CHAPTER 20: GENES WITHIN POPULATIONS

CHAPTER SYNOPSIS

Variation in the genetic composition of living organisms is the driving force behind evolution as a whole. Darwin proposed that natural selection is the mechanism through which it occurs. As a population evolves it becomes better adapted to exist in it's local environment. His ideas contrast with Lamarck's who proposed a mechanism by which evolution occurred via inherited characteristics acquired over an organism's lifetime.

Population genetics explains the behavior of alleles within populations. Most alleles are highly polymorphic within a population and provide for greater variation than that caused by mutations alone. The Hardy-Weinberg equation was derived to explain why dominant alleles did not drive out recessive alleles and eliminate genetic variation. In large populations exhibiting random mating, the original proportions of a genotype remain constant over time. The genotypes of such populations are in equilibrium. The Hardy-Weinberg equation is a binomial expansion of the sum of the frequency of the recessive and dominant alleles. One can determine the frequency of one allele given the frequency of the other, as the sum of the two alleles must equal one. The number of heterozygote dominant individuals can also be calculated from such information.

Although the Hardy-Weinberg principle predicts consistency in allele frequencies over time, actual frequencies change as a result of (1) mutation, (2) gene flow, (3) nonrandom mating, (4) genetic drift, and (5) selection. The goal of selection is to have the individuals that are best suited to an environment leave the most progeny. Although the fate of any one individual cannot be determined, the long term fate of an entire population can be predicted using statistics. Several theories have been advanced to explain the evolutionary forces that maintain polymorphisms. Lewontin's adaptive selection theory suggests that selection is the sole important force. Kimura's neutral theory purports that a balance between mutation and genetic drift maintains polymorphisms. Selection acts only on phenotypes that interact with the environment and is complicated by interactions between genes. Elimination of undesirable traits is difficult because selection does not operate on rare recessive alleles. Natural selection can also maintain variation in a population through the existence of successful heterozygotes. An example of this principle is sickle-cell anemia and its association with malaria in Central Africa. Individuals with the heterozygous condition are more likely to survive and reproduce than either homozygote, one which succumbs to sickle-cell anemia and the other to malaria. Disruptive selection, directional selection, and stabilizing selection act to eliminate one or both extremes or to eliminate the intermediate from an array of phenotypes. Although all five forces cause genetic variation, only selection produces evolutionary change as only it depends on the nature of the environment.

CHAPTER OBJECTIVES

ä Know why natural selection is the correct mechanism to explain evolution.

ä Understand the importance of and sources of genetic variation.

ä Be able to solve various problems associated with Hardy-Weinberg equilibrium.

ä List the five factors that affect Hardy-Weinberg equilibrium and understand how each produces evolutionary change.

ä Compare and contrast the founder effect and the bottleneck effect.

ä Describe the neutral theory and compare it to the adaptive selection theory.

ä Understand what is meant by "the heterozygote advantage."

ä Describe and give examples of the three kinds of selection.

ä Understand the limitations of selection.

KEY TERMS

adaptation	electrophoresis	inbreeding
adaptive selection theory	fitness	inheritance of acquired characteristics
adaptive topography	frequency	natural selection
allele frequency	gene flow	outcrossing
artificial selection	genotype frequency	polymorphic
blending inheritance	genetic drift	population genetics
bottleneck effect	Hardy-Weinberg equilibrium	selection
directional selection	heterozygosity	stabilizing selection
disruptive selection	heterozygote advantage	

CHAPTER OUTLINE

20.0 Introduction

I. MOST ORGANISMS HAVE DIFFERENT GENETIC COMPOSITIONS

A. Genetic Variation Provides Raw Material for Selection

B. Genetic Variation Exists in Natural Populations fig 20.1

20.1 Genes vary in natural populations

I. GENE VARIATION IS THE RAW MATERIAL OF EVOLUTION

A. Evolution is Descent with Modification
1. Evolution explains how any entity changes over time
   a. Modern concepts refer to Darwin's *On the Origin of Species*
   b. His original phrase "descent with modification"
2. Clearly captures essence of biological evolution
   a. All species arise from other, pre-existing species
   b. Accumulate differences over time, ancestors and descendants not identical

