BIOL 359 - Cumulative Notes

ddtnguye

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Contents

1 Introduction

- **Learning Outcomes:**
  - apply basic evolutionary principles to the HIV pandemic
  - understand the scientific meanings of some commonly used terms
  - gain knowledge on the history of evolutionary biology

1.1 Studying Adaptation

- evolution is a **scientific fact**; it has been repeatedly confirmed by comparative physiology studies, morphological studies, embryological studies and direct observation
- evolution is also a **scientific theory**; a well substantiated explanation to evolution
- **fact**; an observation that has been repeatedly confirmed and for all practical purposes is accepted as "true"
- **hypothesis**; a tentative statement about the natural world leading to deductions or predictions **that can be tested**. If the deductions are verified, it becomes more probable that the hypothesis is correct
- **law**; a descriptive generalization about how some aspect of the natural world behaves under specified circumstances
- **theory**; a well substantiated explanation of some aspect of the natural world that incorporates facts, laws, and tested hypothesis
- **Catastrophism**; the early tenet that the Earth's physical features were sculpted by catastrophic forces that no longer operate today
- **Principle of Uniformitarianism**; the geological forces that we see operating today are the same as those that operated in the past
- **Lamarckism**; a flawed early notion of evolution based on the inheritance of acquired characteristics

1.2 Short History of Evolution

- **Anaximander, around 500 BCE**; believed that species came from water, and that humans and other humans descended from fish
- **Empedocles, around 400 BCE**; proposed that body parts were joined together as random and only some combinations were fit for survival
- **Plato, around 300 BCE**; developed the concept of **idealism**; a notion that all natural phenomena that we see in the world today are imperfect representations of an idealized unseen world
- **Aristotle, around 300 BCE**; believes species were organized on a ladder moving from the least perfect to the most perfect
- **Carolous Linnaeus, 1735**; father of taxonomy; a framework for the modern classification system using the binomial nomenclature of genus and species naming
- **Jean Baptiste Lamarck, 1809**; believed that species change over time and evolve into different species. he believed that organisms evolved by the inheritance of characters that they acquire during their lifetime
- **Erasmus Darwin I, 1794**; proposed that species also evolved and are descendants of earlier life-forms. He also alluded to natural selection but didn't have evidence to support his claims
- **Georges Cuvier,1801**; father of comparative anatomy and paleontology; major proponent of the notion of catatrophism. Recognized that some species have gone extinct

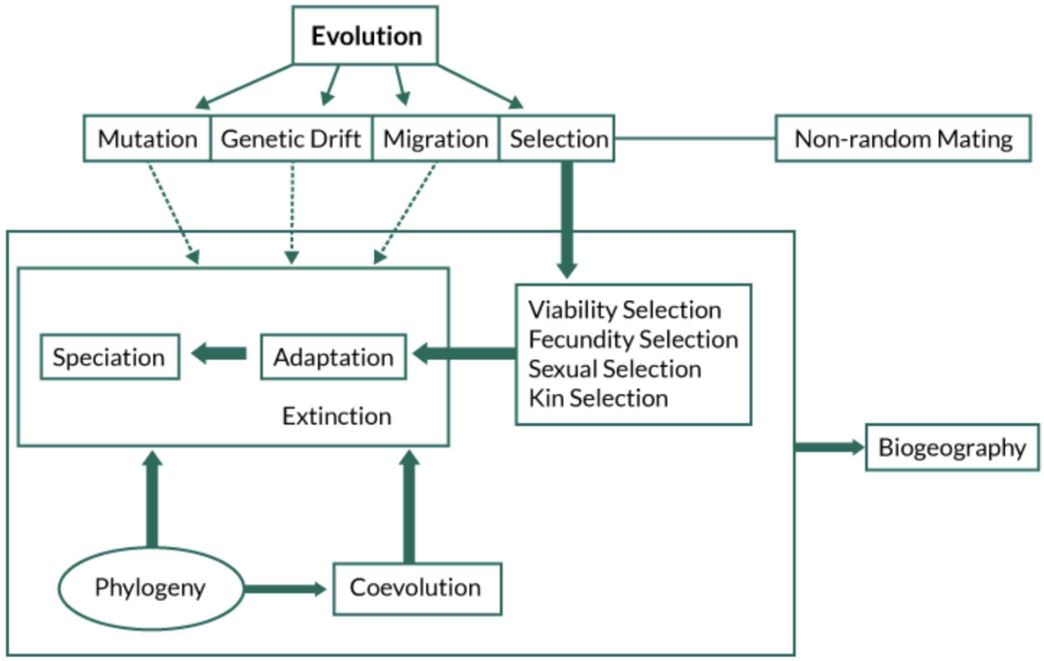


Figure 1: Evolution Connections

1.3 Catastrophism and Christianity

- arose as a consequence of trying to reconcile geological history with the age of the Earth according to the Bible
- believed that the Earth was about 5650 years old

1.4 Modern Synthesis or Neo-Darwinian Synthesis

- notable scientists were:
  - Theodosius Dobzhansky
  - Ernst Mayr
  - George Gaylord Simpson
  - Stebbins and Rensch
- establish that selection acts on genetic variation and that it is consistent with the evolution of taxa at various levels, from the population level all the way up to higher phylogenetic levels

2 Evidence for Evolution

- **Learning Outcomes**
  - understand the different lines of evidence for evolution
  - differentiate between **homology** and **analogy**
  - understand and interpret phylogenetic trees
  - understand geologic time scale and dating

2.1 Introduction

- Evidence for evolution includes:
  - selective breeding and biological change
  - direct observation of evolutionary change
  - vestigial structures
  - laboratory experiments
  - evidence from natural populations
  - extinction and the fossil record
  - transitional forms
  - homologies
  - the age of the Earth
  - the correlations among data sets(geological and biological)
- evolution can be described as:
  - descent with modification
  - a change in population allele frequencies
- **homology**; similarity resulting from common ancestry(the same origin), often despite differences in function
- **analogy**; similarity in function, but not having the same evolutionary origin
- **special creation**
  - species do not change
  - lineages do not split
  - each species is separately created
  - each species is independently created
  - Earth and life are young
- **descent with modification**
  - species change over time(**microevolution**)
  - lineages split and diverge(**speciation**)
  - new life-forms derive from older forms(**macroevolution**)
  - all life-forms are related(**common ancestory**)
  - Earth and life are old

2.2 Selective Breeding

- **microevolution**; small evolutionary changes within species or populations
- **speciation**; the splitting and divergence of lineages, an ancestral species can give rise to two or more descendent or daughter species
- **macroevolution**; refers to larger phenotypic changes sufficient to place an organism in a different higher level taxon(eg) phylum). Over time, microevolution results in both speciation, as well as macroevolutionary differences
- phylogenetic analyses unambiguously show that all domestic dogs are descended from wolves

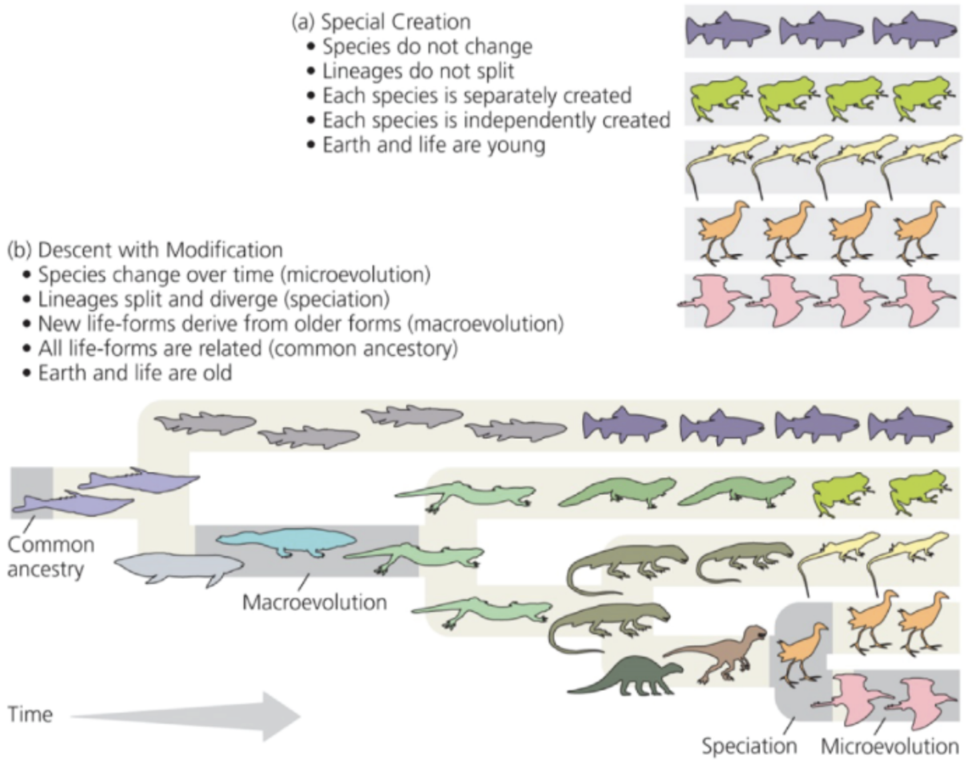


Figure 2: Special Creation vs Descent with Modification

2.3 Direct Observation of Evolutionary Change

- **incipient species**; two populations that have nearly completed the process of becoming separate species

- One powerful line of evidence for evolution is that we can observe it directly in a wide variety of settings. For example, consider the evolution of the apple maggot fly (Rhagoletis pomonella).

