I. Overview: The Smallest Unit of Evolution

A. Smallest unit of evolution is the population.
   1. some traits become more common within the population, while other traits become less common, but the individual does not evolve

II. Population genetics provides a foundation for studying evolution:

A. microevolution: evolutionary change on the smallest scale
   1. change in the genetic makeup of a population from generation to generation
      i. Darwin did not describe or define evolution in this way
      ii. Darwin did not have an explanation for heritable variation required for a population
         a. it was suggested and later proven wrong that information from the parent was blended in the offspring
   2. Gregor Mendel proposed a hypothesis to explain this
      i. stated that parents pass on discrete heritable units (genes) that retain their identities in offspring

B. The Modern Synthesis: when Mendel’s work was rediscovered many scientists thought his theories were at odds with Darwin
   1. Darwin considered the raw material for natural selection to be “quantitative” characters- those characteristics in a population that vary along a continuum, such as fur length in mammals or the running speed of animals fleeing predators.
   2. Mendel worked with discrete “either/or” traits, so it was not obvious that there was a genetic basis to Darwin’s theory
      i. geneticists eventually determined that quantitative characters are influenced by multiple genetic loci and that the alleles at each of these loci follow Mendelian patterns of inheritance
   3. population genetics: the study of how populations change genetically over time
   4. modern synthesis: a comprehensive theory of evolution that integrated ideas from many other fields
      i. comes from population genetics
      ii. R. A. Fisher (statistician) demonstrated the rules by which Mendelain characters where inherited
         iii. J.B.S. Haldane (biologist) studied the rules of natural selection
   5. modern synthesis is still expanding to integrate genetic changes in populations caused by mechanisms other than natural selection

C. Gene Pools and Allele Frequencies:
   1. population: is a localized group of individuals that are capable of interbreeding and producing fertile offspring
      i. individuals near the population center are more likely to breed with members of their own population than other populations and thus on average are more closely related to one another than to members of other populations
   2. gene pool: the aggregate of genes in a population at any one time
      i. consists of all alleles at all gene loci in all individuals of the population
ii. if only one allele exists at a particular locus in a population, that allele is said to be fixed in the gene pool
   a. all individuals are said to be homozygous for that allele
   b. heterozygous individuals have two different alleles at a locus
   c. if there are two or more alleles for a particular locus in a population individuals may be either homozygous or heterozygous

3. each allele has a frequency(proportion) in the population
   i. when there are two alleles at a particular locus
      a. p is used to represent the frequency of one allele
      b. q is used to represent the frequency of the other allele
      c. the sum of the allele frequencies must equal 1(100%)
      d. loci with more than two alleles, the sum of allele frequencies must still equal 100%
   ii. example:
      a. population of 500 wildflowers with two alleles red (C\textsuperscript{R}C\textsuperscript{R}) and white(C\textsuperscript{W}C\textsuperscript{W}), heterozygous would be pink (C\textsuperscript{R}C\textsuperscript{W})
      b. sample population shows: 320 red, 160 pink, 20 white
      c. organisms are diploid, two alleles per gene, so in a population of 500 individuals there are 1000 copies of the gene
      d. CR allele account for 800(80%), for C\textsuperscript{R}C\textsuperscript{R} = 320 \times 2 = 640, and for C\textsuperscript{R}C\textsuperscript{W} = 160 \times 1 = 160, 160 + 640 = 800, 800/1000 = .8 or 80%
      e. p frequency = 80% or .8
      f. q frequency = 20% or .2

D. The Hardy-Weinberg Theorem: measures properties of gene pools that are not evolving(preserves genetic variation from one generation to the next in populations that are not evolving)(provides the opportunity for natural selection to act over many generations)
   1. states that the frequencies of alleles and genotypes in a population’s gene pool remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work

E. Preservation of Allele Frequencies:
   1. allele frequencies in all the gametes produced by the population will be the same as in the original population.
      i. provided that gametes are contributed to the next generation at random, allele frequencies will be unchanged

