a given genotype divided by the total number of individuals in the population.
  - The proportion (i.e.,  $0 < f < 1$ ) of genotypes in a population.
- ▷ **Allele frequencies:** relative frequency of an allele at a particular locus in a population.
  - **Locus:** a fixed position on a chromosome where a particular gene or genetic marker is.
  - Monoploids: frequency of an allele is the result of the number of copies of the allele divided by sample size.
    - $p = i/N$
    - $p$ : frequency |  $i$ : copies of alleles |  $N$ : sample size
  - Diploids: frequency of alleles within three possible genotypes at a locus with two alleles.
    - $p = f(AA) + \frac{1}{2}f(AB)$  frequency of A-allele
    - $q = f(BB) + \frac{1}{2}f(AB)$  frequency of B-allele
  - Allele frequency can always be calculated from genotype frequency, whereas the reverse requires the *Hardy-Weinberg principle* of random mating apply.
- ▷ **Hardy-Weinberg principle:** allele and genotype frequencies in a population will remain constant in the absence of evolutionary influences.
  - Allele frequencies do not change from one generation to the next.
  - Genotypic frequencies after one generation of random mating:
 
$$p^2 + 2pq + q^2$$
  - Evolutionary influences: genetic drift, mate choice, assortative mating, natural selection, sexual selection, mutation, gene flow, meiotic drive, genetic hitchhiking, population bottleneck, founder effect, and inbreeding.
    - *Most of these influences will be discussed later.*



## Selection

- ▷ **Fitness:** success at which a organism produces fertile offspring.
- ▷ **Competition:** an interaction between organism in which the fitness of one is lowered by the presence of another.
- ▷ **Selection:** the act on a heritable phenotypic trait due to competition.
  - Can be members of the same of different species.
  - Not always directional and adaptive, instead selection pressure is applied and removes the less fit variants.
  - Can be classified in different ways, such as effect on a trait, on genetic diversity, by life cycle, by unit of selection, or by the resource in competition.
  - Most effective on large populations.

### By Effect on a Trait

- **Stabilizing selection:** the simplest case in which selection acts to hold a trait at a stable optimum.
  - Reduces the individuals in the tails of the trait's distribution, reducing variation.
- **Directional selection:** favours extreme values of a trait.
  - Directional selection on a continuous trait changes the average value of the trait in the population.
  - Can reduce variation in the population, generally not by large amounts though.
- **Disruptive selection (diversifying selection):** acts during transition periods when current mode is sub-optimal, but alters trait in more than one direction.
  - **Univariate:** when the trait is both quantitatively favoured in either direction and can lead to speciation.
  - Generally **increases the variance** on continuous traits.
  - May be more common than generally recognized.
- All three increases the mean fitness of the population.

### By Effect on Genetic Diversity

- **Purifying selection:** aka negative selection; acts to remove genetic variation from the population.
- **de novo mutation:** introduces new variation and opposes negative selection.
- **Balancing selection:** acts to maintain genetic variation, even in absence of *de novo* mutation by frequency-dependent selection.
  - **Frequency-dependent selection:** fitness that depends of the phenotypic or genotypic **composition** of a population.
    - **Positive:** fitness **increases** as frequency of the trait **increases**.
    - **Negative:** fitness **decreases** as the frequency of the trait **increases**.
  - **Overdominance**, aka *heterozygote advantage*: when a combination of alleles confers a selective advantage over individuals with one allele.
  - **Underdominance**, aka *heterozygote disadvantage*: when the heterozygote has lower fitness than either homozygote.

### By Life Cycle Stage

- **Viability selection:** aka *survival selection*: increases probability of survival.
  - Can act to improve probability of survival before and after reproduction.
- **Fecundity selection:** increases the rate of reproduction given survival.
  - May be split into sub-components including sexual selection, gametic selection, gamete viability, compatability selection, and zygote formation.

