

Study Guide for Exam 3 Fall 09. Evolution.

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Chapters 10. Drift

Define:

genetic drift – random allele fluctuations between two genes with the same fitness in which their outcome cannot be predicted but their probabilities can be calculated.

gene flow – transfer of genes from one population to another.

founder effect – when a population is started by a few (or one) member.

bottleneck effect – when a population experiences a major killing event or limitation in reproduction.

deme – small independent population

coalescence – tracing of an allele back to its origin in an ancestor.

What are effects of drift?—allele frequency **fluctuates** ; heterozygotes **decrease**, probability of fixation = **allele frequency**. Alleles are lost faster in **smaller** populations.

Explain table 10.1 in Drift ppt.

TABLE 10.1 Frequency of alleles at two loci relative to population size of house mice

Estimated population size	Number of populations sampled	Mean allele frequency		Variance of allele frequency ^a	
		<i>Es-3b</i>	<i>Hbb</i>	<i>Es-3b</i>	<i>Hbb</i>
Small (median = 10)	29	0.418	0.849	0.0506	0.1883
Large (median = 200)	13	0.372	0.843	0.0125	0.0083

Source: After Selander 1970.

^aNote that the variance of allele frequency is greater among small than among large populations.

Why does genetic drift and inbreeding tend to increase homozygosity in populations, and how can this be harmful? Inbreeding occurs more frequently in a small population and increases the likelihood that two rare genes will meet in an offspring. Homozygosity increases just like in diffusion in which concentration of a substance reaches equilibrium, so too are genes spreading outwards to the population until the concentration of genes is in equilibrium.

What two processes offset the loss of alleles and “march toward homozygosity” caused by genetic drift? Mutation & Gene Flow.

The Neutral Theory of Molecular Evolution proposes that most mutations are **neutral**, and that they occur at a **fixed** rate, so that they can provide a **molecular clock** to determine time of divergence from different species.

Evidence suggests that base substitutions occur more in the **3rd Base** of the codon than in the second-base, and the rate of base substitutions is higher in **Introns** than in coding regions of the gene, and highest in pseudogenes, and that highly important genes (ie. those that code for histones) evolve **slower** than less important genes. This is good evidence that most base substitutions are **neutral**.

What determines effective population size—why may it vary from actual size? Effective population size is the number of individuals in a population that contribute their genes via reproduction. Often measured by a simple count of all adults within the population, this is often inaccurate as not every adult will breed. Within humans the minimum viable population is 4,500 – 11,200.

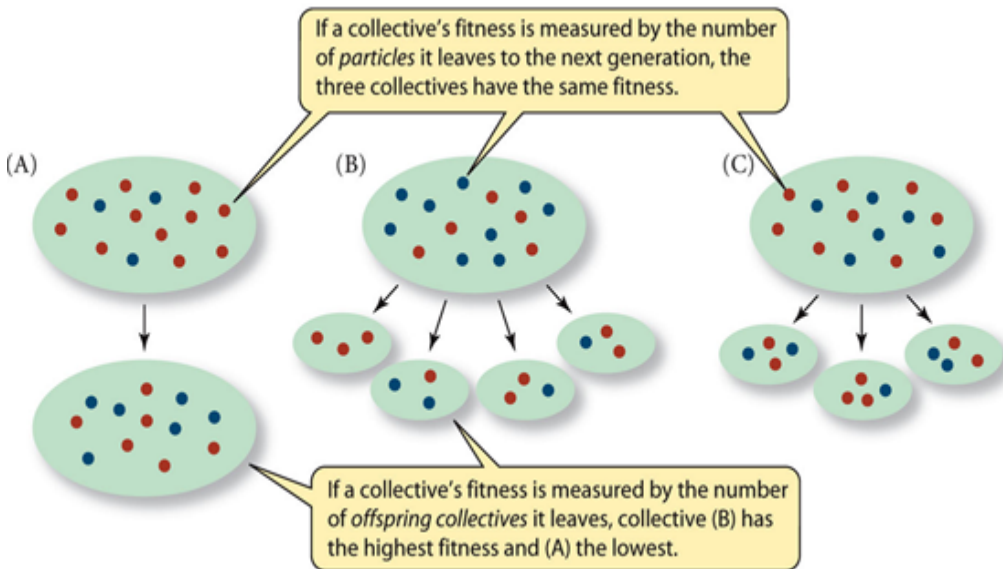
Studies of mitochondrial genes in women and the Y-chromosome in men suggest that all humans descend from an effective population of about **40,000** people living in Africa, about **100,000** years ago.