F. Hardy-Weinberg Equilibrium:
   1. if gamete donation from one generation to the next, and mating practices are random, populations , from one generation to the next will have the same allele frequency which can lead to prediction of the genotype frequency
   2. Hardy-Weinberg Equilibrium: populations are in a state of Hardy Weinberg equilibrium when they are in a state of genetic equilibrium
   3. using the rule of multiplication, frequencies of three possible genotypes(assuming random unions of sperm and ova) can be calculated
      i. the probability of one allele coming together (p \times p = p^2)
      ii. the probability of the other allele coming together (q \times q = q^2)
      iii. the probability of the heterozygote(which can arise in two different ways= 2pq)
      iv. summarized: p^2 + 2pq + q^2 = 1
4. If a population were in Hardy-Weinberg equilibrium and its members continued to mate randomly generation after generation, allele and genotype frequencies would remain constant.
   i. Population does not need to be in Hardy-Weinberg equilibrium for its allele frequencies to remain constant
   a. Self fertilization of pea plants

G. Conditions for Hardy-Weinberg Equilibrium: Departure from these conditions results in evolution—many populations appear to be in HW equilibrium because evolution is slow, but rarely are
   1. Extremely large population size: the smaller the population, the greater the role played by chance fluctuations in allele frequencies from one generation to the next (genetic drift)
   2. No gene flow. Gene flow, the transfer of alleles between populations, can alter allele frequencies
   3. No mutations: by introducing or removing genes from chromosomes or by changing one allele into another, mutations modify the gene pool
   4. Random mating: If individuals preferentially choose mates with certain genotypes, including close relatives (inbreeding), random mixing of gametes does not occur
   5. No natural selection: Differential survival and reproductive success of individuals carrying different genotypes will alter allele frequencies

H. PTC- the ability to taste PTC—bitter taste— is conveyed by a single gene that codes for a taste receptor on the tongue (PTC gene- TAS2R38)
   - PTC- phenylthiourea/ phenylthiocarbamide
   - Two common alleles (tasting/Non-tasting)- codes for a bitter taste receptor protein with a slightly different shape, shape determines how strongly it can bind to PTC—intensely bitter taste, slightly bitter taste or no bitter taste
   - There are five rare forms of the alleles

III. Chapter 23.2: Mutation and sexual recombination produce the variation that makes evolution possible.

A. Mutation: Changes in the nucleotide sequence of DNA.
   i. Cannot be predicted
   ii. Most occur in somatic cells and are lost when the individual dies
   iii. Mutations of the sex cells are the only ones passed to offspring
      a. Only a small percentage spread through the population
   1. Point mutations: Change of as little as a single base in a gene
      i. Sickle cell anemia
      ii. Most are harmless because large portion of the human genome does not code for proteins, and they also may not alter the amino acid composition for section of the genome that do code for proteins
      iii. Some have a significant impact on a phenotype
         a. Some non-coding regions of the DNA regulate expression of a gene, so a point mutation at this loci may have profound effects
         b. May, but very rarely will have a positive impact on the bearer
   2. Mutations that alter gene number or sequence:
      i. Gene duplication: Important source of variation
         a. Duplications of chromosome segments are nearly always harmful
         b. Smaller pieces are often introduced by transposable elements
1. Transposable elements are sections of DNA that can move from one location to another within a genome (color variation in Indian corn)
   c. if effects are not harmful they can persist and expand the genome providing new loci that may take on new functions by further mutations
2. New genes may be formed when shuffling of exons occurs
d. Example: human olfactory genes, about 1000
3. Mutation rates: low in animals and plants, about one in every 100,000 genes per generation
   i. Much higher in microorganisms
   ii. Can rapidly generate variation
   iii. Example: HIV, generation span of two days, RNA genome that has a much higher mutation rate than typical DNA