## Mutation

- ▷ **Mutation:** alteration in the nucleotide sequence of the genome of an organism.
  - May not produce discernible phenotypic changes.
  - The ultimate source of genetic variation.
  - Have several types of changes, from no effect, to small changes, or complete loss of function.

### Large-Scale Structural Mutations

- **Gene duplications**, *aka amplifications*: repetition of a chromosomal segment or attachment of extra piece of chromosome to another, leading to multiple copies of chromosomal regions.
- Deletions of large chromosomal regions.
- **Fusion genes**: mutations that join previously separated genes into one new distinct gene.
- **Chromosomal rearrangement**: large scale changes in structure of chromosomes, leading to speciation in isolated, inbred populations. Includes:
  - **Chromosomal translocations**: interchange of genetic parts from nonhomologous chromosomes.
  - **Chromosomal inversions**: reversing the orientation of a chromosomal segment.
  - Non-homologous chromosomal crossover.
  - **Interstitial deletions**: inverse of fusion genes; removes a segment of DNA joining distant genes.
- **Loss of heterozygosity**: loss of one allele, by deletion or genetic recombination, in a organism that previously had two different alleles.

### Small-Scale Mutations

- **Point mutation**: a single nucleotide base change, that can result in a variety of effects.
- **Insertions**: add one or more extra nucleotides into the DNA.
  - Usually caused by transposable elements, or errors during replication or repeating elements.
  - Can cause *reading frame shift*, possibly effecting how many codons are read, and thus altering the gene product.
- **Deletions**: remove one or more nucleotides from the DNA.
  - Also can cause a reading frame shift like insertions.
  - Generally irreversible.
- **Substitutions**: exchange of a single nucleotide for another.
  - Often classified as transitions or transversions.
  - Generally a purine (A-G) for a purine, or a pyrimidine (C-T) for a pyrimidine.
  - Can be reversed by another point mutation.

### Impact on Protein Sequence

- Effect of mutation depends heavily on where it occurs, particularly in a coding or non-coding region.
- Regulator sequences, e.g. promoters, enhancers, silencers, can alter gene expression but are less likely to alter protein sequence.
- **Frameshift mutation:** caused by insertion or deletion of nucleotides that is not divisible by three, resulting in a different translation from the original.
- **Synonymous substitution:** a codon replacement with another that codes for same amino acid.
  - **Silent substitution:** no phenotypic difference after a synonymous substitution.
- **Nonsynonymous substitution:** a codon replacement that codes for a different amino acid.
  - **Missense mutation:** codon replacement that renders the resulting protein nonfunctional.
  - **Nonsense mutation:** codon replacement that results in a premature stop codon that produces a truncated and often nonfunctional protein.

### Migration

- ▷ **Gene flow:** movement of alleles, or genetic variation, between populations.
  - If the rate of gene flow is high enough, then two populations are considered to have equivalent allele frequencies and thus a single population.
  - Constrains speciation by combining gene pools of the groups.
  - May result in the addition of novel genetic variants in the gene pool.
- ▷ Gene flow is expected to be lower in species that:
  - have low mobility or dispersal.
  - occur in fragmented habitats.
  - have long distances between populations.
  - have small population sizes.
- ▷ **Allopatric speciation:** when gene flow is blocked by **physical** barriers that inhibit gene flow.
- ▷ **Sympatric speciation:** result of gene flow that is blocked due to **non-physical** barriers that inhibit gene flow.

## Genetic Drift

- ▷ **Genetic drift:** the change in the **allele frequencies** in a population due to **random sampling**.
  - Not influenced by environmental factors.
- ▷ May cause certain gene variants to become fixed or lost by chance.
- ▷ Generally drives populations towards genetic uniformity over time, **decreasing heterozygosity**.
- ▷ Only mutation or gene flow can introduce new alleles, which acts against genetic drift.
- ▷ **Founder effect:** result of sampling error which has an increased likelihood on populations with low numbers.
  - By chance certain alleles can be dominant when they otherwise wouldn't be in a new founding population.
  - Often acts to drastically increase rate of genetic drift.
- ▷ **Genetic bottleneck:** a sharp reduction in the size of population due to environmental events.
  - Can essentially cause a founder effect, though it's not a new population.

## Coalescent Theory

- **Coalescent theory:** how gene variants sampled from a population may have **originated** from a common ancestor.
  - Assumes no recombination, no natural selection, no gene flow in the simplest case.
- Aims to look backward in time by merging alleles into a single ancestral copy according to a random process in coalescence events.
- Many theoretical genealogies are made in order to compare to observed data in order to test assumptions about demographic history of a population.
  - Used to make inference about population genetic parameters, such as migration, population size, and recombination.
- **Coalescent time:** number of preceding generations where the coalescence took place, not calendar time.
  - Estimation of the time can be made multiplied by  $2N_e$  with the average time between generations.
  - Time to coalescence for a pair of alleles at a locus is **dependent** on population size.

- Formula:  $P_c(t) = \left(1 - \frac{1}{2N_e}\right)^{t-1} \left(\frac{1}{2N_e}\right)$
- Can also be used to model the amount of variation in DNA sequences expected from genetic drift and mutation.

## Molecular Evolution

- ▷ **Molecular evolution:** the process of change in the sequence composition of cellular molecules across generations.
- ▷ **Polymorphism:** occurrence of two or more clearly different morphs, or alternative phenotypes, in the population of a species.
  - **Substitution:** when alleles become fixed or lost in a population and polymorphism is ended.
    - Substitution rate ( $k$ ):  $k = sN\mu$
    - $s$  = probability of fixation.
    - $N\mu$  = mutation rate of population.

## Recombination

- **Recombination:** the process that results in genetic exchange between chromosomes or chromosomal regions.
  - Can also cause mutations due to misalignment after recombination.
  - **Gene repair:** a type of recombination that is the product of DNA repair that corrects damage using a homologous template.
    - Often responsible for homogenizing sequences of duplicate genes over long periods of time, which reduces nucleotide divergence.
- **Genetic hitchhiking:** change in allele frequency not because of natural selection, but due to proximity to a gene undergoing selective sweep.
  - **Selective sweep:** a beneficial mutation that increases frequency and generally becomes fixed.

### Neutral Theory

- **Neutral theory of molecular evolution:** most evolutionary changes occur at the molecular level.
- Most variation is due to random genetic drift of mutant alleles that are selectively neutral.
- Compatible with phenotypic evolution, as phenotypes are driven by molecular changes.
- Most mutations are neutral with respect to fitness.
- A minority of mutation are advantageous.
- Substitution rate predicted to be neutral, equal to per-individual mutation rate, **independent** of population size.
- $K_A/K_S$  test used to determin direction selection based on evolutionary history.
  - $K_A$ : number of nonsynonymous substitutions (replacement).
  - $K_S$ : number of synonymous substitutions (silent).
  - $K_A > K_S$  signals for **diversifying selection**.
  - $K_A < K_S$  signals for **purifying selection**.

### Molecular Clocks

- **Molecular clocks:** the average rate at which species' genomes accumulates **neutral mutations** over time.
  - A linear rate is often easy to establish.
  - Used to measure evolutionary divergence.

## Nonrandom Mating

- ▷ **Inbreeding:** production of offspring from closely genetically related individuals.
  - Results in homozygosity, which can increase chances of offspring being affected by deleterious or recessive traits.
  - **Inbreeding depression:** the reduced fitness in a given population due to inbreeding.
    - Usually caused by population bottlenecks or the founder effect.
  - Can also result in purging of deleterious alleles through purifying selection.
  - Can allow for the expression of advantageous phenotypes, which if outweighs the disadvantages, then could potentially lead to speciation.
  - **Coefficient of inbreeding:** the probability that two alleles at any locus in an individual are identical by descent.
  - Nonrandom mating does not alter allele frequencies and not a mechanism of evolution.
    - Can alter the frequencies of genotypes, changing the distribution of phenotypes in a population, which can alter patterns of natural selection.
- ▷ **Assortative mating:** mating based on phenotypic factors.
  - Can play a role in sympatric speciation.
  - A form of sexual selection.
  - Can be either positive or negative, selecting for similar or different phenotypes respectively.



## 8 Evolution at Multiple Loci

### Linkage Equilibrium and Disequilibrium

- ▷ **Linkage equilibrium:** when the genotype of a chromosome at one locus is **independent** of its genotype at another locus.
- ▷ **Linkage disequilibrium:** the non-random association of alleles at different loci in a given population.
  - Occurs when frequency of the association between loci's different alleles is higher or lower than expected.
- ▷ **Haplotype:** a group of alleles in an organism that are inherited together from a single parent.
  - Used to mean the collection of specific alleles that represent a phenotype and likely to be conserved.
  - Also can be used to mean a set of linked single-nucleotide polymorphism alleles that are associated statistically.
- ▷ Factors that influences disequilibrium: selection, rate or genetic recombination, mutation rate, genetic drift, system of mating, population structure.
  - Understanding linkage disequilibrium in a genome can be a powerful signal of the population genetic processes that structure it.
  - Selection, genetic drift, assortative mating, and population admixture act to **create disequilibrium**.
  - Recombination and outbreeding act to **reduce disequilibrium**.
- ▷ Level of linkage disequilibrium can between  $A$  and  $B$  can be quantified by the **coefficient of linkage disequilibrium**,  $D_{AB}$ .
  - Formula:  $D_{AB} = P_{AB} - P_A P_B$
  - $P_{AB}$ : the frequency with which both occur together on same gamete, or the frequency of the  $AB$  haplotype.
  - $P_A P_B$ : product of the probabilities give the probability they occur together.
  - When there is a difference, the magnitude of the coefficient rises, indicating linkage disequilibrium.
  - Strong recent selection can be indicated by linkage disequilibrium of alleles located next to neutral alleles.

### Recombination's Effect on Linkage Disequilibrium

- Linkage disequilibrium ( $D$ ) will converge to zero depending of the magnitude of the recombination rate ( $c$ ) between two loci the absence of natural selection, inbreeding, and genetic drift.
- The smaller the distance between the two loci, the smaller the rate of convergence of  $D$  to zero.
- Genetic recombination tends to randomize genotypes, thus it tends to reduce frequency of overrepresented chromosome haplotypes and increases underrepresented haplotypes.
- In short, recombination reduces linkage disequilibrium.

### Adaptive Significance of Sex

- ▷ **Parthenogenesis:** a natural form of **asexual reproduction** in which growth and development of embryos occur without fertilization.
- ▷ **Hermaphrodite:** an organism that has complete or partial reproductive organs and can produce gametes normally associated with both sexes.
  - Allows the either partner to act as male or female in sexual reproduction.
  - **Sequential:** born as one sex, but later changes into the opposite.
  - **Simultaneous:** fully functioning male and female genitalia.

### Maynard Smith Assumptions

1. A female's reproductive mode does not affect how many offspring she makes.
2. A female's reproductive mode does not affect the probability that her offspring will survive.
  - Designed to question advantage of either mode of reproduction (asexual vs sexual).
  - Predicts asexual females should be dominant reproduction form.
    - Due to the **two-fold cost of sex**: requires two individuals and some of the offspring are male.
    - Asexual reproduction of females would have all of the individuals reproduce and pass on genes, leading to quick dominance.
  - The prediction is not seen, so it raises question of what the benefits of sexual reproduction are.

### Violations of Maynard Smith Assumptions

1. Male parental care can influence how many offspring survives or can be made, though this violation is rare.
2. Presence of self-compatible hermaphrodites and males in same organism means males must:
  - collectively fertilize a proportion of eggs that exceed their own frequency in the population ( $\alpha$ );
  - and/or produce offspring that have a higher relative fitness ( $w$ ).
  - Condition for male persistence:  $\alpha w > 2$
- Raises the question how male fertilization increases relative fitness.

### Consequences of Sex

- **Sexual reproduction:** meiosis with crossing over and mating between unrelated individuals.
  - Meiosis results in genetic recombination.
  - Mating between unrelated individuals (outcrossing) results in allelic segregation.
- **Segregation** tends to restore the population to the **Hardy-Weinberg equilibrium**.
- **Recombination** tends to restore the population to **linkage equilibrium**.

### Maintenance of Sex

- More attention is given to the maintenance of sex via its effects on linkage disequilibrium.
- Sex **purges deleterious mutations**.
  - **Genetic load:** the burden imposed by the accumulating mutations in a population.
  - **Muller's ratchet:** mutations should accumulate in asexual lineages.
    - Lack of ability to purge mutations means that drift has higher chance of removing smaller proportion of mutation free individuals.
    - Thus, number deleterious mutations increases in individuals remaining, overtime lowering fitness of lineage.
  - A higher mutation rate selects for more frequent outcrossing; thus more males (more sexual reproduction).

- More frequent outcrossing results in more recombination, which opposes genetic drifts tendency of creating linkage disequilibrium.
  - Recombination recreates lost genotypes caused by random chance due to drift.
- Even if two individuals mate carrying deleterious mutations, then there is still a chance that they can produce mutation free offspring.
- Genes responsible for sex are maintained because they help create zero-deleterious-mutation genotypes.
- Sex **accelerates adaptive evolution**.
  - Natural selection also helps create linkage disequilibrium, creating chances at losing advantageous genotype.
    - Sex again introduces recombination allowing for recovery of lost advantageous genotypes.
    - Recombination can be also disadvantageous once optimal genotypes arise, raising question how it remains useful.
  - **Red Queen hypothesis**: sex remains beneficial indefinitely in populations subject to ever-changing selection.
    - Results in coevolutionary arms races.
    - Genotypes in lower-than-equilibrium frequencies due to previous disadvantage may soon become advantageous.
  - Thus, sex is continually selected for as recombination is continually favored in changing conditions.
    - Creates an accelerated rate of adaptive evolution in genes that take advantage of changing fitness of genotypes relative to each other.
  - Genes for sex are maintained in populations due to higher frequencies of genetic hitchhiking in genotypes they create.

## 9 Quantitative Genetics

### The Nature of Quantitative Traits

- ▷ **Quantitative genetics:** deals with phenotypes that vary continuously due to multilocus traits and environmental factors.
  - Allows for the prediction of how a population will respond to selection, even when we do not know the genetic basis of the trait.
- ▷ **Qualitative traits:** discrete traits that can be assigned individual categories by observation of simple genetic test.
- ▷ **Quantitative traits:** continuous traits determined by the combined influence of the genotype at multiple loci and the environment; the focus of quantitative genetics.
  - Study of continuous distribution requires many other statistical methods such as the effect size, mean, and variance, to link phenotypes to genotypes.

### Heritable Variation

- ▷ **Heritability:** the degree of **variation** in a phenotypic trait in a population that is due to genetic variation between individuals in that population.
- ▷ **Phenotypic variance ( $V_P$ ):** the genetic variance ( $V_G$ ) combined with the environmental variance ( $V_E$ ).
  - $V_P = V_G + V_E + V_{GE}$
  - $V_{GE}$  represents variance associated with **intereaction** of genetic and environmental factors.

### Genetic Variance

- **Additive genetic variance ( $V_A$ ):** how much the phenotypic trait is influenced by traits that show an additive effect on the quantitative traits.
  - Measures the magnitude to which individual phenotypic differences can be predicted due to additive effects of allelic substitutions.
  - The greater the additive genetic variation for the trait, the greater is response to selection can be.
- **Dominance genetic variance ( $V_D$ ):** associated with the dominant gene actions which cover the influence of the recessive alleles at the particular locus.
- **Epistasis ( $V_I$ ):** occurs due to statistical interaction among loci, i.e., gene-by-gene modification.