Chapter 11.

Define:

“natural selection” and under what conditions can it occur? Natural Selection is any consistent difference in fitness among phenotypically different classes of biological entities.

What is “fitness” or “reproductive success” and how can it be estimated in real populations?



Define and give examples of:

adaption - is where a feature lost its function in one way but found another use, an example is the penguins wing is no longer useful for flight but is useable in water.

Exaptation – is where a feature can be used for another purpose, such as the bird called the auk’s wing is suitable for air and water.

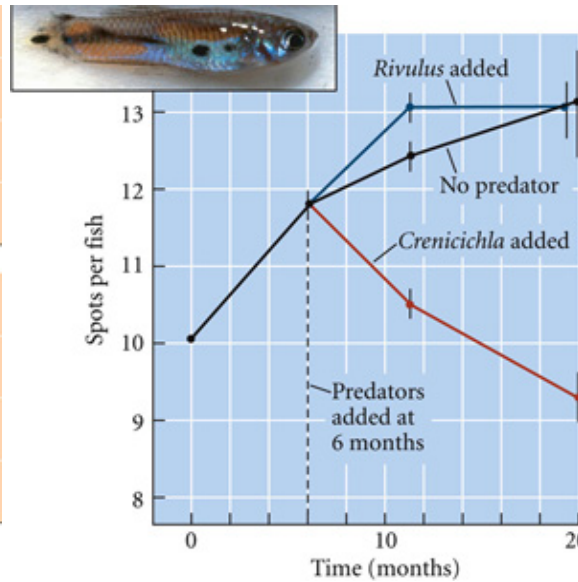
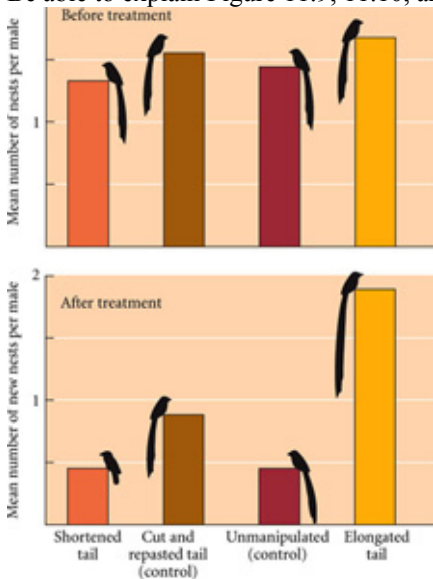
Distinguish:

group selection – Genes favoring the function of the group vs the individual.

kin selection – Genes favoring relatives vs the group, examples are altruism and selfishness.

species selection – A type of group selection in certain genes are transmitted into further generations and those without may go extinct.

Be able to explain Figure 11.9, 11.10, and 11.12.



Discuss: relationship of Natural Selection to:

necessity – a change in environment doesn’t necessitate the need for adaptation

perfection – adaptation does not produce perfection because we have not been selected for or against every conceivable trait.

progress – evolution isn’t always progressive or moving forward towards “better”.

harmony – the natural balance for example between prey and predator can’t be exclusively attributed to the predators self-control in the take of prey, but also attributable to the prey’s ability to persist.

morality – doesn’t relate to natural selection as it isn’t steered by anyone it simply is a process neither cruel nor kind.

Chapter 12.

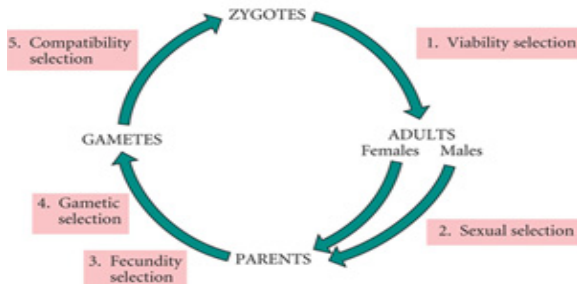
Distinguish the 3 types of selection and provide examples:

directional – pushes the selection towards an extreme (on bell curve) with the homozygote having advantage. An example is the peppered moth of England.

stabilizing – doesn't change the mean but may change the variance (of the bell curve) with heterozygote having advantage. An example is Sickle-Cell Anemia.

diversifying – shifts the mean (of the bell curve) producing asymmetry with the heterozygote having a disadvantage. An example is birds with medium sized beaks.

Contrast types of zygotic vs gametic selection.