- The apple maggot fly's native North American host plant is the hawthorn tree, which produces a fruit in the fall very similar to a crab apple. The flies lay their eggs on the fruit, and the larvae develop in it.

- The apple tree was introduced to North America from Europe around 300 years ago, and the fly was first observed parasitizing apples in the mid 1800s when it made a host plant shift. Detailed genetic, ecological, and life history studies have shown that the fly populations parasitizing apple trees have evolved considerable heritable differences related to the fact that apples ripen earlier than hawthorn fruits, and apple and hawthorn maggot flies are now considered to be incipient species.

- Host plant shifts have been an important factor that induces speciation in insects, and several other examples are well documented

- **vestigial structures**; body parts that are useless, or rudimentary in one or more organisms, but have an important function in related organisms

2.4 The Biological Species Concept

- **Species are**:

- difficult to define
- controversial
- difficult to come up with a definition that encapsulates the tremendous biological diversity

- **reproductive isolation**; key operational criterion
- can only be applied to species that are sexually reproducing
- not a universal definition
- evidence for evolution in natural populations
- if evolution occurs we should be able to look at natural populations and observe different stages on the way to reproductive isolation

2.5 Extinction and the Fossil Record

- the entire collection of fossils that we have globally
- paleontology is the study of fossils
- in 1801, Georges Cuvier published a list of extinct species
  - eg) Irish Elk
- Treating Evolution as a Hypothesis and Testing it with the Fossil Record
  - (null hypothesis) if Evolution has not occurred;
    * we should see the same organisms that exist today throughout the entire Fossil Record
  - (alternative hypothesis); Evolution has occurred
    * we should see changes in the organisms that have inhabited the Earth throughout the fossil record
    * there should be strong geographic patterns with respect to the similarity of organisms that within the fossil record and those that exist today
- **The Law of Succession**; fossils in a given geographic region are more closely related to the **extant(opposite of extinct)** fauna of that region than they are to organisms in a different geographic region

2.6 Homology

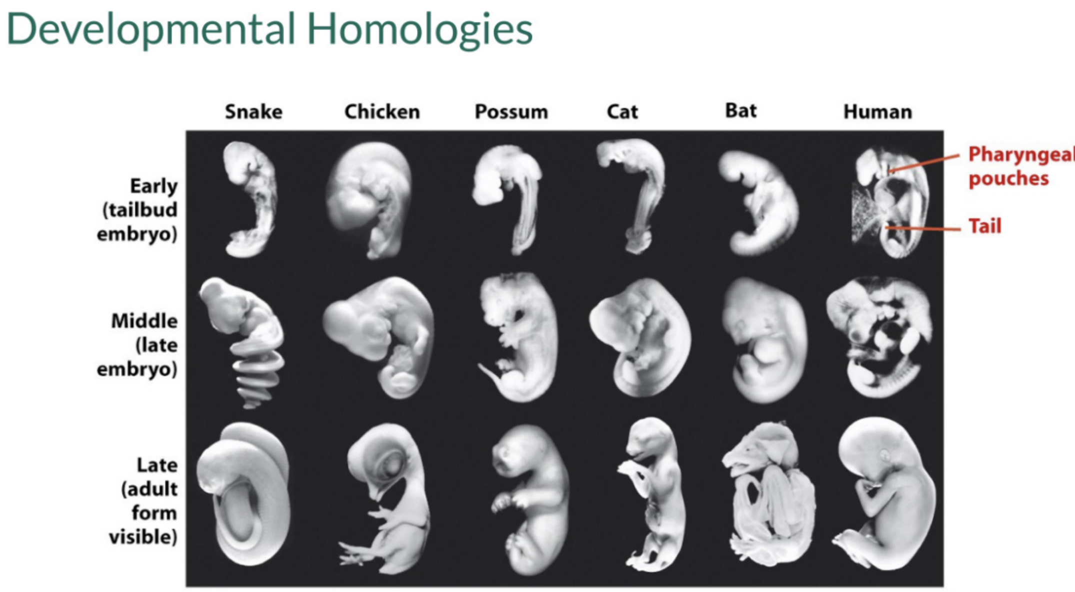


Figure 3: Developmental Homologies of various animals

2.7 Summary

- The theory of evolution provides a logical framework in which the diversification of life can be understood
- It makes predictions that can, and have been tested in the natural world
- It is strongly supported by selective breeding, direct observation of evolutionary change, vestigial structures, laboratory experiments, evidence from natural populations, extinction and the fossil record, transitional forms, homologies, the age of the Earth, and the correlations among data sets

3 Introduction to Natural Selection

- Learning Outcomes
  - describe and apply the selective elements of **fitness**
  - understand and articulate Darwin's postulates in the context of examples of natural selection in nature
  - apply the principles of natural selection to human management regimes in natural populations

3.1 Introduction

- Darwin's great contribution to science was the forma ldevelopment of a mechanism that explains how evolution can occur through natural selection
- **Natural Selection** is the difference in the survival and reporduction of phenotypes, which leads to differences in their contribution to the next generation, resulting in a change in the frequency of heritable phenotypic variations in populations over time

- natural selection is not the only mechanism by which evolution can occur, but it is the principal mechanism of adaptive evolution
- **The Components of Natural Selection**
  - living things produce more offspring than can be supported
  - there is a constant struggle for existence
  - individuals in a population vary in their phenotypes
  - some of this variation is hertiable(based on genotypes)
  - those individuals best adapted to current conditions are most likely to survive and reproduce themselves
  - if these adaptations are heritable, they will be passed on to their offspring
- natural selection acts on **phenotypes**, but evolution only occurs if there is a change in population **allele frequencies**
- the process of natural selection is fundamentally driven by differences in evolutionary fitness among individuals
- **evolutionary fitness or Darwinian fitness** represents an individual's contribution to the **next** generation in terms of **numbers of offspring**
- the more offspring an individual contributes to the next generation, the greater the individual's evolutionary fitness
- there are three components that contribute to an individual's evolutionary fitness:
  1. **viability or mortality selection**; an individual's ability to survive and reach reproductive age
  2. **sexual selection**: an individual's ability to procure a mate(**mating success**)
  3. **fecundity selection**; family size, which is usually measured as the number of female gametes(eggs) produced
- **adaptation**; trait or characteristic that increases an individual's fitness, in comparison to individuals that do not possess the trait

3.2 Darwin's Theory of Natural Selection

- Darwin's Four Postulates
  1. individuals within species are **phenotypically variable**
  2. some of these variations are **heritable**
  3. in every generation, **more offspring are produced than survive**, some are more successful at survival and reproduction than others
  4. the survival and reproduction of individuals is **not random**. Those who reproduce, or reproduce the most are those with the most favourable variations and are **naturally selected**
- **Note:**
  - within the public and popular press, natural selection is often defined as "survival of the fittest"
  - however, we can see that this definition is high problematic(and very inaccurate) because it makes no mention of an individual's contribution to the next generation
  - in the context of selection, survival on its own is meaningless if there is no contribution to the next generation

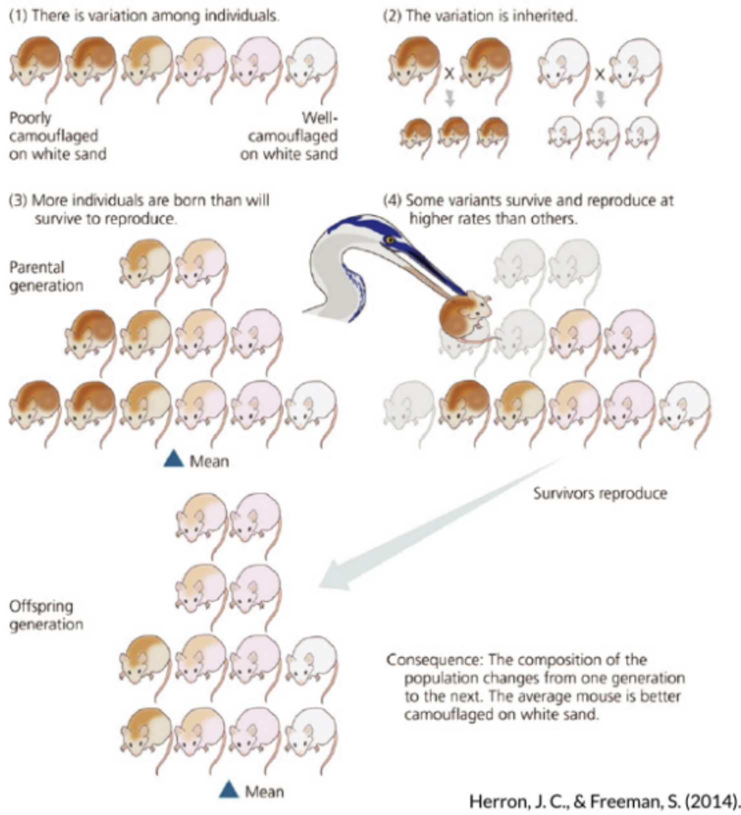


Figure 4: Beach Mice example

3.3 Natural Selection in Action

- natural selection is dynamic; phenotypes favoured in one generation may be very different than the phenotypes favoured in a subsequent generation
- natural selection does not produce anything new, it acts on heritable phenotypic variation already present in the population, and altered the frequency of different heritable phenotypic variants
- **heritability** is a key component of natural selection and can be defined as the proportion of trait variation in a population that is attributable to genetic factors as opposed to environmentally induced differences
- the mechanisms that can produce new variation are:
  - mutations
  - recombinations