B. Sexual recombination: produce variations that make adaptations possible - rearranges alleles into fresh combinations every generation
   1. Most phenotypic variation is a result of sexual recombination (allele variation originates from past mutations)
   2. Populations have many possible mating combinations
   3. Shuffles alleles but does not change frequencies

C. Nonrandom and assertive mating: cause a shifting of different genotypes
   1. Nonrandom mating = inbreeding
   2. Assertive mating = establishing pair bonds on the basis of phenotypes

IV. Chapter 23.3: Natural selection, genetic drift, and gene flow can alter a population's genetic composition - there are three major factors that alter allele frequencies and cause most evolutionary change are: natural selection, genetic drift and gene flow.

   A. Natural selection: individuals within a population exhibit variations in their heritable traits, and those with variations that are better suited to their environment tend to produce more offspring than those with variations that are less well suited.
      1. Results in alleles being passed to the next generation in proportions different from their relative frequencies in the present generation
         i. White flowers more attractive to predators less chance of reproducing
         ii. Red flowers more attractive to pollinators, more chance of reproducing
         iii. Frequency of the white allele would decline

   B. Genetic drift: the smaller the sample size the greater chance of deviation from the predicted results - unpredictable fluctuations of allele frequencies from one generation to the next
      1. Indiscriminate events causing the loss of an allele from a small population
      2. Two types:
         i. Bottle neck effect: sudden change in the environment such as flood, fire, volcano, earthquake that causes a drastic reduction in the population size
            a. Survivor gene pool may not be a reflection of the original populations gene pool
            b. Over, or under representation of alleles
            c. Some alleles may be eliminated all together
            d. Has long term effect until population is large enough that chance fluctuations have less effect
            e. Human actions can create bottle neck effect for other species
               1. Elephant seals of California
2. wolves
3. polar bears
   ii. founders effect: new population being established from the isolation of a few individuals from a larger population
      a. gene pool may not reflect source population
      b. a few individuals colonize a new location
      c. pass through an isolated bottle neck
      d. may account for relatively high frequency of certain inherited disorders
      e. maybe when humans left Africa

C. gene flow: gaining or losing of alleles resulting from the movement of fertile individuals or gametes
   1. reduces differences between populations
   2. can amalgamate neighboring populations into a single population with a common gene pool if extensive enough
   3. important agent of evolutionary change in the human population do to ability to travel around the globe with ease

V. Chapter 23.4: Natural selection is the primary mechanism of adaptive evolution. (Connection: The 10,000 year explosion- Balanced Polymorphisms and the Heterozygote Advantage – pgs. 71-74)

A. Genetic Variation:
   1. variations that are heritable are the raw material for natural selection
   2. populations have extensive genetic variation that can only be observed at the molecular level
   3. not all phenotypic variation is heritable
      i. product of genotype and environmental influences
   4. the genetic component of variation can have evolutionary consequences as a result of natural selection

B. Variation Within a Population:
   1. discrete characters- are determined by a single gene locus with different alleles that produce distinct phenotypes
   2. quantitative characters- found in most heritable variation- vary along a continuum with a population – influence of two or more genes on a single phenotypic character
   3. polymorphism-
      i. individuals that differ in a discrete character are called morphs
      ii. phenotypic polymorphism- occurs when two or more distinct morphs are each represented in high enough frequencies to be really noticeable
      iii. genetic polymorphism- alleles at several loci influencing a trait
         a. example: height- does not have two or more separate and distinct morphs- it varies along a continuum
   4. measuring genetic variation: determining the amount of heterozygosity at both the level of the whole gene(gene variability) and the molecular level of DNA (nucleotide variability)
      i. average heterozygosity- measured as the average percent of these loci that are heterozygous
      ii. nucleotide variability is measured by comparing the nucleotide sequences of DNA samples from two individuals and then averaging the data from many such comparisons
iii. average heterozygosity tends to be greater than nucleotide variability because a gene can consist of thousands of bases of DNA - a difference at one of these bases is sufficient to make two alleles of that gene different and increase average heterozygosity
iv. nucleotide variability between humans is only 0.1% which encompasses the entire heritable component of the many different ways that people look