Zygotic:

A. Viability. The probability of survival of the genotype through each of the ages at which reproduction can occur. After the age of last reproduction, the length of probability of survival does not usually affect the genotypes contribution to subsequent generations, and so does not usually affect fitness.

B. Mating success. The number of mates obtained by an individual. Mating success is a component of fitness if the number of mates affects the individual's number of progeny, as is often the case for males, but less often for females, all of whose eggs, may be fertilized by a single male. Variation in mating success is the basis of sexual selection.

C. Fecundity. The average number of viable offspring per female. In species with repeated reproduction, the contribution of each offspring to fitness depends on the age at which it is produced. The fertility of a mating may depend only on the maternal genotype (number of eggs or ova), or it may depend on the genotype of both mates (if they display some reproductive incompatibility).

Gametic:

D. Segregation advantage (meiotic drive or segregation distortion. An allele has an advantage if segregated into more than half the gametes of a heterozygote.

E. Gamete viability. Dependence of a gamete's viability on the allele it carries.

F. Fertilization success. An allele may affect the gamete's ability to fertilize an ovum (e.g. If there is variation in the rate at which a pollen tube grows down a style).

Heterozygote advantage is due to **stabilizing**-selection

Multiple niche polymorphisms are due to **diversifying**-selection

Anagenesis is due to **directional**-selection.

Describe changes in the peppered moth populations in England—is this a good example of natural selection? The peppered moth was mostly white with a few darker colored individuals present, after the industrial revolution in England the timber bark started darkening and the lighter colored peppered moth were heavily predated leaving a higher population of the darker colored peppered moth. This is a great example of natural selection.

Study 4 major points on page 304 and 9 summary statements on page 334.

- Natural Selection is not the same as evolution. Evolution is a two-step process: the origin of genetic variation by mutation or recombination, followed by changes in the frequencies of alleles and genotypes, caused chiefly by genetic drift or natural selection. Neither natural selection nor genetic drift accounts for the origin of variation.
- Natural selection is different from evolution by natural selection. In some instances, selection occurs- that is, in each generation, genotypes differ in survival or fecundity-yet the proportions of genotypes and alleles stay the same from one generation to another.
- Although natural selection may be said to exist whenever different phenotypes vary in average reproductive success, natural selection can have no evolutionary effect unless phenotypes differ in genotype. For instance, selection among genetically identical members of a clone, even though they differ in phenotype, can have no evolutionary consequences. Therefore, it is useful to describe the reproductive success, or fitness, of genotypes, even though genotypes differ in fitness only because of differences in phenotype.

- A feature cannot evolve by natural selection unless that feature affects reproduction or survival. The long-haired tail of a horse, used as a fly-switch, could not have evolved merely because it increases a horse's comfort; it must have resulted in increased reproductive success, perhaps by lowering mortality caused by fly-borne disease.

10 – Summary Points

1. Even at a single locus, the diverse genetic effects of natural selection cannot be summarized by the slogan “survival of the fittest.” Selection may indeed fix the fittest genotype, or it may maintain a population in a state of stable polymorphism, in which inferior genotypes may persist.
2. The absolute fitness of a genotype is measured by its rate of increase, the major components of which are survival, female and male mating success, and fecundity. In sexual species, differences among gametic (haploid) genotypes may also contribute to selection among alleles.
3. Rates of change in the frequencies of alleles and genotypes are determined by differences in their relative fitness, and are also affected by genotype frequencies and the degree of dominance at a locus.
4. Much of adaptive evolution by natural selection consists of replacement of previously prevalent genotypes by a superior homozygote (directional selection). However, genetic variation at a locus often persists in a stable equilibrium condition, owing to a balance between selection and recurrent mutation, between selection and gene flow, or because of any of several forms of balancing selection.
5. The kinds of balancing selection that maintain polymorphism include heterozygote advantage, inverse frequency-dependent selection, and variable selection arising from variation in the environment.
6. Often the final equilibrium state to which selection brings a population depends on its initial genetic constitution: there may be multiple possible outcomes, even under the same environmental conditions. This is especially likely if the genotypes' fitnesses depend on their frequencies, or if two homozygotes both have higher fitness than the heterozygote.
7. When genotypes differ in fitness, selection determines the outcome of evolution if the population is large; in a sufficiently small population, however, genetic drift is more powerful than selection. When the heterozygote is less fit than either homozygote, genetic drift is necessary to initiate a shift from one homozygous equilibrium state to the other.
8. Studies of variable loci in natural populations show that the strength of natural selection varies greatly, but that selection is often strong, and is thus a powerful force of evolution.
9. Variation in DNA sequences can provide evidence of natural selection. Compared with the level of variation expected under neutral mutation and genetic drift alone, positive selection (of an advantageous mutation) causes “selective sweeps” that reduce the level of neutral variation at closely linked sites. It can also create linkage disequilibrium among neutral variants in the region of the advantageous mutation. Purifying (background) selection against deleterious mutations also reduced linked neutral variation. Balancing selection results in higher levels of linked variation than under the neutral theory. Studies of DNA sequence variation in humans and other species have provided evidence of extensive recent directional selection.
10. Selection can also be inferred from DNA sequence comparisons among different species, as indicated by the incidence of nonsynonymous versus synonymous nucleotide substitutions.