3.4 Natural Selection Example

- **Introduction of the Cane Toad to Australia**
  - native to South America
  - introduced into Australia in 1935 to control Sugar Cane Beetle populations
  - rapidly spread; Australian population now numbers in the hundreds of millions
  - cane toads possess skin glands which secrete highly toxic substances

- predators that feed on native Australian frogs and toads died in large numbers as a result of cane toad ingestion
  - eg) red-bellied black snake vs green tree snake

- **What Happened?**
  - snakes with large jaws and stout bodies were able to ingest cane toads, and were eliminated from the population
  - snakes with small jaws and slender bodies could not ingest toads, survived and reproduced
  - there has been a marked decrease in jaw size, and increase in slenderness within populations of these snake species as a result of the cane toad's introduction and subsequent natural selection

- **Darwin's Postulates and Snakes**
  1. there was variation in the snake populations with respect to jaw size and body slenderness
  2. some of this variation had a genetic basis(heritable)
  3. more snakes were produced each generation than survived, some were better at survival and reproduction than others
  4. survival and reproduction were non-random, variation in slenderness and jaw sizze resulted in different fitnesses among snakes

3.5 How Natural Selection Operates

- natural selection **acts on individuals** but consequences occur in populations
- natural selection acts on phenotypes, but evolution consists **changes in allele frequencies**

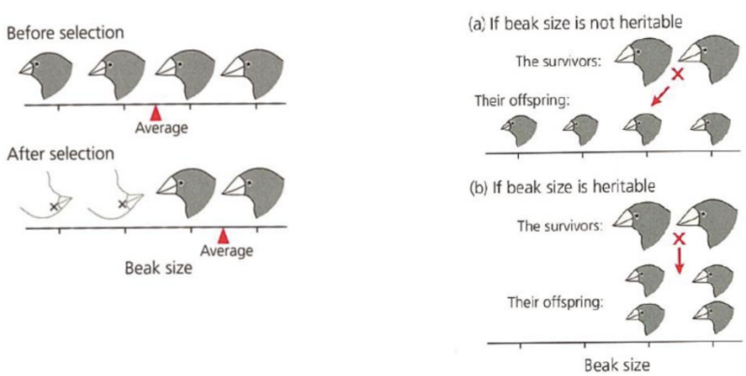


Figure 5: Natural Selection acting on beaks of a population

- **The Measure of "Fitness"**
  - fitness is a measure of reproductive success, which is affected by three different elements of natural selection
    1. **viability or mortality selection**; an individual's ability to survive and reach reproductive age
    2. **sexual selection**; an individual's ability to procure a mate(mating success)
    3. **fecundity selection**; family size, which is usually measured as the number of female gametes(eggs) produced

- **Antagonistic Selection**

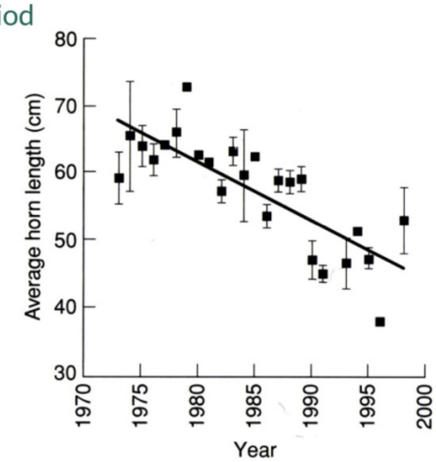
- when any of the 3 selective elements of fitness act in opposition to each other
- antagonistic selection is one of the reasons why natural selection does not lead to perfectly adapted organisms

- **How Natural Selection Operates**
  - natural selection is **non-random**
  - evolutionary forces such as mutation are random, natural selection is not one of them
  - misconception of somehow natural selection is progressive and that it is leading up to some kind of an objective
  - natural selection acts on individuals, it does not act on groups of individuals

3.6 Human Induced Selection Regimes in Natural Populations

- **Ram Mountain Alberta**
  - at Ram Mountain Alberta, there has been no restriction on the number of rams killed during the hunting season, except that their horns be greater than a minimum specified size
  - in addition, there are typically killed prior to breeding season, meaning males with large horns have reduced fitness
  - this has resulted in a regime of directional selection for small horn size being imposed on the population
  - horn size is a polygenic character, but has been demonstrated to be heritable

Mean Male Population Horn Length at Ram Mountain Alberta Declined Over a 30 Year Period



3.7 Evolution of Bacterial Resistance to Antibiotics

- **Evolution of Tuberculosis Infection**

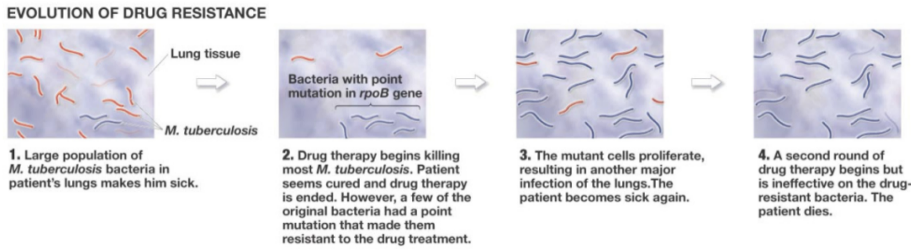


Figure 6: The Evolution of Bacterial Resistance to Antibiotics

3.8 Summary

- Natural selection is the principal mechanism of adaptive evolution, although as we shall see, three other evolutionary mechanisms can potentially be adaptive as well. Natural selection cannot result in new variants on its own; it is a statistical mechanism that alters the frequency of variations that already exist. It does so by altering the population gene (allele) frequencies that underlie phenotypic variation. Recall that one way that evolution can be defined is a change in population allele frequencies.

- An **evolutionary mechanism** can be more stringently defined as **any force that can change population allele frequencies**, and natural selection is an important one.

4 Variation and Mutation

- Learning Outcomes
  - understand and differentiate between the factors that result in phenotypic variation
  - understand the different types of mutations, and their associated fitness effects

4.1 The Kinds of Variation

- **genetic variation**; individuals can possess different phenotypes as a result of genetic differences(different genotypes), transmitted from parents to offspring

- **environmental variation**; individuals can possess different phenotypes as a result of exposure to different environments, despite identical genotypes

- **genotype by environment interactions**; individuals can possess different phenotypes as a result of the interaction of their genotypes with the environment

- **phenotypic plasticity**; refers to the fact that genetically identical individuals can have different phenotypes in different environmental conditions, it is the result of environmental variation

- **reaction norm**; refers to the pattern or range of phenotypes that the same genotype can possess as a result of different environments

4.2 DNA, Point Mutations and Indels

- mutations can be broadly classed as somatic cell mutations, and germline mutations
  - only germline mutations are heritable and have evolutionary consequences
- **permutation**;
- **point mutation**;
- **transition**;
- **transversion**
- **synonymous substitution**;
- **nonsynonymous substitution**;
- **nonsense mutation**;
- the ratio of transitions to transversions observed among DNA sequences is often greater than 10:1
  - this is because transversions are more easily detected by proof reading and mismatch repair systems
- **indels**; refers to the insertion or deletion of one or more nucleotides in a DNA sequence, and frequently result in frameshifts, which are often highly deleterious