B. Natural Selection is an Important Mechanism of Evolutionary Change
1. Darwin not first to propose theory of evolution
2. He uniquely proposed mechanism for evolution – natural selection
   a. Individuals with some inherited characteristics produce more offspring than others
   b. Population gradually includes more individuals with those characteristics
   c. Population evolves, becomes better adapted to local circumstances
3. Rival mechanism proposed by Lamarck
   a. Evolution occurred via inheritance of acquired characteristics
   b. Changes in body and behavior gained in life were passed onto offspring
4. Example: Giraffes
   a. Lamarck fig 20.2a
      1) Necks stretched as they feed on tree leaves
      2) Extension passed to subsequent generations
   b. Darwin fig 20.2b
      1) Variation not from experience of individuals

    2) Results from pre-existing genetic differences

5. Other processes can lead to change in population's genetic makeup
    a. Change in alleles frequency due to repeated mutations
    b. Introduction of new alleles from migrants
    c. Chance events cause random changes in small populations

II. GENE VARIATION IN NATURE

A. Evolution Results from Changes in a Population's Genetic Makeup
1. Modern theory of population genetics
2. Variation among individuals of a species is raw material for selection

B. Measuring Levels of Genetic Variation
1. Blood groups
    a. Over 30 blood group genes in humans, in addition to ABO
    b. 45 other variable genes encoding other proteins in blood and plasma
    c. More than 75 variable genes associated with blood system alone
2. Enzymes
    a. Measure variation in alternative alleles for enzymes via electrophoresis
    b. Great deal of variation at enzyme-specifying loci
    c. 5% of enzyme loci in humans are heterozygous
3. Almost all people are different from one another

C. Enzyme Polymorphism
1. Polymorphic loci have more variation than can be explained by mutation fig 20.3
    a. Modern study based on techniques like gel electrophoresis
    b. Insect and plants polymorphic at over half of loci
2. Heterozygosity: Probability that a randomly selected gene will be heterozygous
    a. About 15% in *Drosophila* and other invertebrates
    b. Between 5 and 8% in vertebrates
    c. Around 8% in outcrossing plants
3. High levels of genetic variation provide ample raw material for evolution

D. DNA Sequence Polymorphism
1. Gene technology enables examination of variation at level of DNA sequence
2. Example: Sequencing of ADH genes isolated from 11 *Drosophila* individuals
    a. Found 43 variable sites
    b. Only one was detected by electrophoresis
3. Abundant variation exists in coding regions and noncoding introns

20.2 Why do allele frequencies change in populations?

I. POPULATION GENETICS

A. Study of the Properties of Genes Within Populations

B. Genetic Variation Was a Puzzle Before the Discovery of Meiosis
1. Genetic variation in populations puzzled Darwin and contemporaries
2. Selection should always favor an optimal form
3. Blending inheritance widely accepted at that time
    a. Offspring would be phenotypically intermediate to parents
    b. Effects of new genetic variant quickly diluted
    c. Would disappear totally in later generations

II. THE HARDY-WEINBERG PRINCIPLE

A. Development of Principle
1. Persistence of variation solved independently by two researchers
2. Original proportions of genotypes in populations will remain constant
3. Requires meeting five assumptions
   a. Large population size
   b. Random mating occurs
   c. No mutation takes place
   d. No genes are introduced from other sources (no migration)
   e. No selection occurs
4. Dominant alleles do not replace recessive ones
5. Hardy-Weinberg equilibrium: Proportions of genotypes do not change
6. Frequency:
   a. Proportion of individuals falling in a category compared to total
   b. Specific case/total number of individuals
7. Example: Coat color in cats
   a. Initial counts: Black= 84; white= 16; total = 100 cats
      1) Frequency for black = 0.84 = 84%
      2) Frequency for white = 0.16 = 16%
      3) Frequency of B allele = p
      4) Frequency of b allele = q
      5) $p + q = 1$
   b. Assume that white cats are homozygous recessive, *bb*
   c. Black cats are therefore either BB or Bb
8. Mathematical basis: Binomial expansion of algebraic equation
   a. $(p + q)^2 = p^2 + 2pq + q^2$
      1) p^2 = individuals homozygous for B
      2) $2pq$ = individuals heterozygous, alleles B and b
      3) q^2 = individuals homozygous for b
   b. Calculate allele frequencies of each allele in population
      1) Frequency of bb: $q^2 = 0.16$
      2) Frequency of b: $q = 0.4$
      3) Since $1 = p + q$; frequency of B: $p = 0.6$
   c. Calculate genotype frequencies
      1) Frequency of BB: $p^2 = 0.6 \times 0.6 = 0.36$ (36 individuals out of 100)
      2) Frequency of Bb: $2pq = 2 \times 0.4 \times 0.6 = 0.48$ (48 individuals out of 100)