Chapter 15. Sexual selection

Define:

Syngamy - union of two gametes to form a zygote.

Dioecious – dual sexed (m & f)

Monoecious – single sexed (m or f)

vegetative reproduction – a form of asexual reproduction in which daughter is the same as parent.

Parthenogenesis – formed from a single egg (unfertilized).

What is the paradox of sex?

Sexual reproduction vs asexual reproduction, both offer benefits.

Table 15.1, be able to discuss 3 examples.

Table 15.1 Mechanisms of competition for mates and characters likely to be favored

<i>Mechanism</i>	<i>Characters favored</i>
Same-sex contests	Traits improving success in confrontation (e.g., large size, strength, weapons, threat signals); avoidance of contests with superior rivals
Mate preference by opposite sex	Attractive and stimulatory features; offering of food, territory, or other resources that improve mate's reproductive success
Scrambles	Early search and rapid location of mates; well-developed sensory and locomotory organs
Endurance rivalry	Ability to remain reproductively active during much of season
Sperm competition	Ability to displace rival sperm; production of abundant sperm; mate guarding or other ways of preventing rivals from copulating with mate
Coercion	Adaptations for forced copulation and other coercive behavior
Infanticide	Similar traits as for same-sex contests
Antagonistic coevolution	Ability to counteract the other sex's resistance to mating (by, e.g., hyperstimulation); egg's resistance to sperm entry

Mate Preference by Opposite Sex – (Duck – females initiate courtship; seahorse – males carry young)

Examples of male contests, sperm contests, and sexual selection of mate.

Male Contests – Horns in a variety of animals

Sperm Contests – Damselfly with penis that is barbed to remove sperm packet from females body

Sexual selection of a mate – Male tiger moth provides alkaloids to female during mating; male cricket gives 'nuptial' gift to female cricket of spermatophore to eat.

PP. 409-410, 11 statements.

1. Alleles that increase mutation rates are generally selected against because they are associated with the deleterious mutations they cause. Therefore, we would expect mutation rates to evolve to the minimal achievable level, even if this should reduce genetic variation and increase the possibility of a species' extinction.
2. Asexual populations have a high extinction rate, so sex has a group-level advantage in the long term. But this is unlikely to offset the short-term advantage of asexual reproduction.
3. In a constant environment, alleles that decrease the recombination rate are advantageous because they lower the proportion of offspring with unfit recombinant genotypes. In addition, asexual reproduction has approximately a twofold advantage over sexual reproduction because only half of the offspring of sexuals (i.e., the females) contribute to population growth, whereas all of the (all-female) offspring of asexuals do so. Therefore, the prevalence of recombination and sex requires explanation.
4. Among the several hypotheses for the short-term advantage of sex are: (a) in asexual populations, fitness declines because genotypes with few deleterious mutations, if lost by genetic drift, cannot be reconstituted, as they are in populations with recombination (Muller's ratchet); (b) deleterious mutations can be more effectively purged by natural selection in sexual than in asexual populations, thus maintaining higher mean fitness; (c) recombination enables the mean of a polygenic character to evolve to new, changing optima in a fluctuating environment; (d) the rate of adaptation, by fixing combinations of advantageous mutations, may be higher in sexual than asexual populations, if the populations are large.
5. In large, randomly mating populations, a 1:1 sex ratio is an evolutionarily stable strategy, because if the population sex ratio deviates from 1:1, a genotype that produces a greater proportion of the minority sex has higher fitness. If, however, populations are characteristically subdivided into small local groups whose offspring then colonize patches of habitat anew, a female-biased sex ratio can evolve because female-biased groups contribute a greater proportion of offspring to the population as a whole.
6. The evolution of hermaphroditism versus dioecy (separate sexes) depends on how reproductive success via female or male function is related to the allocation of an individual's energy or resources. Dioecy is advantageous if the reproductive "payoff" from one or the other sexual function increases disproportionately with allocation to that function.
7. Outcrossing can be advantageous because it prevents inbreeding depression in an individual's progeny. Conversely, self-fertilization may evolve if fewer resources need to be expended on reproduction, if an allele for selfing becomes associated with advantageous homozygous genotypes, or if selfing ensures reproduction despite low population density or scarcity of pollinators.
8. Differences between the sexes in the size and number of gametes give rise to conflicts of reproductive interest and to sexual selection, in which individuals of one sex compete for mates (or for opportunities to fertilize eggs). The several forms of sexual selection include direct competition between males, or between their sperm, and female choice among male phenotypes.

9. Females may prefer certain male phenotypes because of sensory bias, direct contributions of the male to the fitness of the female or her offspring, or indirect contributions to female or offspring fitness. Indirect benefits may include fathering offspring that are genetically superior with respect to mating success (“runaway sexual selection”) or with respect to components of viability (“good genes models”). Sexually selected male features may also evolve by antagonistic coevolution: selection on females to resist mating, and on males to overcome female resistance with irresistible stimuli.
10. The evolution of reproductive effort by males is governed by similar principles as in females. Delayed maturation may evolve if larger males are more successful in attracting or competing for mates. Similar principles explain phenomena such as sequential hermaphroditism (sex change with age) and alternative mating strategies.
11. The evolution of features of genetic systems, such as rates of mutation and recombination, sexual versus asexual reproduction, and rates of inbreeding, can usually be understood best as consequences of selection at the level of genes and individual organisms, rather than group selection.

Chapter 3.

Define and give examples—

paedomorphosis vs peramorphosis, Paedomorphosis is the possession of juvenile characters in an adult, whereas peramorphosis is the delayed maturity while the development of the adult is extended.

allometry vs heterotopy – Allometry involves size and shape such as the bones of limbs (similarity), whereas heterometry involves the number of structures for example the diminishment of the number of bones in the skull in mammals.

individualization vs heterochrony – Individualization is the process by which a structure changes such as teeth in reptiles vs. humans. Heterochrony is the timing of development for example the differences in chimpanzee and human brain development are very similar for a period of time, then humans continue developing as the chimpanzees brain stops.

homoplasy (evolutionary reversal vs convergent vs parallel evolution) – Evolutionary reversal is where a character reverts back to a less derived form, whereas convergent is where a similar structure forms via a different pathway, and in parallel evolution a similar character evolved in two separate species from the same pathway independently.

evolutionary trend vs adaptive radiation, Evolutionary trends often are unidirectional, whereas adaptive radiation is more omnidirectional.

What are patterns of selection at gene level? 1) size of **genome**; 2) number of functional **genes**; and **comparison** of whole genome or groups of genes.

Explain major evidences of evolution and give examples (Box 3A page 50)—

hierarchical organization of life – example Linnaeus hierarchical system of organization

homology – similarity of structures despite differences in function, example is hand of human in comparison to a bats wing.

Embryology – similarity in embryologic development, for example tooth development in an anteater that is later discarded.

vestigial features – retention of potentially useless structures such as coccyx in humans.

Convergence – similar function yet yet remarkably different in structure (example cephalopod’s eye).

suboptimal design – poorly designed systems such as the pharynx for food and air creating potential for choking.

geographic distributions – location of species such as marsupials showing a common ancestor on another continent.

intermediate forms. – fossil records showing “in-between” species showing successive changes.

Chapt 6. Evol Biog

Define:

Biogeography – location and distribution of species

Endemic – a restricted local population

Cosmopolitan – found in many places

Disjunct – separation of populations

Vicariance – separation of organisms by a geographic barrier.

Fundamental vs realized niche – Fundamental niche is where the species could exist, whereas realized niche is where it is actually found.

historical vs ecological factors – historical factors are those which could not be explained by ecological factors such as whether a species may not have been able to get to certain regions, or that a species could have been excluded by a competitor.

What were Darwin’s observations about islands (the fill in the blank slide in ppt)

- 1.) Islands are inhabited by kinds of organisms with capability to reach the islands.
- 2.) Many island animals were brought there by humans.
- 3.) Most island species are related to nearby mainland species.
- 4.) Islands that are difficult to reach have more endemics
- 5.) Island species bear ancestral structures not needed on islands.