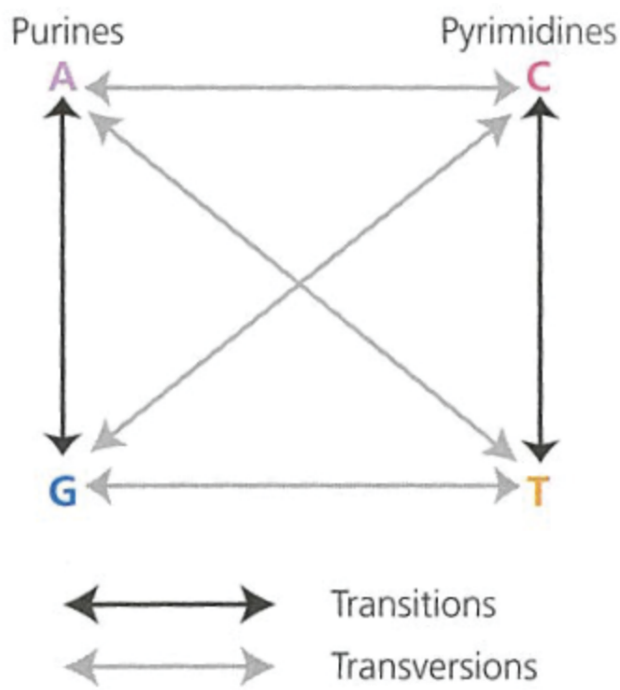


Figure 7: Transitions vs Transversions

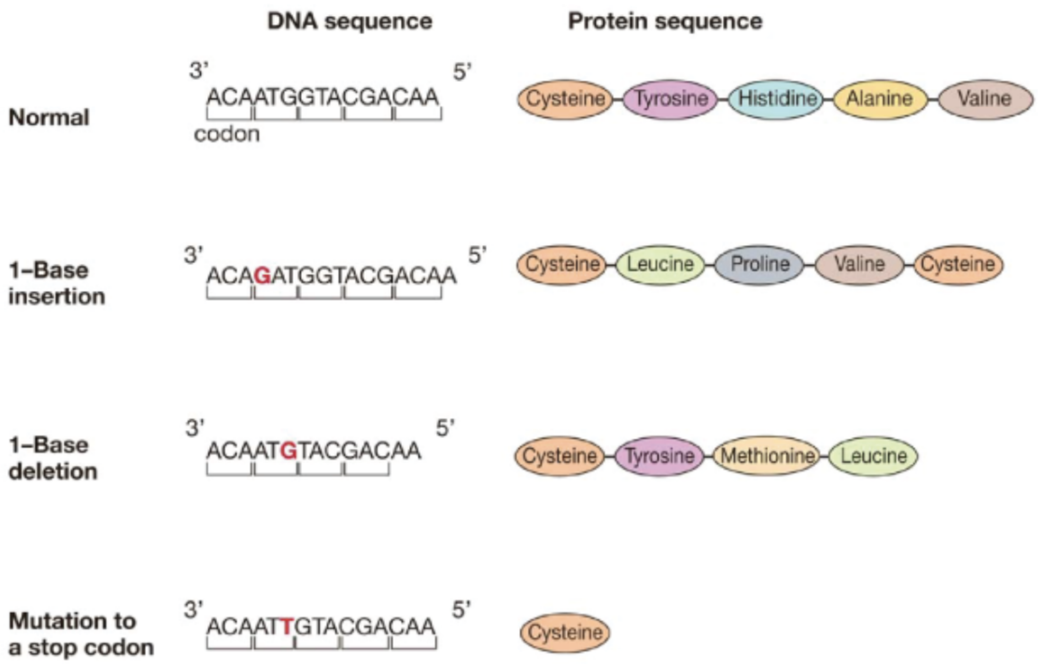


Figure 8: Effects of Indels

4.3 New Gene Formation and Chromosome Mutation

- gene duplication has been very important in evolution, and can occur as a result of unequal crossing over during meiosis, or as a consequence of **retroposition**(also called **retroduplication**)
- gene duplication can result in the formation of multigene families
- chromosomal mutations include inversions(that affect gene order and recombinations) as well as polyploidization events, which involve the duplication of entire genomes

4.4 Mutation Rates and Fitness Effects

- overall mutation rates are a function of generation times(lesser generation times have more opportunities to produce mutations) and mutation rates
- mutation rates are typically measured in terms of generations to facilitate meaningful comparisons among different organisms
- mutation rates can vary among organisms as a result of the fidelity of their polymerases'(that can differ quite dramatically), as well as the effectiveness of their proof reading and mismatch repair mechanisms
- additionally, mismatch repair mechanisms work more effectively on regions that are coded, and frequently transcribed, resulting in mutation rate variation across the genome
- **neutral mutations**; have no effect on fitness
- **deleterious mutations**; reduce the fitness of an individual
- **beneficial mutations(or advantageous)**; increase the fitness of an individual
- **lethal mutations**; deleterious mutations that result in an organism's death before it can reproduce

- deleterious and lethal mutations are much more common than beneficial mutations
- even thought the substitution may be synonymous, it can still be non-neutral
  - this is because different codons for the same amino acid will still require a different transfer RNA during protein synthesis
  - although there may be multiple different codons for the same amino acid, most organisms use one or a couple of codons for a given amino acid(**codon bias**)
  - if the synonymous substitution results in a codon for which the transfer RNA is in very short supply, or unavailable, it can slow down the process of protein synthesis
- not all nonsynonymous substitutions are non-neutral
  - some amino acids such as alanine and valine have very similar biochemical properties, and such substitutions could potentially have no effect on fitness

4.5 Summary

- an organism's phenotype depends on its genotype, and the environment in which that genotype is located
- selection can only occur on variation that has a genetic basis, not on variation that is controlled by the environment
- mutation is the source of all genetic variation, and mutation rates can vary markedly among organisms, and genes
- the fitness effects associated with different mutations will govern the nature of their interactions with selection
- selection will act to increase the frequency of advantageous mutations

5 Population Genetics

- Learning Outcomes
  - conduct basic population genetic calculations and statistical tests
  - apply the **Hardy-Weinberg Principle** to natural populations
  - understand and integrate the population genetic mechanisms of evolution
  - understand the types and consequences of non-random mating
  - apply the principles of population genetics to population conservation
- evolution is a change in population allele frequencies

5.1 Measuring Genetic Variation

- **The Classical Hypothesis**; populations contain very little variation, selection maintains a single best allele at any locus, and heterozygotes are rare. Heterozygotes occur as a result of rare deleterious mutations that are quickly eliminated by selection
- **The Balance Hypothesis**; individuals are heterozygous at many loci, and balancing selection maintains lots of genetic variability within populations
- **balancing selection**; any form of selection that results in the maintenance of genetic variation(allelic diversity)

- **Population Heterozygosity**;

  $\frac{heterozygotes}{total\ number of\ individuals}$

- **Protein Electrophoresis**
  - to measure the diversity of populations at a locus, you need to determine an individual's **genotypes**
  - protein electrophoresis was the first method used to do this
  - today, this is typically done by **direct DNA sequencing**

- **Heterozygosity in Natural Populations**
  - protein electrophoretic studies in the 1960s and 70s revealed substantial genetic variation
  - this provided strong support for the balance hypothesis(the classical hypothesis was clearly wrong)
  - variation at the DNA level is even greater

- the high genetic variability resulted in a new debate
  - **The Selectionist Hypothesis**; balancing selection results in the maintenance of high genetic variability
    - heterozygotes usually have higher fitness
  - **The Neutral Hypothesis**; most alleles in natural populations are neutral, and do not affect fitness

- this debate resulted in the development of the neutral theory of molecular evolution

- **Note**: always make sure allele and genotype frequencies add up to 1

5.2 The Hardy-Weinberg Principle

- shows us how allele and genotype frequencies behave in natural populations if no external forces are acting on them
- population is mating randomly
- the HW Principle is a model of random mating in the absence of evolutionary mechanisms
- serves as a starting point or null hypothesis in population genetic studies
- for a two allele system, the HW principle is mathematically stated as:
  - $p^2 + 2pq + q^2 = 1$
  - p and q are the frequencies of the alleles
  - the HW principle can be expanded to any number of alleles
- **Panmictic Population**; a sexually reproducing population where each male has an equal probability of mating with each female, and each emale has an equal probability of mating with each male(randomly mating)
- **Meiosis**; reduction divisions that produces haploid(1 set of chromosomes)**gametes**(eggs/sperm) from diploid parent cells
  - gametes unite to form offspring(**zygotes**)
- the probability that two gametes(alleles) unite to form a zygote(diploid genotype) is equal to the product of their frequencies(allele frequencies)

- "What does the HW Principle do?"
  - given **allele** frequencies, it allows us to calculate **expected genotype frequencies**
- **Assumptions of the HW Principle**
  1. no selection
  2. no mutation
  3. population is diploid
  4. no migration
  5. population reprpduces sexually
  6. infinitely large population(no chance events) with **random mate selection**(panmictic)
- **Important Points of the HW Principle**
  1. if a population is out of HW equilibrium,(say we deliberately remove individuals with certain genotypes), it wil take a **single** generation of random mating to restore HW equilibrium
  2. if there are no violations of its assumptions, the HW principle shows that genotype and allele frequencies will not change from one generation to the next
- all in all, the HW Principle provides a null model to predict genotype frequencies from allele frequencies in the **absence of evolutionary forces, and non random mating**

5.2.1 Testing Hypotheses Using the HW Principle

- the HW Principle is typically the starting point in investigation on natural populations
- population geneticists will genotype individuals in a population, and then estimate allele frequencies from these **observed genotypes**
- subsequently, the estimated allele frequencies will be used to calculate the **expected genotype** numbers assuming the population is in HW equilibrium
- if the observed genotype numbers are different than those expected, something is interesting is occurring in the population
- the HW Principle provides a **Null Hypothesis** about expected genotype frequencies in natural populations, which we use to test an **alternate hypothesis**
- the alternate hypothesis can take the form of violations of the assumptions of the HW Principle
- the chi square (χ^2) goodness of fit test is a generalized statistical procedure used to determine if an observed number entities are statistically equivalent to the number of entities expected on the basis of a model, hypothesis or some other criterion
- the chi square test statistic is calculated as follows:
  - $\chi^2 = \Sigma \frac{(obs-exp)^2}{exp}$
- once the test statistic has been calculated, it must be compared to its critcal value, which is obtained from a statistical table
  - if the calculated test statistic is less than or equal to the critical value, we accept the null hypothesis that a population is in Hardy-Weinberg equilibrium
  - if it is greater than the critical value, we have statistical evidence to reject the null hypothesis of Hardy-Weinberg equilibrium
- when we conduct a chi-squared goodness of fit test, we need to calculate a second number, **the degrees of freedom**
  - in general, the degrees of freedom is equal to the nubmer of classes of data(number of different **genotypes**, denoted K) minus 1, minus the number of parameters **estimated** from the data
- HW disequilibrium will always result as a consequence of a **heterozygote deficit**, or a **heterozygote excess**
  - both evolutionary, and non-evolutionary forces can result in HW deviations

5.2.2 Selection and the HW Principle

- the big four evolutionary mechanisms are:
  * selection
  * mutation
  * migration
  * genetic drift
- other evolutionary mechanisms include:
  * founder effects
  * population bottlenecks
- evolutionary mechanisms result in the change of allele frequency