B. Using the Hardy-Weinberg Equation
1. Simple extension of Punnett square, alleles assigned frequencies p and q fig 20.4
   a. Trace genetic reassortment during sexual reproduction
   b. See how it affects frequencies of B and b genes in next generation
   c. Assume union of egg and sperm is random, all combinations of b and B equally likely
   d. Genetic reassortment during sexual reproduction
      1) Random mating, alleles b and B randomly mixed
      2) Individual chance to get B allele = 0.6
      3) Individual chance to get b allele = 0.4
   e. In next generation
      1) Chance for $BB = p^2 = 0.6 \times 0.6 = 0.36$ = 36% =36 individuals out of 100
      2) Chance for $bb = q^2 = 0.4 \times 0.4 = 0.16$ = 16% =16 individuals out of 100
      3) Chance for $Bb = 2pq = 2 \times 0.6 \times 0.4 = 0.48$ = 48% = 48 individuals out of 100
2. Example: Cystic fibrosis in North Americans of Caucasian descent
   a. Frequency of allele: 22 per 1000 = 0.022 = q
   b. Frequency of double recessive (affected) = 0.022 x 0.022 = 0.00048 = 1 per 2000

c. Frequency of dominant allele: $p = 1 - 0.022 = 0.978$
d. Frequency of carriers: $2pq = 2 \times 0.978 \times 0.022 = 0.043$ = 43 per 1000
3. Calculations are accurate for many genes
4. Some genes do not match predicted values

C. Why Do Allele Frequencies Change?
1. Hardy-Weinberg predicts consistency from generation to generation
a. Large, randomly mating population
b. No mutation, no gene flow, no selection
c. These stipulations are crux of Hardy-Weinberg principle
2. Individual allele frequencies do change
a. Some alleles more common
b. Other alleles decrease in frequency
3. Used as convenient baseline to measure changes
4. Identify many factors that affect proportion of homozygotes and heterozygotes
5. Five factors alter proportions enough to cause deviation from equilibrium tbl 20.1
a. Mutation
b. Gene flow (immigration into and emigration out of a population)
c. Nonrandom mating
d. Genetic drift (random loss of alleles, more likely in small population)
e. Selection
1) Only factor that produces evolutionary change
2) Only one dependent on nature of environment

III. FIVE AGENTS OF EVOLUTIONARY CHANGE

A. Mutation
1. Change from one allele to another
2. Alters proportion of alleles in population
a. Generally low rate
b. Rare for population to be stable enough to slowly accumulate mutations
c. Ultimate source of genetic variation making evolution possible
d. Likelihood of mutation occurring is not affected by natural selection

B. Gene Flow
1. Movement of alleles from one population to another
a. Powerful agent of change due to exchange of genetic material between populations
b. May be obvious as when an individual moves from one place to another
1) Characteristics of newcomer must differ from individuals already present
2) Newcomer must be adapted well enough to survive in new area
3) Newcomer must mate successfully for genetic composition to change
c. Includes subtle movements of drifting immature stages or gametes fig 20.5
2. May also result from mating with individuals of adjacent populations
3. Can alter genetic characteristics of population, doesn't maintain equilibrium
a. Even low levels homogenize allele frequency in populations
b. Prevent divergence

C. Nonrandom Mating
1. Mating of individuals with certain genotypes more common than expected
2. Inbreeding: Mating with relatives
a. Does not change frequency of alleles
b. Increases proportion of homozygote individuals
c. Self-fertilizing plant populations tend to be mostly homozygous individuals

3. Outcrossing: Mating with nonrelatives
   a. Plants breed with individuals other than self
   b. Have higher proportion of heterozygotes
4. Faults associated with inbreeding
   a. Promotes occurrence of double recessive alleles, with expression of that allele
   b. Increases likelihood of genetic disorders

D. Genetic Drift
1. Changes in allele frequency in small population caused by chance alone
   a. Appears to be random event as if frequencies drifted
   b. Small, isolated populations become very different fig 20.6
   c. Harmful alleles may increase in frequency, despite selective disadvantage
   d. Favorable alleles may be lost, despite selective advantage
   e. May be major factor in human evolution
2. Large populations can feel effect of genetic drift too
   a. If population was small in past, genetic drift acted then
   b. Example: Two alleles B and b in equilibrium ($p = q = 0.5$)
      1) Large population frequency expectations: $BB = bb = 0.25$
      2) Small sample produces next generation, large deviations occur by chance
      3) Assume four individuals produce next generation (2 BB, 2 Bb)
      4) New allele frequencies: $p = 0.75$, $q = 0.25$
      5) Repeat experiment 1000 times, 1 of 2 alleles absent in 8/1000 populations
3. Genetic drift leads to loss of alleles in isolated populations
4. Founder effects
   a. Few individuals begin new, isolated population
   b. Source population rare, allele may be significant in new population
   c. Important factor in oceanic island evolution
5. The bottleneck effect
   a. Populations greatly reduced in size, due to flood, drought, disease
   b. Surviving individuals represent random genetic sample of original population
   c. Resultant change in and loss of genetic variability
   d. Example: Northern elephant seal
      1) Hunted to near extinction, reduced to a single population
      2) Numbers now in tens of thousands, genetic variation very limited

E. Selection
1. Artificial selection: Breeder selects characteristics
2. Natural selection: Environment determines characteristics that confer more offspring
3. Must meet three conditions for natural selection to occur
   a. Variation must exist among individuals in a population
      1) Favors individuals with certain traits over others
      2) No variation = no selection
   b. Variation results in different numbers of offspring surviving in next generation
      1) Success due to certain phenotypes or behaviors
      2) Some individuals then produce more offspring, pass characteristics on
   c. Variation must be genetically inherited
      1) Selected differences must have genetic basis
      2) Some variation due to environment not genes
      3) Example: Turtle shell shape often due to moisture of soil
4. Natural selection and evolution are not the same
   a. Natural selection is a process
   b. Evolution is an outcome, not a process
   c. Processes other than natural selection can lead to evolution
   d. Natural selection can occur without causing evolutionary change

5. Selection to avoid predators
    a. Include many dramatic documented instances of adaptation
    b. Example: Larva of common sulphur butterfly
        1) Larvae exhibit color that enables them to blend in with leafy surroundings
        2) Alternate bright blue color kept at low frequency by bird predation
    c. Example: Shell markings of land snail
        1) Enable snail to blend into surroundings
        2) Avoid predation by camouflage
    d. Example: Animals inhabiting deserts with interspersed lava flows fig 20.7
        1) Black rocks of lava contrast with desert sand
        2) Populations of animals on rocks are dark in color
        3) Populations of animals in sand are lighter
        4) Predatory birds pick out individuals on contrasting backgrounds
6. Selection to match climatic conditions
    a. Natural studies examine genes encoding enzymes, consequences are easy to assess
    b. Enzyme allele frequencies often vary latitudinally (north/south) fig 20.8
        1) Allele more common in northern location
        2) Allele less common in southern location
    c. Example: Variation among mummichog fish *Fundulus heteroclitus*
        1) Gene produces enzyme lactase dehydrogenase
        2) Catalyzes conversion of pyruvate to lactate
        3) Enzymes formed by alleles function at different temperatures
        4) Northern form better catalyst at colder temperatures
        5) At low temperatures fish with northern allele swim faster, survive better
7. Selection for pesticide resistance fig 20.9
    a. Widespread use of pesticides led to rapid evolution of resistance in 400 insect pests
        1) Resistance allele at *pen* gene decreases uptake of insecticide
        2) *kdr* and *dld-r* genes decrease number of target sites, decrease binding ability
        3) Other alleles improve enzymes' ability to identify and detoxify insecticides
    b. Single gene Triazine resistance in pigweed plant *Amaranthus hybridus*
        1) Triazine inhibits photosynthesis, binds to protein in chloroplast membrane
        2) Single amino acid substitution decreases Triazine's ability to affect plant
    c. Norway rats have developed resistance to Warfarin
        1) Warfarin causes hemorrhaging by preventing blood clotting
        2) Single gene alters metabolic pathway, Warfarin ineffective

IV. IDENTIFYING THE EVOLUTIONARY FORCES MAINTAINING POLYMORPHISM

A. The Adaptive Selection Theory
1. What evolutionary force maintains polymorphism?
    a. Gene flow and nonrandom mating are not major influences in natural population
    b. Mutation, genetic drift or selection are most likely forces
2. Adaptive selection theory suggests selection is the force that maintains polymorphisms
    a. Lewontin proposed that natural populations are quite heterogeneous
    b. Selection pulls gene frequencies in different directions in different microhabitats
    c. Generates a condition in which many alleles persist

B. The Neutral Theory
1. Kimura suggests a balance between mutation and genetic drift maintains polymorphism
    a. Demonstrated by elegant mathematics
    b. Mutation rates need to be high to generate the variation
    c. Population size needs to be small to promote genetic drift
    d. Selection is not an acting force, differences between alleles are "neutral to selection"

2. Kimura's equation: $\overline{H} = 1/4N_e\mu + 1$
    a. $\overline{H}$ (mean heterozygosity): Likelihood that a random individual will be heterozygous at a randomly selected locus
    b. Value is influenced by population size (N_e) and mutation rate (μ)
    c. Level of polymorphism = very large number (N_e) x very small number (μ)
    d. Both values hard to measure with any precision
    e. Theory can thus account for almost any value of $\overline{H}$
    f. Difficult to prove or disprove, source of controversy

C. Testing the Neutral Theory
1. Difficult to chose between two theories
2. Both account equally well for most data on natural populations
3. Attempt to test neutral theory by examining large-scale patterns of polymorphism
4. Complications regarding population size
    a. Polymorphism ($\overline{H}$) should be proportional to effective population size N_e
    b. Assume mutation rate (μ) is constant
    c. $\overline{H}$ should be greater in insects (*Drosophila*) than humans
        1) When DNA sequence variation is measured, it is by sixfold
        2) When enzyme polymorphism examined, levels are similar
5. The nearly-neutral model
    a. Assume many variants are slightly deleterious, not strictly neutral to selection
    b. Helps explain patterns
    c. Little evidence that enzyme polymorphism is slightly deleterious
6. Detailed picture of DNA sequence variation is emerging
    a. Most nucleotide substitutions are disadvantageous and are eliminated
    b. Protein alleles not so clear, may be neutral or advantageous
7. Level of polymorphisms at enzyme-encoding genes may depend on both
    a. Adaptive selection theory: Action of selection on the gene
    b. Nearly-neutral theory: Population dynamics of the species
    c. Relative contribution varies from one gene to next
8. Control in natural populations
    a. Adaptive selection maintains some enzyme polymorphisms
    b. Genetic drift plays major role in variation at DNA level
    c. Most enzyme-level polymorphisms fit selection theory or nearly-neutral theory

D. Interactions Among Evolutionary Forces
1. Levels of variation determined by relative strength of different processes
2. Mutation rates versus natural selection
    a. If *B* mutates to *b* at high rate, *b* maintained even if selection strongly favors *B*
    b. Mutation rates in nature not usually high enough for this to occur
3. Genetic drift versus natural selection
    a. Both processes act to remove variation from a population
    b. Selection is deterministic, increases enhancing alleles
    c. Genetic drift is random, may also lead to decrease of enhancing allele
    d. In extreme case, allele could be removed from the population
    e. Natural selection expected to overwhelm drift, except in small populations