C. Variation Between Populations:
   1. geographic variation: differences between the gene pools of separate populations or population subgroups

D. A Closer Look at Natural Selection:
   1. Evolutionary Fitness:
   2. Directional, Disruptive, and Stabilizing Selection
      i. Directional selection: most extreme phenotype is most fit
         1. one allele becomes more common until fitness is reached (w (frequency/ relative fitness = 1)
         2. eliminates genetic variation over time
         3. examples: peppered moth, black bear size
      ii. Disruptive selection (Diversifying) intermediate has low fitness, two extreme phenotypes are most fit.
         1. not very common
         2. increases variance
      iii. Stabilizing selection: phenotypes, close to the mean are most fit
          (intermediate phenotypes.
          1. selects, maintains the mean value for the trait
          2. decreases genetic variation
          3. examples: birth weight in humans, clutch size in birds
      iv. Balancing Selection: type of stabilizing selection - maintains two different alleles of a gene
         1. heterozygous individuals have greater fitness than homozygous individuals - heterozygous advantage
         1. examples: sickle cell anemia
            a. in countries with out malaria: homozygous recessive (sickle cell anemia) are selected against - they rarely survive long enough to reproduce (directional selection against this allele)
            b. in countries with malaria- sickle cell allele has some resistance to malaria
               i. heterozygote becomes most fit (heterozygous advantage)
               ii. selection acts to balance and maintain both alleles

E. The Preservation of Genetic Variation:
   1. Diploidy:
      i. most eukaryotes are diploid
      ii. diploidy: genetic variation is hidden from selection in the form of recessive alleles
a. recessive alleles are propagated in the heterozygous individuals
b. recessive variation is exposed to natural selection when the individual is homozygous recessive

2. Balancing Selection: occurs when natural selection maintains stable frequencies of two or more phenotypic forms in a population- this is a state called balanced polymorphism
   i. this includes heterozygote advantage and frequency dependent selection
      a. Heterozygote Advantage: if individuals who are heterozygous at a particular gene locus have greater fitness than the homozygous, natural selection will tend to maintain two or more alleles at that locus-
         example: sickle cell anemia- the homozygous recessive will develop the disease, where as the heterozygous form will not develop the disease but will still be resistant to the severe effects of malaria
      b. Frequency-Dependent Selection: the fitness of any one morph declines if it becomes too common in the population
         aa. predators may recognize and target the more common prey decreasing its population

3. Neutral Variation: some variation has little or no impact on reproductive success
   i. pseudogenes: genes that have become inactivated by mutations, genetic “noise” is free to accumulate in all parts of the gene
   ii. relative frequencies of neutral variations are not affected by natural selection

F. Sexual Selection: natural selection for mating success
1. sexual dimorphism: marked differences between the sexes in secondary sexual characteristics, which are not directly associated with reproduction
   i. distinctions include differences in size, color and ornamentation.
   ii. in vertebrates, males are usually the showier sex
2. intrasexual selection: selection within the same sex is a direct competition among individuals of one sex for mates of the opposite sex
   i. most obvious in males
3. intersexual selection: (mate choice)- individuals of one sex(usually females) are choosy in selecting their mates from the other sex
   i. usually depends on the showiness of males
   ii. female only gains an advantage over other females if she chooses a mate that enables her to produce more fit offspring

G. The Evolutionary Enigma of Sexual Reproduction:
H. Why Natural Selection Cannot Fashion Perfect Organisms:
1. Evolution is limited by historical constraints:
2. Adaptations are often compromises:
3. Chance and natural selection interact:
4. Selection can edit only existing variations: