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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 (α);
 - 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 (μ)
 - $S = \bar{x} - \mu$
 - 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.

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