E. Gene Flow Versus Natural Selection
1. Gene flow is either constructive or constraining
    a. Increase adaptedness by spreading beneficial mutation between populations
    b. Can impede adaptation by importing inferior allele from other population
2. Example: Two populations, different environments, alleles *B* and *b*
    a. Opposite alleles favored in each population
    b. Without gene flow, *B* frequency would reach 100% in one, 0% in other

c. With gene flow, less favored allele continually reintroduced from other population
d. *B* and *b* balanced between flow of inferior gene in and its removal by selection
3. Example: Effects of metal ions on plants around mines in Great Britain fig 20.10
a. Metal ion concentration at mine sites greater than in surrounding areas
b. Metals generally toxic, certain plants have developed resistance
1) Plants with resistance grow better in contaminated soils
2) But grow slower in uncontaminated soils
c. Resistance gene found at intermediate levels
1) Pollen dispersed by wind, leads to substantial gene flow
2) Counters effects of natural selection
4. Extent of competition dependent on nature of individuals involved
a. Species with strong gene flow include birds and wind-pollinated plants
b. Frequency of less favored allele may be high
c. Species with low gene flow include sedentary species like salamanders
d. Favored allele frequency should approach 100%

V. HETEROZYGOTE ADVANTAGE

A. Natural Selection Can Also Act to Maintain Variation in a Population
1. Heterozygous advantage favors individuals with copies of both genes
2. Selection works to maintain copies of both alleles in a population

B. Sickle-Cell Anemia
1. Causes red blood cells to assume irregular, elongated shapes
2. Common among African Americans
a. Disorder affects 3 in 1000 individuals
b. Determine frequency with Hardy-Weinberg: $\sqrt{0.003} = 0.054$
c. Frequency in white Americans is only 0.001
3. Disease is often fatal
a. Recent therapies enable individuals to survive through childhood
b. Still 31% of affected individuals in U.S. die by age of 15
4. Disease affects shape of hemoglobin molecule
a. Nonpolar hydrophobic valine substituted for polar glutamic acid
b. Creates "sticky" patch on surface of hemoglobin
c. With oxygen, patch is shielded, no unusual interactions
d. Without oxygen, "sticky" patches bind to other patches
e. Molecules form long, fibrous clumps that deform blood cell fig 20.11
5. Individuals with sickle-cell trait are heterozygous or homozygous for *S*
a. Heterozygotes produce few sickle-shaped cells
b. Only half of the molecules have "sticky patches"
c. Cannot produce lengthy clumps, cells don't sickle

C. Malaria and Heterozygous Advantage
1. Frequency of *S* allele in Central African population = 0.12
a. 1 per 5 are heterozygous
b. 1 per 100 heterozygous are recessive and die before reproducing
c. Recessive homozygotes die before reaching reproductive age
2. Recessive allele maintained at unusually high levels
a. Heterozygotes less susceptible to malaria
b. Heterozygous women more fertile than homozygotes
3. Malaria parasite causes low oxygen tension in the infected cells
a. Such cells removed from bloodstream by spleen
b. Parasite is effectively removed from the bloodstream
c. Filtering process causes anemia in homozygote individuals

4. Environment acts to maintain allele frequency
   a. Maintenance of allele has adaptive value in Africa — fig 20.12
   b. No advantage to having resistance to malaria
   c. In nonmalarial areas selection acts to eliminate *S* allele
   d. Only 1 in 375 African Americans develop sickle-cell anemia

20.3 Selection can act on traits affected by many genes

I. FORMS OF SELECTION

A. Complex Interactions When Traits Are Affected by Many Genes
1. Many traits in nature affected by more than one gene
2. Example: Determining human height — fig 13.18
   a. Selection operates on all genes
   b. Strongest influence on genes making greatest contribution
   c. Changes to population depends on which genotypes are favored

B. Disruptive Selection — fig 20.13a
1. Eliminates intermediate type
2. Example: Beak sizes in seedcracker finch, *Pyronestes ostrinus*
   a. Population contains large and small beak sizes, few intermediates
   b. Seeds are of two categories, large or small
   c. Large-beaked birds eat tough-shelled large seeds
   d. Small-beaked birds adept at eating small seeds
   e. Selection acts to eliminate intermediates
      1) Unable to eat large seeds
      2) Inefficient at handling small seeds

C. Directional Selection
1. Eliminates one extreme from array of phenotypes — fig 20.13b
2. Decreases frequency of genes promoting extreme
3. Example: *Drosophila* behavior with light — fig 20.14
   a. Eliminate flies that move toward light
   b. Fewer of this allele found in population
   c. Population changed in favor of lower light attraction