- **fixed(or fixation)**; when an evolutionary mechanism results in an allele moving to a frequency of 1, we say that the population has become fixed for that allele, or moved to fixation for that allele
- **heterozygote superiority**; when (in a two allele system; eg) 3 possible genotypes), the heterozygote has the highest fitness. Heterozygote superiority is a form of balancing selection
- **heterozygote inferiority**; when (in a two allele system, eg) 3 possible genotypes), the heterozygote has lowest fitness
- the magnitude of the impact that selection has on allele and genotype frequencies will depend on whether alleles are common or rare, dominant or recessive, as well as the fitness of the different genotypes

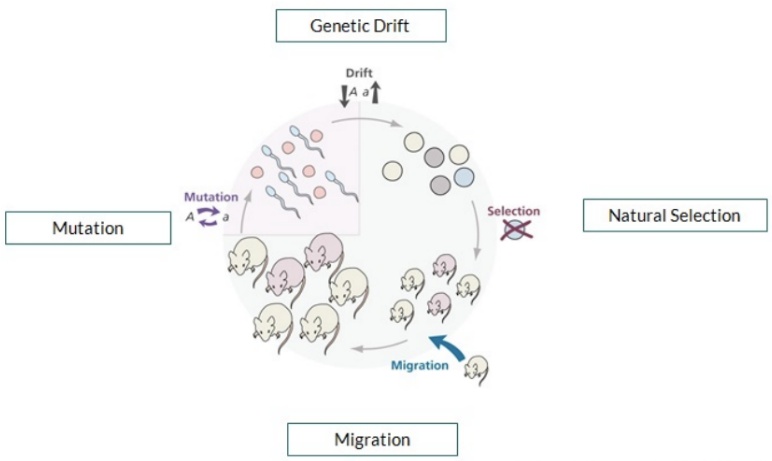


Figure 9: Forces impacting Genotype and Allele Frequencies

- **What happens if Selection occurs in a population?**
  - for HW equilibrium, we assumed that all individuals survive at equal rates and contribute equally to the next generation
  - selection occurs when individuals with a particular phenotype have greater survival and reproduction than those individuals with a different phenotype, provided that phenotypes at least in part have a genetic(genotypic) basis
- **Change Due to Selection**
  - in nature, there are not usually differences in survival rates large enough to make a big impact over a single generation(but sometimes there can be)

- smaller changes typically accumulate over numerous generations

- **Selection and HW Principle**
  1. selection can change allele frequencies, therefore it is an evolutionary force or an evolutionary mechanism
  2. it can also change population genotype frequencies
  3. it can change genotype and allele frequencies in a way that causes HW disequilibrium in the form of heterozygote excess and deficit

- **Selection on Heterozygotes and Homozygotes**
  - fitness of heterozygotes
    * if one allele is recessive and the other is dominant, then the fitness of the heterozygote is equal to that of one of the homozygotes
    * fitness can be between that of the two homozygotes(codominant)
    * fitness can also be superior or inferior to that of either homozygote
  - heterozygote inferiority(underdominance) or superiority(overdominance) can produce interesting outcomes

5.2.3 Modes of Selection on Quantitative Traits

- traits affected by many loci are referred to as quantitative traits
- phenotypic characteristics that varies continuously, as opposed to discretely, and involve multiple loci
- there are 3 important modes of selection on quantitative traits:
  * directional selection
  * stabilizing selection
  * disruptive selection
- **quantitative trait**; phenotypic characteristic that varies continuously as opposed to discretely, and involves multiple loci
  * eg) weight and height
- directional and stabilizing selection are more common and disruptive is believed to be more rare
- directional and stabilizing selection reduce phenotypic variation in a population
- "Why do natural populations exhibit significant variation and why is it maintained in the population?"
  1. populations are not in evolutionary equilibrium with respect to directional or stabilizing selection
  2. in most populations, there is a balance between mutation and selection
  3. disruptive selection may be more common than thought

5.2.4 Mutation and the HW Principle

- mutation is the ultimate source of all population genetic variation
- mutation changes allele frequencies, but only in a very subtle way from one generation to the next
- mutation does not change allele frequencies in a way that causes Hardy-Weinberg disequilibrium
- mutation **will not result in HW disequilibrium** in a randomly mating population, even though it changes allele frequencies(albeit slightly)

- in other words, not all violations of the assumptions of the HW principle result in Hw disequilibrium
  - however, mutation does change allele frequencies
  - when all of the assumptions of the HW principle are met, allele and genotype frequencies are stable from generation to generation
- **selective sweep**; the rapid fixation of a new advantageous mutation by selection
- **mutation-selection balance**; the equilibrium allele frequency established when the mutation rate of a deleterious allele into a population is equal to the rate of its removal by selection. This is another reason why deleterious alleles can persist in populations
  - many mutations are deleterious
  - selection will remove these mutations from the population, but mutation will re-introduce them
  - at some point, the rate at which new copies of a deleterious allele appear through mutation will equal the rate at which selection moves them
  - this cann account for a persistence of deleterious alleles within a population

5.2.5 Migration and the HW Principle

- migration refers to the movement of alleles into(or among) populations, and is typically referred to as geneflow
- the rate of **geneflow** among populations will be in part dependent on the dispersal capabilities of the organism in question
- migration can change allele frequencies and result in HW disequilibrium with either heterozygote deficits or excesses
- it is an evolutionary force that can potentially act against selection or work with selection and aid the fixation of a beneficial allele
- migration is a mechanism that homogenizes populations, or makes them more similar to each other in terms of allele frequencies
- **Migration**
  - movement of alleles between population
  - **gene flow**
  - caused by anything that moves alleles from one population to another
  - island populations are excellent "laboratories" for examining migration
  - it takes one round of random mating to restore HW equilibrium
  - migration is a force that can change allele frequencies and where the HW Principle is concerned, it can result in heterozygote deficits/excesses depending on the situation
  - it is important to remember that migration might not necessarily result in HW disequilibrium depending on the circumstances
  - although migration can result in heterozygote excesses/deficits, it doesn't mean that it will do that all the time
- **Fixation Index**
  - is a measure of how much populations differ in allele frequencies at a locus, or quantifies genetic variability among populations
  - it can be computed for 2 or more populations, and can take on values from 0 to 1
  - when F_{st} is equal to 0, all populations have identical allele frequencies
  - when F_{st} is equal to 1, no alleles are shared among populations
  - migration reduces the value of F_{st} among populations

5.2.6 Genetic Drift and the HW Principle

- genetic drift can change population allele frequencies from one generation to the next in a completely unpredictable, random manner, but it does not result in HW disequilibrium
- genetic drift results from **sampling error** during the gamete phase of an organism's life cycle
- genetic drift is very powerful when population size is small, and will have the greatest impact on allele frequencies from one generation to the next
- conversely, genetic drift will be weak or non-existent when population size is very large
- although drift changes allele frequencies in a manner that does not cause HW disequilibrium, allele frequencies will be stable from one generation to the next when all of the HW principle's assumptions are met
- over time, genetic drift reduces population heterozygosity and allelic variability, and causes alleles to randomly go to fixation
- when population size is small, genetic drift can overpower natural selection and result in the random fixation of a deleterious allele
- however, because it is random and unpredictable, it could also work with selection and aid selection with the fixation of an advantageous allele
- migration and genetic drift are evolutionary mechanisms that act in opposition to each other
- **founder effect**; allelic sampling error that occurs when a group of individuals from a population colonize a new area, and start(or found) a new population. This new population can differ in allele frequencies in comparison to the source population as a result of sampling error
- **population bottleneck**; a sharp reduction in population size that can alter allele frequencies as a result of sampling error
- an evolutionary mechanism(or force) is anything that can change population allele frequencies
  1. natural selection is a **non-random** mechanism of evolution
  2. mutation is a **random** mechanism
  3. migration can either be **random** or **non-random**
- **Genetic drift**
  - refers to chance fluctuations in allele frequencies as a result of **randomly sampling gametes** each generation
  - gametes unite to form zygotes
  - to conceptualize drift, think of each generation as **random sample** of gametes produced by the previous generation
  - think of drift as **sampling error** spread across generations
  - genetic drift is a very important, random evolutionary force
  - it changes population allele frequencies in a stochastic and unpredictable manner, but not in a way that creates Hardy-Weinberg disequilibrium
  - genetic drift is most powerful when population is very small

5.3 The Nature and Consequences of Genetic Drift

- genetic drift results from sampling error during the gamete phase of an organism's life cycle
- genetic drift is very powerful when population size is small, and will have the greatest impact on allele frequencies from one generation to the next
  - genetic drift will be very weak or non-existent when population size is very large
- over time, genetic drift reduces population heterozygosity and allelic variability, and causes alleles to randomly go to fixation
- when population size is small, genetic drift can overpower natural selection, and result in the random fixation of a deleterious allele
  - because it is random and unpredictable, it could also work with selection and aid selection with the fixation of an advantageous allele
- genetic drift is a mechanism that results in the divergence of populations in terms of allele frequencies, and increases the value of FST
- **Founder Effect**; allelic sampling error that occurs when a group of individuals from a population colonizes a new area, and start(or found) a new population
  - the new population can differ in allele frequencies in comparison to the source population as a result of sampling error
- **Population bottleneck**; a sharp reduction in population size that can alter allele frequencies as a result of sampling error
- **Genetic Drift**
  - every population follows a unique and independent path
  - genetic drift is most powerful when population size is small
  - the larger a population, the **weaker** that drift will be as an evolutionary mechanism
  - genetic drift can produce substantial changes in allele frequencies
  - genetic drift can cause allele frequencies to "wander" over generations, which has two effects
    1. alleles drift to fixation or loss
    2. the frequency of heterozygotes, or heterozygosity decreases over time
  - the effect of genetic drift is much more pronounced when population size is small, the smaller the population, the stronger the genetic drift, and the fast heterozygosity will decline, and alleles will be fixed
- both bottlenecks and founder effects can result in HW disequilibrium
- they can cause heterozygote deficits or heterozygote excesses
- however, after the initial founder/bottleneck event, one round of random mating will restore HW equilibrium
- migration is a force that will oppose genetic drift
  - drift results in population divergence(increases FST) but migration acts to homogenize populations(decrease FST)
  - it takes little migration to counter the effects of drift

5.4 Non-Random Mating

- outbreeding is the opposite of inbreeding; a higher incidence of mating among distantly related individuals than expected in a randomly mating population. Outbreeding causes HW disequilibrium with heterozygote **excesses**, but it does not change allele frequencies, and on its own is not a mechanism if evolution
- assortative mating describes cases where individuals with similar phenotypes mate eg) large individuals only mate with other large individuals(**Positive assortative mating**) or individuals with dissimilar phenotypes mate(eg) small individuals mate with large individuals)(**negative assortative mating**) at a higher frequency than occurs in a randomly mating panmictic population
- inbreeding and outbreeding affect **all loci**
- the major assumption of the HW principle is that individuals mate randomly,(panmictic population)
- non-random mating can indirectly affect evolution, but does not change allele frequencies on its own and includes:
  - inbreeding
  - outbreeding
  - positive assortative mating
  - negative assortating mating
- **inbreeding**; refers to mating among closely related individuals(eg) relatives) and results in **deviations from HW equilibrium** as a result of heterozygote deficits(or increase in homozygosity)
- self fertilization is the strongest form of inbreeding, and occurs among numerous plants and animals(snails, worms, and even some fish)
- **What effect will inbreeding have on genotype frequencies?**
  - inbreeding causes changes in genotype frequencies, **but not allele frequencies**
  - creates a heterozygote deficit, or homozygote excess(HW disequilibrium)
  - it is not a mechanism of evolution on its own(it does not change allele frequencies), but it can have important evolutionary consequences in conjunction with selection
- **Inbreeding Depression**
  - a reduction in the average fitness among individuals within a population due to inbreeding
  - **consider recessive deleterious alleles**
    * these are alleles that will reduce survival and reproduction(fitness) when in homozygous form

5.5 Population Genetics and Conservation

- working with small population sizes have population genetic reasons:
  1. genetic drift will be strong, and will reduce heterozygosity by randomly fixing alleles, removing variation and **adaptive potential**
  2. drift can overpower natural selection, and randomly fix deleterious alleles
  3. the probability of mating among close relatives **increases** in small populations, resulting in inbreeding depression
- **Genetic rescue effect**; an increase in average population fitness as a result of the restoration of genetic diversity

- this is typically achieved by the deliberate introduction of individuals into a population suffering the ill effects of small population size, from a different population that harbors greater levels of allelic diversity

- **Linkage Corridors**; connects fragmented and isolated habitats, creating a single larger habitat, where the negative evolutionary effects of small population size will be less pronounced

5.6 Summary

- **Selection**
  - can shift both allele and genotype frequencies, and result in HW disequilibrium with either heterozygote deficits, or excesses
- **Mutation**
  - a weak evolutionary mechanism in terms of the magnitude of allele frequency changes, but it provides the raw material for evolution
  - it does not change HW equilibrium
- **Migration**
  - when source and recipient populations differ in alelle frequencies, migration can cause the recipient population to evolve
  - it can cause HW disequilibrium with heterozygote deficits or excesses
  - it tends to homogenize allele frequencies among populations
- **Genetic Drift**
  - random evolution that occurs due to sampling error in the gamete phase of the life cycle
  - it can change allele frequencies and genotype frequencies from one generation to the next, but not in a way that causes HW disequilibrium
  - it is most powerful when population size is small, and results in the divergence of populations
- **Non-random mating**
  - does not change alelle frequencies on its own
  - does change genotype frequencies and creates HW disequilibrium with heterozygote deficits or excesses, depending on the type

6 Phylogeny

- **Learning Outcomes**
  - understand the basic properties of phylogenetic trees
  - understand how phylogenetic trees are constructed
  - understand homoplasy and how it can arise
  - interpret phylogenies and apply them to evolutionary questions

6.1 Introduction to Phylogeny

- **phylogeny**; is a hypothesis of ancestor descendant relationships
- **phylogenetic tree**; is a graphical summary of a phylogeny
- **phylogenetics**; is the study of ancestor descentdent relationships. The objective of phylogeneticists is to construct phylogenies
- all life forms are related by common ancestry and descent
- construction of phylogenies provides explanations of the diversity seen in the natural world
- phylogenies can be based on morphological data, physiological data, molecular data, or all three
- a group that includes **all** of the descendants of a common ancestor is a monophyletic group or **clade**
- a non-monophyletic group is any case that does not satisfy the above, such as:
  - **paraphyletic**; a group that includes some, but not all of the descendants of a common ancestor
  - **polyphyletic**; assemblages of taxa that have been erroneously grouped together on the basis of homoplasious characters
- the principle objective of phylogenetic analysis and reconstruction is to identify groups of organisms that are monophyletic
- monophyletic groups represent organisms with a shared evolutionary history, and form the basis of modern taxonomic classification

6.2 DNA Sequences and Distance Measures

- DNA sequences are most commonly used to assess phylogenetic relationships
- **Distance Measures: Models of DNA Sequence Change**
  - must align sequences such that **homologous positions** are adjacent to each other, and then estimate the number of base pair differences between each pair of sequences
- **Nucleotide Sequence Divergence(d)**
  - the proportion of nucleotide differences between 2 sequences
  - the proportion is equal to the number of differences over sequence length and it is often expressed as a percentage
  - d = $\frac{number of differences}{sequence length}$
  - this is called the **p-distance, or proportion of differences**
    * p-distance does not account for the evolutionary process of sequence divergence
    * does not consider how the number of differences arose
- **Multiple Hits and Models of Sequence Change**
  - to develop more accurate measures of sequence differences(distances), and to more accurately estimate phylogenetic relationships, we must account for multiple substitutions at sequence positions, more frequently referred to as **multiple hits**

6.3 Phylogenetics I

- **Clustering Methods**
  - simplest way of constructing phylogenies using DNA sequences
  - they first require that we use a model of sequence evolution to estimate the distances between all of the taxa or species that we are studying
  - clustering methods utilize a matrix of **pairwise** distances or similarity values between all possible pairs of taxa, sequences, populations, or whatever it is we are studying
  - this matrix is used in conjunction with a clustering algorithm to produce a bifurcating tree, called a **phenogram**
- **Neighbour-Joining(clustering) Algorithm**
  - **advantage**; is a very fast algorithm
  - **disadvantages**; the major disadvantage is that it produces a **single tree** based on a distance matrix, out of **many possible trees**. It offers **no** evaluation of these other possible trees, but it performs quite well

6.4 Phylogenetic Characters, Homology and Homoplasy

- **Phylogenetic Characters**
  - a character is any atrribute of an organism that can provide us with insights into history(shared ancestry)
  - in molecular phylogenies, characters are typically nucleotide positions in a gene sequence, and each position can possess four **character states**:
    - A
    - C
    - G
    - or T
  - a character state that is shared between two DNA sequences or taxa may be so because they inherited it from a common ancestor, or it is **homologous**(a homology/synapomorphy)
  - alternatively, the shared character might occur because they were evolved independently, in which case they are called a **homoplasy**
  - parallel evolution, convergent evolution and reversals are forms of homoplasy that can result in erroneous phylogenetic groupings, or **polyphyletic groups**
  - as a result, homoplasious characters are the arch enemy of phylogenetic reconstruction

6.5 Phylogenetic Methods II

- optimality criteria are more sophisticated methods of phylogenetic reconstruction, and can be of two types:
  - frequency probability methods (maximum likelihood and Bayesian methods)
  - parsimony (also called cladistics)
- **plesiomorphy**; refers to the ancestral character state
- **apomorphy**; a character state different than the ancestral state, or **derived state**
- **synapomorphy**; a derived character state(apomorphy) that is **shared** by two or more taxa due to inheritance from a common ancestor: these characters states are phylogenetically informative using the parsimony or cladistic criterion
- **autapomorphy**; a uniquely derived character state

6.6 Parsimony/Cladistics

- **The Principle of Parsimony** is a method of constructing phylogenetic trees and it operates on a very logical principle
- the more parsimonious option is simpler and has less steps
- when construct a phylogenetic tree using the principle of parsimony, we need that we refer to as an outgroup/ingroup of the taxa of interest
- **ingroup**; the group of organisms for which we wish to develop an understanding of relationships
- **outgroup**; taxon or organisms which is **not** part of the ingroup but also **not** too distantly related to our ingroup organisms
- the outgroup is used to polarize or infer the direction of character change
- the character state possessed by the outgroup is defined as being **ancestral or pleisiomorphic a priori**

7 Adaptation

- **Learning Outcomes**
  - apply the evolutionary forces discussed in natural selection and population genetics to adaptation
  - understand, differentiate, and apply the three approaches that evolutionary biologists use to study adaptation
  - understand and differentiate the factors that hinder adaptation
  - interpret phylogenies and apply them to evolutionary questions