- $V_G = V_A + V_D + V_I$
- ▷ **Broad-sense heritability ( $H^2$ ):** all genetic contributions to a populations phenotypic variance, including additive, dominant, and epistatic, and maternal/paternal effects.
  - $H^2 = \frac{V_G}{V_P}$
- ▷ **Narrow-sense heritability ( $h^2$ ):** proportion of the total phenotypic variance that is due to the additive effects of genes.
  - $h^2 = \frac{V_A}{V_P}$
  - Allows prediction of how a population will respond to selection.
  - The greater the additive genetic variation for the trait, the greater its response to selection can be.

### Estimating Heritability

- Heritability is often estimated by measuring correlations between parents and offspring.
- **Midparent:** the average of the trait value between parents.
  - The mother's value often has a scaling value applied to help account for developmental sex differences.
- **Midoffspring:** the average value of a trait among offspring.
- Correlations are determined through a line of best fit.
  - Heritability of the trait is measured between 0 and 1 determined by the slope of the best fit line plotted against midparent and midoffspring values.
  - Using a method of **least-squares linear regression**, which minimizes the sum of the squared vertical distances between points, the heritability slope represents **narrow-sense heritability**.
- If a trait is heritable, monozygotic twins will resemble each other more than dizygotic twins.

### Predicting Evolutionary Responses

- **Selection differential (S)**: the difference between the mean of the selected individuals ( $\bar{x}$ ) and the mean of the entire population ( $\mu$ )
  - $S = \bar{x} - \mu$
  - Can be used to create a statical selection gradient, which is used to represent the strength of selection.
- **Breeder's equation**: evolutionary response (R) can be predicted using narrow-sense heritability and the selection differential.
  - $R = h^2 S$
  - The greater the heritability and selection differential, the greater the response to selection.
- When characters are genetically correlated, selection for one can drag the other along through genetic hitchhiking.
- Selection on the alleles at any single locus affecting a quantitative is often very weak; substantial genetic variation may persist at equilibrium between mutation and selection.
- Low heritability often represents populations effected by strong selection, as selection removes variation.
- Higher heritability represents high variance within the population.

# 11 Sexual Selection

## Sexual Dimorphism and Sex

- ▷ **Sexual Dimorphism:** when two sexes of the same species exhibit different characteristics beyond differences in sexual organs.
  - **Primary sexual characteristics:** differences that contribute directly to reproduction and serve no purpose in courtship.
  - **Secondary sex characteristics:** traits that give advantage over rivals in courtship or competition and are not directly related to reproduction.
  - Males and females often have different equilibrium strategies, due in large part to relative parental investment.

### Asymmetries Between the Sexes

- **Parental investment:** the energy and time expended constructing and caring for the offspring.
  - Typically higher in females.
  - Ultimately the investment is measured in fitness.
- Females produce eggs which often require substantial investment; often limiting mating availability.
- Males produce many small gametes; allowing for frequent and multiple mating.
- Variation in mating success is predicted to be highest in males, as females are often the limiting factor and have no trouble reproducing.

## Sexual Selection

- ▷ **Sexual selection:** differences in reproductive success due to variation among individuals in success at getting mates.
  - **Intersexual selection:** when members of one sex choose mates of the other sex.
  - **Intrasexual selection:** when members of same sex compete for access to members of the opposite sex.
- ▷ If sexual selection is strong for one sex, and weak for the other, then we predict that:
  - members of the sex subject to strong sexual selection will be competitive (intersexual).



- members of the sex subject to weak sexual selection will be choosy (intersexual).

### Selection on Males: Competition

- Male-male competition results in mainly combat, alternate mating strategies, sperm competition, and infanticide.
- **Combat:** fighting over access to mates that favours morphological traits such as body size, weaponry, armor, and tactical cunning.
  - Typically leads to a select few dominant males mating with majority of females.
- **Alternative strategies:** other strategies that are often employed by the less combat prone males.
  - Variety of examples, such as pretending to be female, sneaking, false displays of strength, and more.
  - Generally less successful, as it still requires the fooling of females or avoidance of dominant males and only works well in small relative frequency.
- **Sperm competition:** competition between gametes can continue after physical mating is complete.
  - Large quantities of ejaculation, guarding of mates, prolonged copulations, deposit of a copulatory plug, applications of disadvantage pheromones, and more.
- **Infanticide:** improvement of males reproductive success at cost of females due to killing of previous males offspring.

### Selection on Males: Female Choice

- Intrasexual selection that occurs when males cannot monopolize access to females, allowing for females to choose mates.
- Models for female preference include: good genes, direct benefits, preexisting sensory bias, and runaway sexual selection.
- **Good genes:** traits that code of ornamented displays can indicate higher fitness.
  - Often causes a handicap, which may be due to preexisting sensory bias and runaway sexual selection, or just a further display of fitness.
  - Sometimes displays end up being directly beneficial to reproduction or competition by chance.

- Other times it's just clear evidence of direct fitness advantages for partners.
- **Preexisting bias:** preexisting preference, which arose before male trait, selecting for further evolution of the trait.
  - Different biases can help lead to speciation.
- **Runaway sexual selection:** when a locus for a trait in males becomes linked to a trait that codes for mating preferences in females.
  - Can be direct preferences, or indirect. Can lead to overrepresentations of a trait that does nothing, or even harms the fitness of males.
- Gender roles can be reversed, but female choice is more common.

### Selection on Females

- Selection can occur when:
  - a single insemination delivers vastly more sperm than a female needs,
  - mating exposes females to diseases and other dangers,
  - when traits that females possess increases fitness of offspring,
  - when males provide parental care,
  - or when traits can attract more fit males that females can choose from.
- **Polyandry:** multiple mating by females.
  - Monogamy appears common, indicating little selection on females, but it turns out it's more common than once thought.
- ▷ **Sex allocation theory:** when individuals can change sex when the reproductive value of the other sex exceeds that of its present sex.
  - Has occurred in a variety of species, and is common in fish.

## 12 Evolution of Social Behavior

### Four Kinds of Social Behavior

- ▷ **Mutally beneficial (cooperation):** when both the recipient's and actor's fitness is increased due to the interaction between them.
  - Often has the greatest overall benefits over long term.
- ▷ **Selfish:** when the actor benefits, often to a greater degree, at the cost of the recipient.
  - Greatest benefits over short term, and the what is expected to be selected for.
- ▷ **Altruistic:** when the actor sacrifices, or loses, on behalf of the recipient's success (selfish + cooperation).
- ▷ **Spiteful:** when the actor suffers a loss in order to impose a penalty on the recipient (selfish + selfish).

### Kin Selection and Costly Behavior

- ▷ **Hamilton's rule:** a rule centered around a parameters of relatedness ( $r$ ) that shows how altruistic behavior, and thus cooperation, can spread.
  - Altruism will spread when:  $Br - C > 0$
  - $B$ : benefit to the recipient, and  $C$ : cost to the actor; both measured in units of surviving offspring.
  - Indicates that altruism will spread when the benefits ( $Br$  to the recipient) are great, and the cost ( $C$ ) is low.
- ▷ Relatedness values:
  - Parents-offspring: 0.5
  - Full siblings: 0.5
  - Half-siblings: 0.25
  - Cousins: 0.125
- ▷ **Inclusive fitness:** the sum of direct and indirect fitness of an individual.
  - **Direct fitness:** reproduction and individual achieves on its own.
  - **Indirect fitness:** additional reproduction by relatives made possible by individual's actions.
- ▷ **Kin selection:** natural selection that leads to the spread of genes that increase the indirect component of inclusive fitness.

## 13 Evolution of Human Health



## 16 Mechanisms of Speciation



## 17 Origin of Life; Major Transitions

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## 18 Fossil Record and Extinctions



## 20 Human Evolution





## 15 Genome Evolution