D. Stabilizing Selection
1. Eliminates both extremes from array of phenotypes — fig 20.15
2. Indirectly increases frequency of intermediate, already the most common
3. Examples:
   a. Human infant birth weight: Intermediate has highest survival rate
   b. Duck/chicken egg weight: Intermediates have highest hatching success

E. Components of Fitness
1. Reproductive success is quantified as fitness
   a. Individuals with one phenotype leave more offspring than another allele
   b. Fitness = the number of offspring left in the next generation
   c. Natural selection characterized as survival of the fittest
   d. Differences in survival only one component of fitness
2. Selection may still operate if some individuals are more successful at attracting mates
   a. Important in territorial species
   b. Large males mate with many females, small males rarely mate

3. Number of offspring produced per mating is also important
   a. Large female fish and frogs lay more eggs than smaller ones
   b. May leave more offspring in next generation

II. LIMITS TO WHAT SELECTION CAN ACCOMPLISH

A. Limits of Selection
1. Alternative alleles may interact with other genes
   a. Example: Chicken clutch size
   b. Strong selection results in rapid change initially
   c. Change dies out as interactions between genes increase
2. Restrict maximums achieved by selective breeding

B. Evolution Requires Genetic Variation
1. Analysis of performance of thoroughbred horses fig 20.16
   a. 80% of stock today trace back to 31 individuals
   b. Despite intense directional selection, speed hasn't improved in 50 years
   c. Probably not due to depletion of genetic variation
   d. Difficult to devise alternative explanations
2. Phenotypic variation for trait may not have genetic basis
   a. Different number of ommatidia between left and right eyes of insects
   b. Cannot breed insects with consistently more on one side than other
   c. No separate genes for left and right eyes
   d. Number of ommatidia dependent on developmental processes fig 20.17

C. Selection Against Rare Alleles
1. Selection acts only on phenotype
2. Only expressed characteristic can affect ability to produce progeny
   a. Selection does not operate on rare recessive alleles
   b. Cannot select against recessive unless present as homozygotes fig 20.18
3. Selection against undesirable traits difficult unless heterozygotes detected
   a. If recessive allele *a* has frequency of $q = 0.2$
   b. Only 4 out of 100 (q^2)individuals will be double recessive
4. Effect is more dramatic if frequency of allele is lower
   a. If frequency of allele $q = 0.01$
   b. Frequency of homozygous recessives is 1 in 10,000
5. Selection against undesirable traits is difficult unless heterozygotes can be detected
   a. If undesirable trait *r* has frequency of $q = 0.01$, no homozygotes allowed to breed
   b. Would take 1000 generations (25,000 years) to lower frequency to 0.005
   c. Frequency still 1 in 40,000 (25% of initial value)

D. Selection in Laboratory Environments
1. Action of selection assessed by artificial selection in experiments
2. Develop strains that are genetically identical except for gene studied
3. Discounts potential for linkage disequilibrium
4. Example: Hartyl's crosses with bacteria 6-PGD enzyme
   a. All strains grew at same rate
   b. Different alleles were selectively neutral in a normal genetic background
   c. Under different conditions certain alleles were superior to others
   d. Selection operated on alleles, only under certain conditions

INSTRUCTIONAL STRATEGY

PRESENTATION ASSISTANCE:

It may prove necessary to review manipulation of fractions and other basic algebraic skills so that students can work with the Hardy-Weinberg equation. Prepare many practice problems if you intend to test heavily on that material. This isn't as necessary if your intent is to understand the basic concepts of Hardy-Weinberg without relying too heavily on the mathematics.

Discuss the rationale behind nonrandom mating. Certain physical traits are more "appealing" (*i.e.* long tails in many tropical species of birds) as are certain behaviors. One could extrapolate on this idea in terms of human appearance, body style, and dress and how it has varied over time and with society and social status.

Genetic drift is perhaps the most difficult factor affecting equilibrium to understand. Discuss the rapid radiation of life forms in newly opened territories and after mass extinctions.

VISUAL RESOURCES:

Photographs or actual samples of gels showing various polymorphisms are helpful to explain the concept. Photos or drawings of various morphological polymorphisms are additionally valuable.