7.1 Studying Adaptation

- an adaptation is a trait that increases the fitness of an individual in comparison to individuals that don't posses the trait
- must proven through hypothesis testing that a trait is considered **adaptive**

7.2 The Approaches to Studying Adaptation

- **Things to Keep in Mind When Studying Adaptations**
  1. differences among populations are not always adaptations
     - eg) differences in DNA sequences among different populations may be neutral differences which have been fixed by genetic drift
  2. not every trait an organism possesses is adaptive
     - eg) vestigial structures
  3. not every adaptation is perfect
     - eg) mosquitofish male gonopodium
- **Methods to Study Adaptation in Evolutionary Biology**
  1. experimental studies
     - the most powerful
     - carefully control conditions so we can investigate a single effect and learn about what potentially could cause it

2. observational studies
   - when experimental studies are not possible
   - leads us into important insights
3. comparative studies
4. require an understanding of the phylogeny among the organisms being considered

7.3 Phenotypic Plasticity and Adaptation

- phenotypes arise as a consequence of genotypes and their interations with the environment
- identical genotypes can result in different phenotypes in different environments, which is referred to as **phenotypic plasticity**
- some studies have indicated that plasticity itself is an adaptive trait

7.4 What can Hinder Adaptation?

- natural selection is the primary agent of adaptive evolution, with mutation providing the raw material for it to act on
- two other evolutionary mechanisms can both either help or hinder natural selection in the adaptive process:
  1. genetic drift(and other types of sampling error such as population bottlenecks)
  2. migration
- when population size is small, genetic drift can be powerful and fix deleterious alleles that selection is acting to remove
- genetic drift is entirely random and unpredictable, and could also potentially work alongside selection and aid the fixation of a beneficial allele.
- migration is another force that can either aid or hinder adaptation
- two additional factors that can hinder adaptation are:
  - **trade-off**; a compromise between one trait and another, which cannot be avoided
  - **constraint**; a factor that tends to retard the rate of adaptive evolution, or prevent a population from optimizing a trait
  - we will be focusing on three types of constraints:
    1. functional/developmental constraints
    2. genetic constraints
    3. ecological constraints

7.5 Summary

- the study of adaptation is an important component of evolutionary biology
- requires the development and testing of hypotheses
- requires proper study designs which can be, experimental, observational, or comparative65

8 Evolution and Sexual Reproduction

- **Learning Outcomes**
  - know the major forms of asexual reproduction
  - understand the difference between asexual reproduction(parthenogenesis) and hermaphrodism
  - characterize the two-fold cost of sex and its implications
  - know the effects of outcrossing and recombination and their implications with respect to fitness
  - apply the principles of sex and selection to evolutionary arms races

8.1 Asexual Reproduction and the Two-Fold Cost of Sex

- existence and maintenance of sexual reproduction has been a paradox for evolutionary biology

8.2 The Effects of Sex

8.3 Recombination

- crossing over and recombination during gametogenesis is a very important component of sexual reproduction, and has two important effects:
  - it breaks down linkage disequilibrium
  - it increases genetic diversity in offspring by creating new combinations of alleles
- linkage disequilibrium constitutes a violation of Mendel's second law
- linkage disequilibrium can be defined as non-random associations between alleles at different loci
- it can arise when different loci are situated close together on the same chromosome, resulting in them being inherited as a single unit, instead of segregating independently
  - this will result in less genetic diversity in offspring
  - linkage disequilibrium can also be caused by selection, migration and genetic drift

8.4 Sex, Evolutionary Arms Races and the Red Queen Hypothesis

- consider host/parasite and predator/prey dynamics
  - in such systems, one participant will need to evolve to meet the challenge of a new innovation or defense that has evolved in the other
  - this can lock the participants in these types of dynamics in a perpetual evolutionary arms race, where both must continually evolve better means for coping with the other
- the idea that different sex is adaptive in such circumstances bec ause it provides new and/or different allelic combinations across loci is referred to as the Red Queen hypothesis

8.5 Summary

- the existence of sexual reproduction was once challenging for evolutionary biology to explain because of the numerical reproductive advantage offered by asexual reproduction (the two-fold cost of sex)
- genetic diversity produced by outcrossing and recombination offers the best defense against pathogens, parasites and changing environments
- vast majority of asexual species are evolutionarily very young, inferring that this form of reproduction is a ticket to extinction
- given that most mutations are deleterious, obligate asexuals are doomed to accumulate them, while outcrossing and recombination provides a means to purge them

9 Sexual Selection

- **Learning Outcomes**
  - apply the concept of fitness in the context of mating success
  - understand how asymmetries in reproductive potential fundamentally drive sexual selection
  - characterize the major forms of sexual selection
    * male competition
    * female choice
  - integrate viability selection and sexual selection in the context of antagonistic selection

9.1 Introduction to Sexual Selection

- Selective elements that contribute to a sexually reproducing organism's fitness include:
  1. mortality, or viability selection
  2. mating success or sexual selection
  3. family size of fecundity selection
- sexual selection can be defined as differential reproductive success resulting from different abilities to procure a mate
- **Terminology**
  - **sexual dimorphism**; refers to the phenotypic differences between males and females
  - **sexual selection**; differential reproductive success resulting from differential abilities to find a mate
  - **parental investment**; refers to the time, energy, and resources devoted to mating, gestating, and caring for offspring
    * parental investment is typically much greater for females
    * eggs are expensive, sperm are cheap
    * daily female egg production requires 3X the energy needed for daily basal metabolism
    * daily male sperm production requires 4/1000 of the energy needed for daily basal metabolism

9.2 Asymmetric Limits on Reproductive Potential

- usually(not always) females make a much greater parental investment than males, and as a result, their reproductive success is limited by the number of eggs that they can produce and rear
- in 90% of mammals, males provide no parental care for their offspring
- reproductive success in males is potentially enormous as they can essentially produce an infinite quantity of sperm
- as a result, male reproductive success is limited by the number of mates that they can obtain
- asymmetry in reproductive potential predicts that differences in mating behaviour exist between the two sexes:
  - males; usually be competitive(combat, sperm competition, infanticide, strong sexual selection)
  - females; usually be selective, or choosy(weak sexual selection)
- **Intrasexual Selection**; interactions between members of the same sex
- **Intersexual Selection**; interactions between members of opposite sexes

9.3 Sexual Selection on Males: Male-Male Competition

- **direct combat** is a common form of male-male competition for mates, and it often favours the evolution of weaponry, and large body size in males
- male-male competitions also comes in the form of **sperm competition** and **infanticide**
- in certain social structures, when a male take over another male of a pride, **infanticide** of the previous male's offspring typically follows
- when new males take over a group of females, pregnant females will often abort their fetus, rather than continue to invest in offspring that are doomed to infanticide
- **Bruce Effect**; pregnancy termination in the presence of unfamiliar males

9.4 Sexual Selection on Males: Female Choice

- in such instances, males will advertise for mates, and females will choose a male based on the quality of the **advertisement**
  - this can result in the evolution of elaborate calling, singing, and courtship displays, as well as embellished morphological features and extravagant colouration, such seen in the peacock
  - relationship between female display preference and male display
- may be responding to males as a result of a pre-existing sensory bias, which makes them susceptible to certain sensations that mimic cues in their environment
- females may exhibit a certain preference that may result in the acquisition of of resources
- in some species, males provide food, parental care, protection, and other benefits that help the female and her offspring
- females who distinguish between males that can provide high-quality resources from those that do not will garner a **fitness benefit**
- females being picky and choosy only to the highest quality males may get better genes for their offspring

9.5 Sexual Selection on Females

- males frequently mate with more than one female; this is referred to as **polygyny**
- sexual selection can also act on females; males can be choosy, and females can mate with more than one male, which is termed **polyandry**

9.6 Sexual Selection and Sexual Dimorphism in Humans

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9.7 Summary

- **sexual selection**; differences in contribution to the next generation as a consequence of differential abilities to procure a mate
  - arises as a direct result of asymmetries in **reproductive potential** between the sexes
- female choice can result in a **runaway selection**, which can culminate in male characteristics that are highly maladaptive when viewed through the lens of **viability selection**
- sexual selection and viability selection can often oppose each other
  - when this happens it is called **antagonistic selection**

10 A Brief Introduction to Kin Selection

- differentiate between four behaviours and their associated fitness effects
- understand the paradox of altruism in the context of selection
- apply **Hamilton's Rule**

10.1 Introduction to Behaviour and Hamilton's Rule

- in this section, we will introduce the fitness consequences of four different types of behaviours, and then focus on the evolution of altruism
- definitions:
  - **actor**; an individual carrying out an action(or behaviour)
  - **recipient**; an individual on the receiving end of the behaviour
  - **mutually beneficial**; a behaviour resulting in fitness benefits for both the actor and recipient
  - **selfish**; a behaviour resulting in a fitness benefit for the actor, but a fitness reduction for the recipient
  - **altruistic**; a behaviour resulting in a fitness benefit for the recipient, but a fitness reduction for the actor
  - **spite**; a behaviour resulting in fitness reductions for both the actor and recipient

10.2 Altruism

- also known as the **Paradox of Darwinism**
  - can selection favour traits(behaviours in this case) that increase survival and fitness of an actor's close relatives, even if there is decreased fitness for the actor carrying out the behaviour?
- the fitness of an individual can be divided into two components:
  - **direct fitness**
  - **indirect fitness**
- an individual's direct fitness and indirect fitness make up its total fitness, or **inclusive fitness**
- **direct fitness**; an individual's direct contribution to the next generation by reproduction(number of offspring contributed)
- **indirect fitness**; arises from additional reproduction by relatives that results from an actor's actions(eg) assistance)
  - it is additional reproduction that would not have been achieved without the assistance provided by the actor
- the selection for, and spread of alleles that increase **indirect fitness** is **kin selection**

10.3 Hamilton's Rule

- the coefficient of relatedness(r) gives the probability that an allele in the actor and an allele in the recipient at a given locus are **identical by descent** or arose by replication from the same ancestral copy of an allele
- **Hamilton's Rule**; an allele for altrustic behaviour will spread if (B x r) - C ¿ 0, where B is the benefit to the recipient, C is the cost to the actor, r is the coefficient of relatedness
- the costs and benefits are measured in terms of surviving offspring

10.4 Summary

- Hamilton's Rule explains many behavioural observations that have been difficult to explain in the past, including altruism, as well as spite
- Hamilton's Rule also shows that the adaptive value of spiteful behaviours will be highest when the cost to the actor is low, the damage to the recipient is high, and the value of r between the actor and recipient is low

11 Species Concepts and Speciation

- understand the advantages and limitations of the morphological, biological, and phylogenetic species concepts
- apply species concepts in the context of examples
- integrate evolutionary forces with the process of speciation
- differentiate between allopatric and sympatric speciation

11.1 Species Concepts

- we will consider three species concepts:
  - morphological
  - biological
  - phylogenetic
- defining "species" has, and continues to be controversial due to problems with the establishment of practical criteria for recognizing evolutionary independence
  - as a result, there are many species concepts

11.1.1 Typological or Morphological Species Concept

- **Type specimen**; a single individual (usually) that represents the entire species
- individuals are considered to belong to the same species if they look like or morphologically agree with the "**type**" of species
- however, many species show a continuum of morphological variations
- today, the "**type method**" is still used, but there is an attempt to select defining characters that have a genetic basis
- there are clearly written rules for naming and renaming taxa:
  - botanical code
  - zoological code
- **Problems**:
  - **Cryptic Species**; species that cannot be distinguished on the basis of their morphological characteristics
  - **Phenotypic Plasticity**; morphological variation that does not have a genetic basis; environmentally-induced morphological differences

11.1.2 Biological Species Concept

- species are groups of interbreeding natural populations that are reproductively isolated from other such groups
- individuals within a species resemble each other due to gene flow, resulting from **interbreeding**
- evolutionary criteria is **reproductive isolation** and **interbreeding**
- **Problems**:
  * **asexual taxa**; doesn't apply
  * **fossil taxa**; cannot be tested
  * **hybridization**; difficult to apply the biological species concept to taxa that hybridize
- commonly applied to natural populations but is a difficult test
- cannot be applied to "species" that hybridize freely or that reproduce asexually
- cannot be applied to extinct species

11.1.3 Phylogenetic Species Concept

- species consists of a population or group of populations that share a common evolutionary history over the course of time
- species are **monophyletic groups**
  * taxa that contain all of the known descendants of a single common ancestor
- populations must have been **evolutionarily independent** long enough to diagnostic traits to appear
- can be applied to both living and extinct species
- is applicable to species that reproduce asexually or sexually
- based on evolutionary independence
- can be applied without direct observation of species

11.2 Reproductive Isolation

- Reproductive Isolation can be broken down into two categories
  - Premating(prezygotic)
    * ecological isolation
    * behavioural isolation
    * mechanical isolation
  - Postmating(postzygotic)
    * zygotic, embryonic or larval mortality
    * hybrid inviability
    * hybrid sterility
- **Hybridization**:
  - can occur when recently diverged species come back into contact
- **Hybrid zones**:
  - geographic contact zone where interbreeding occurs and the frequency of hybrids can be high
- there are three major generalized outcomes of hybridization:

1. hybrids have lower fitness than parental linages; this will result in **reinforcement** and **character displacement**, and a short-lived hybrid zone
2. hybrids have equal fitness to parental species; the two lineages will interbreed and merge back into a single lineage (**introgressive hybridization**)
3. the hybrids have higher fitness than parental lineages; the hybrids can displace both parental species, or possibly form a new species

11.3 Isolating Mechanisms

- the process of speciation frequently begins with the physical isolation of populations, resulting in a cessation of gene flow between them
  - this is referred to as **allopatric divergence** and **speciation**
  - the **allopatric**, or physical separation of populations can result from two processes:
    * **dispersal**
    * **vicariance**
- allopatric divergence and speciation is the most common, but lineages can become isolated as a result of polyploidization events, and other chromosomal changes
- lineages can also be isolated in time, referred to as **temporal isolation**

11.4 The Process of Divergence

- once populations become allopatrically isolated, mutation, genetic drift, and selection drives their divergence
  - of these, selection(in concert with mutation) is the most important
- **sympatric speciation** is divergence and speciation that occurs in the absence of physical isolating barriers
  - process involves positive assortative mating and **disruptive selection**

11.5 Summary

12 Biogeography

- **Learning Objectives**
  - differentiate between dispersal and vicariance, and provide important examples of each
  - understand the impact of major vicariance events such as the uplifting of the **Panamanian Isthmus** and **Pleistocene glaciations** on population divergence and speciation
  - explain the latitudinal gradient in species diversity and **Rapoport's rule**
  - differentiate between allopatric and sympatric speciation

12.1 The Biogeographical Impact of a Major Geological Event

- **Biogeography** is the study of spatial(geographic) patterns of biodiversity, and is concerned with how and why organisms came to possess their geographic distributions
- biogeography has several different sub-disciplines including:
  - **zoogeography**; animal biogeography
  - **phytogeograph**; plant biogeography

  - **historical biogeography**; the reconstruction of the origin, dispersal and extinction of taxa, as well as entire biotas
  - **phylogeography**; the branch of biogeography that considers the principles and processes that control the geographic distributions of genetic lineages, particularly within species, and among very closely related species

- biogeographic patterns(the geographic distribution of organisms and genetic lineages) result from two processes

  - **dispersal**; the movement of organisms away from their point of origin
  - **vicariance**; the splitting of floras and faunas(or populations) as a result of the formation of a physical barrier

12.2 Biogeographic Patterns and Provinces

12.3 Summary

- Biogeographic patterns arise from dispersal and vicariance, and are frequently modulated by geological events such as the **Pleistocene Glaciations**, and the uplifting of the **Isthmus of Panama(and many others)**

  - provides us the important insights into the process of divergence and speciation

13 The History of Life

- **Learning Outcomes**

  - understand the case for a RNA-based origin of Life
  - describe the three stages in the **Oparin-Haldane model**
  - apply the principles of phylogeny covered in module 7 to the tree of life and last universal common ancestor
  - compare and contrast the **Ediacaran** and **Burgess Shale Faunas**
  - understand **Background Extinction** vs **Mass Extinction**
  - contrast the evolutionary patterns produced by **punctuated equilibrium** and **phyletic gradualism**

13.1 Origins of Life

- Life is that which possesses a genotype and a phenotype, and is capable of evolution by natural selection

- Earth's first life form, the **initial Darwinian ancestor, or IDA** is not the same as the common ancestor of all extant organisms, or **cenancestor** also known as the **last universal common ancestor(LUCA)**

- cenancestor was very likely a community of organisms that exchanged DNA, and had already been evolving for a long period of time, not a single organism

- **Panspermia Hypothesis**; life exists throughout the universe, distributed by space dust carrying unintended contamination by microorganisms

- Stanley Miller's(1953) experiment; stimulations of abiogenesis generated amino acids; capable of developing lifeforms through the **Oparin-Haldane Model**

13.2 The Last Universal Common Ancestor(or Cenancestor) and the Tree of Life

- poses two problems:
  - we need a gene possessed by all representatives of life that is not loaded with homoplasious characters
  - what do we use an outgroup?

13.3 Fossils and the Fossil Record

- the fossil record has three inherent biases:
  - geographic
  - taxonomic
  - temporal
- a geographic bias arises as a consequence of the fact that fossilization is more likely to occur in freshwater, marine or very wet terrestrial habitats
- a taxonomic bias is evident because certain types of organisms(those with hard chitinous, bone, or calcareous body parts) are more likely to fossilize than other, soft-bodied organisms
- the temporal bias stems from the fact that older fossils are more likely to have been lost by **plate subduction** and other geological processes than more recent fossils
- some major transitions include:
  - fish-tetrapod
  - dinosaur-bird
  - reptile-mammal

13.4 Extinction

- the vast majority of organisms that have inhabited the Earth are extinct
- human activity is currently driving an extinction to certain species
- extinction creates opportunity
  - eg) had the dinosaurs not gone extinct, mammals would have remained small, mouse and squirrel sized creatures
- there have been five mass extinction events since the **Cambrian Explosion** but we only have good understanding of the recent one, the **Cretaceous-Paleogene** or also known as **Cretaceous-Tertiary**

13.5 Punctuated Equilibrium vs Phyletic Gradualism

- Niles Eldredge and Stephen Jay Gould argued that much of evolution is characterized by rapid bursts of morphological change, followed by periods of stasis, with little or no morphological change
  - this is referred to as **punctuated equilibrium**
- the prevailing view at the time was that morphological evolution proceeds with slow , steady incremental change, or **phyletic gradualism**
- both ideologies had evidence to support both cases

13.6 Summary

- challenge of modelling the initial evolution of life itself