What are animal-based biogeographic regions of the Americas? What are plant-based regions of the Americas? 3 main ecoregions in KY? Regions based on animal populations. Regions based on plant populations. The Appalachian Plateau, Interior Low Plateaus, and the Mississippi Embayment.

center of origin

dispersal types— Range and Jump, Range involves an extension of an existing range, whereas Jump involves moving across a barrier.

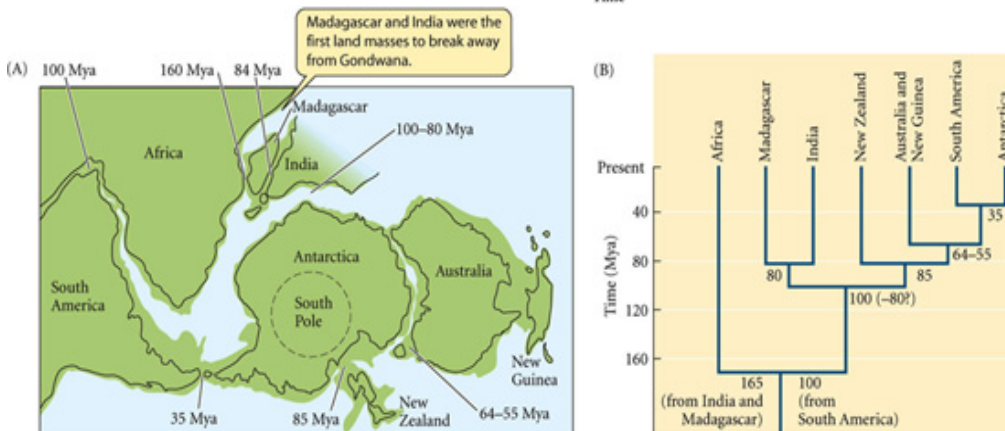
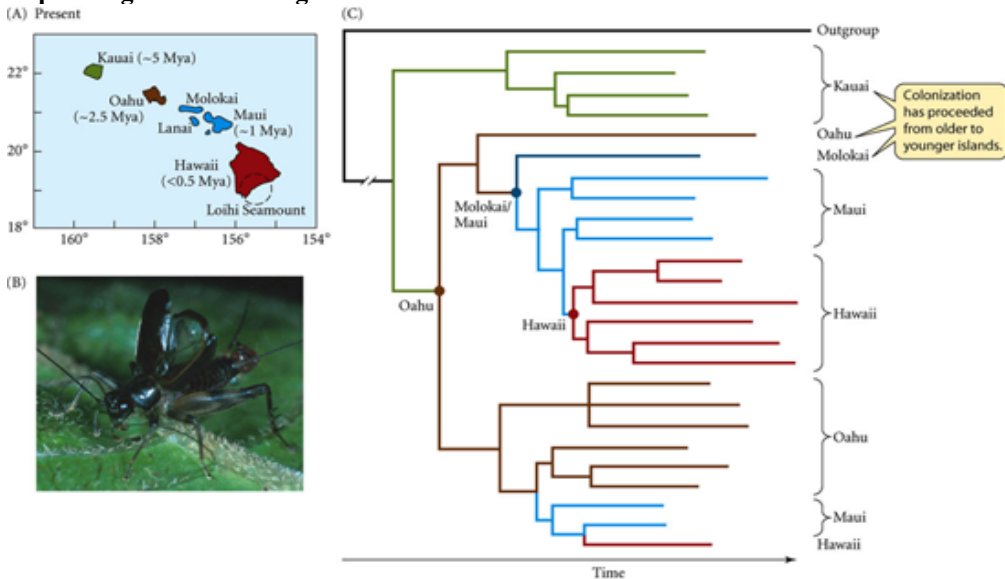
corridors – joined together via landmass such as Texas and and Georgia.

filter bridges – A bridge of land which connects two areas such as the Bearing Strait.

Sweepstakes – Routes are hazardous or accidental dispersal mechanism by which animals move from place to place, in which luck plays a part.

what are major mechanisms of dispersal – Range and Jump dispersal. Range is when one extends the existing range for the species, whereas Jump dispersal is when a species moves beyond a barrier.

Explain significance of Figures 6.10 and 6.11—Hawaiian crickets—is there a creationist explanation?



South America broke from Africa about **100** million years ago, and Madagascar/India broke away about **150** million years ago.

P. 158 summary statements.

1. The geographic distributions of organisms provided Darwin and Wallace with some of their strongest evidence for the reality of evolution.
2. Biogeography, the study of organisms' geographic distributions, has both historical and ecological components. Certain distributions are the consequence of long-term evolutionary history; others are the result of contemporary ecological factors.
3. The historical processes that affect the distribution of a higher taxon include extinction, dispersal, and vicariance (fragmentation of a continuous distribution by the emergence of a barrier). These processes may be affected or accompanied by environmental change, adaptation, and speciation.
4. Histories of dispersal or vicariance can often be inferred from phylogenetic data. When a pattern of phylogenetic relationships among species in different areas is repeated for many taxa, a common history of vicariance is likely.

5. Disjunct distributions are attributable in some instances to vicariance and in others to dispersal.
6. Genetic patterns within species, especially phylogenetic relationships among genes that characterize different geographic populations, can provide information on historical changes in a species' distribution. Studies of this kind are illuminating the origin and spread of human populations.
7. The local distribution of species is affected by ecological factors, including both abiotic aspects of the environment and biotic features such as competitors and predators. Why species do not enlarge their range indefinitely, by incrementally adapting to conditions farther and farther away, is a major question in evolutionary ecology.
8. In some cases, sets of species have independently evolved to partition resources in similar ways, suggesting that competition may limit species diversity and may result in different communities with a similar structure. However, convergence of community structure is usually incomplete, suggesting that evolutionary history has had an important impact on ecological assemblages.
9. Geographic patterns in the number and diversity of species may stem partly from current ecological factors, but they probably cannot be understood without recourse to long-term evolutionary history.

Chapter 17. Species

Define concepts:

cladogenesis vs anagenesis – Cladogenesis is the branching of lineages during phylogeny, whereas anagenesis is the evolution of a feature within a lineage over time. Cladogenesis branches $A \rightarrow B$ and C , Anagenesis is $A \rightarrow B$

Biological vs morphological vs phylogenetic species; Biological species are species that can be interbred, morphological species are ones that one can distinguish by shape, and phylogenetic species are identified by their phylogenetic history.

species vs subspecies vs ecotype – an ecotype is used mostly in botany to designate a phenotypic variant of a species that is associated with a particular type of habitat; may be designated a subspecies. Subspecies are populations that are distinguishable by one or more characteristics and are given subspecific names, in botany there may be sympatric forms. Species are members of a single population sharing similar phylogenetic or morphological similarities.

sibling vs sister species – Sibling species are reproductively isolated species that are difficult to distinguish by morphological characteristics. Sister species are ones that are thought on the basis of phylogenetic analysis to be each other's closest relatives, derived from an immediate common ancestor.

terms in Box 17A.

Geographic isolation – prevention of gene flow between populations by extrinsic barriers to movement.

Reproductive isolation – reduction or prevention of gene flow between populations by genetically determined differences.

Allopatric populations – populations occupying separated geographic areas.

Parapatric populations – populations occupying adjacent geographic areas, meeting at the border.

Sympatric populations – populations occupying the same geographic area and capable of encountering one another.

Hybrid zone – region where genetically distinct populations meet and interbreed to some extent resulting in hybrids.

Introgression – the movement or incorporation of genes from one genetically distinct population (usually considered a species or semispecies) into another.

Sibling species – reproductively isolated species that are difficult to distinguish by morphological characteristics.

Sister species – Species that are thought on the basis of phylogenetic analysis to be each other's closest relatives, derived from an immediate common ancestor (Cf. sister groups in phylogenetic systematic).

Chronospecies – phenotypically distinguishable forms in an ancestor-descendant series in the fossil record that are given different names.

Subspecies – populations of a species that are distinguishable by one or more characteristics and are given subspecific names (see the Elaphe subspecies in Figure 9.26). In zoology subspecies have different (allopatric or parapatric) geographic distributions and are equivalent to "geographic races." In botany they may be sympatric forms.

Race – A vague term, sometimes equivalent to subspecies and sometimes to polymorphic genetic forms within a population.

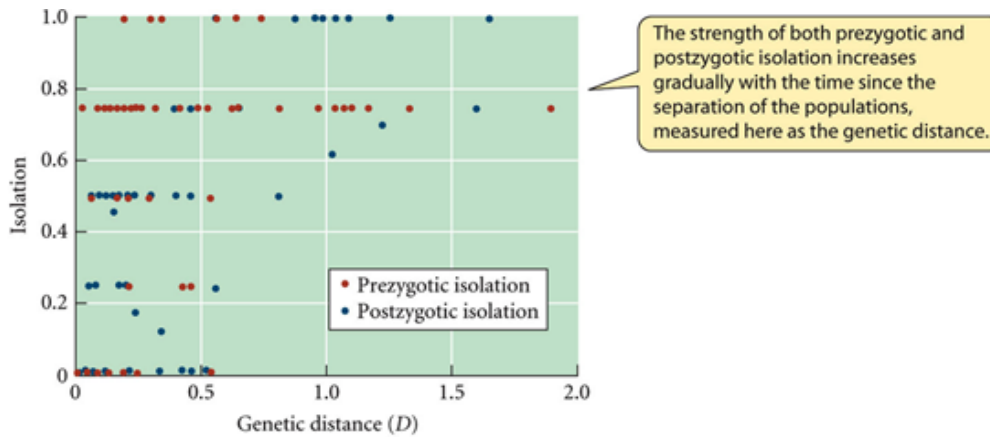
Semispecies – Usually, one or two or more parapatric, genetically differentiated groups of populations that are thought of to be partially, but not fully reproductively isolated; nearly, but not quite, different species.

Superspecies – usually the aggregate of a group of semispecies. Sometimes designates a group of closely related allopatric or nearly allopatric forms that are designated different taxonomic species.

Ecotype – Used mostly in botany to designate a phenotypic variant of a species that is associated with particular type of habitat; may be designated a subspecies.

Polytypic species – a geographically variable species, often divided into subspecies. (Most species are polytypic, whether or not subspecies have been named.)

Explain Figure 17.10.



What are fates of hybrid zones?

- 1.) A hybrid zone may persist indefinitely, with selection maintaining steep clines at some loci even while the clines in neutral alleles dissipate because of introgression. If the hybrid zone is a tension zone, it may move. It may become lodged in a region of low population density, or may eventually move to the far edge of the range of one of the semispecies, resulting in its extinction. If, however, some of the character differences are favored by different environments, the positions of the clines in those characters will be stable.
- 2.) Natural selection may favor alleles that enhance prezygotic isolation, resulting in ultimately in full reproductive isolation.
- 3.) Alleles that improve the fitness of hybrids may increase in frequency. In the extreme case, the postzygotic barrier to gene exchange may break down, and the semispecies may merge into one species.
- 4.) Some hybrids may become reproductively isolated from the parent forms and become a third species.

How can chromosome differences lead to reproductive isolation? Union of species having different chromosome numbers may produce sterile offspring such as that of the Donkey.

Review Table 17.2—be able to explain and give examples: premating examples vs postmating (prezygotic vs postzygotic) examples.

Table 17.2 A classification of isolating barriers (Part 1)	
I. <i>Premating barriers</i> : Features that impede transfer of gametes to members of other species	
A. Ecological isolation: Potential mates (although sympatric) do not meet	
1. Temporal isolation (populations breed at different seasons or times of day)	
2. Habitat isolation (populations have propensities to breed in different habitats in the same general area, and so are spatially segregated)	
B. Potential mates meet but do not mate	
1. Behavioral (sexual or ethological) isolation (in animals, differences prevent populations from mating)	
2. Pollinator isolation (in plants, populations transfer pollen by different animal species or on different body parts of a single pollinator; may also be classified as ecological isolation)	
II. <i>Postmating, prezygotic barriers</i> : Mating or gamete transfer occurs, but zygotes are not formed	
A. Mechanical isolation (copulation occurs, but no transfer of male gametes takes place because of failure of mechanical fit of reproductive structures)	
B. Copulatory behavioral isolation (failure of fertilization because of behavior during copulation or because genitalia fail to stimulate properly)	
C. Gametic isolation [failure of proper transfer of gametes or of fertilization, either due to intrinsic incompatibility or to competition between conspecific and heterospecific gametes (conspecific sperm precedence or pollen tube precedence)]	
Table 17.2 A classification of isolating barriers (Part 2)	
III. <i>Postzygotic barriers</i> : Hybrid zygotes are formed but have reduced fitness	
A. Extrinsic (hybrid fitness depends on context)	
1. Ecological inviability (hybrids do not have an ecological niche in which they are competitively equal to parent species)	
2. Behavioral sterility (hybrids are less successful than parent species in obtaining mates)	
B. Intrinsic (hybrid fitness is low because of problems that are relatively independent of environmental context)	
1. Hybrid inviability (developmental problems cause reduced survival)	
2. Hybrid sterility (usually due to reduced ability to produce viable gametes; also "behavioral sterility," neurological incapacity to perform normal courtship)	