The Modern Theory of Evolution

Although Charles Darwin is credited with the development of the theory of evolution by natural selection, there were many people who contributed ideas upon which he built his own. Since Darwin first proposed his theory, aspects that were problematic (such as the mechanism of inheritance) have now been explained. The theory has undergone refinement and has been expanded to incorporate the modern developments in biology. The development of the modern theory of evolution has a history going back at least two centuries. The diagram below illustrates the way in which some of the major contributors helped to form the currently accepted model, often referred to as the new synthesis (or the Neo-Darwinian theory). Some of the early contributors did not have the concept of evolution in their minds when they put forward their ideas, but their work contributed toward the development of a unifying theory explaining how species can change over time.

**Erasmus Darwin**
1731 - 1802
Evolution by the Inheritance of acquired characteristics. Charles Darwin's grandfather was probably an important influence in developing his thoughts on evolution.

**Hebert Spencer**
1820 - 1903
Proposed concept of the 'survival of the fittest'.

**Alfred Russel Wallace**
1823 - 1913
'Theory of Natural Selection'.

**August Weismann**
1834 - 1914
Proposed chromosomes as the basis of heredity, demolishing the theory that acquired characteristics could be inherited.

**R.A. Fisher**
1890 - 1962
Founding of population genetics and mathematical aspects of evolution and genetics.

**J.B.S. Haldane**
1896 - 1964

**Sewall Wright**
1889 - 1988

**John Baptiste de Lamarck**
1744 - 1829
The first person to publish a reasoned theory of evolution: 'Philosophie Zoologique'. Proposed the idea of use and disuse and inheritance of acquired characteristics.

**Reverend Thomas Malthus**
1766 - 1834
Wrote: 'An Essay on the Principles of Population', attempting to justify the squallid conditions of the poor by stating that poverty and starvation were merely a consequence of overpopulation.

**Charles Lyell**
1797 - 1875
A major influence on Darwin. Lyell's work 'Principles of Geology' proposed that the geological processes we observe today have always been occurring and the earth is therefore very old.

**Gregor Mendel**
1822 - 1884
Developed the fundamentals of the genetic basis of inheritance. Mendel's particulate model of inheritance (the gene idea) was recognized 34 years later as providing the means by which natural selection could occur.

**Julian Huxley**
1887 - 1975
**Ernst Mayr**
1904 - 2005
**T. Dobzhansky**
1900 - 1975
During the 1930s and 1940s these workers collaborated to help formulate the modern or synthetic theory of Darwinian evolution, incorporating developments in genetics, paleontology and other branches of biology.

**The New Synthesis**

Neo-Darwinism: The version of Darwin's theory refined and developed in the light of modern biological knowledge (especially genetics) in the mid-20th century.

*Errnst Mayr died on Feb. 3, 2005. His reflections on his 80 years in the field of evolutionary biology are published in the July 2, 2004 issue of Science.

1. From the diagram above, choose one of the contributors to the development of evolutionary theory (excluding Charles Darwin himself), and write a few paragraphs discussing their role in contributing to Darwin's ideas. You may need to consult an encyclopedia or other reference to assist you.
Gene flow (pages 105-107)

19. Explain how migration leads to gene flow between natural populations, and may affect allele frequencies.

Special events in gene pools (pages 105, 113-115)

20. Explain the founder effect, including reference to its genetic and evolutionary consequences.

21. Explain the population bottleneck effect, including reference to its genetic and evolutionary consequences.

22. Appreciate how the founder effect and population (genetic) bottleneck may accelerate the pace of evolutionary change. Explain the importance of genetic drift in populations that undergo these events.

Speciation (pages 116-121, also see page 390)

23. Recall your definition of evolution and distinguish clearly between microevolution and macroevolution.

24. Define species. Describe how the nature of some species can create problems for our definition.

25. Recognize the role of natural selection and isolation in speciation. Discuss speciation in terms of migration, geographical or ecological isolation (see #26-27) and adaptation (see #7), leading to reproductive or genetic isolation of gene pools.

26. Explain what is meant by reproductive isolation. Describe the mechanisms through which populations may become reproductively isolated. If required, distinguish between prezygotic and postzygotic reproductively isolating mechanisms (RIMs).

27. Contrast allopatic and sympatric speciation. Identifying the situations in which each is most likely to occur. Explain why RIMs tend to be more pronounced between sympatric (as opposed to allopatric) species. Explain the role of polyploidy in instant speciation.

28. Recognize stages in species development, including reference to the reduction in gene flow as populations become increasingly isolated.

Patterns of evolution (pages 122-131)

29. Describe the major stages in a species life cycle extending from origin to extinction.

30. Distinguish between sequential (phylectic) speciation and adaptive radiation (a form of divergent evolution). Appreciate how evolution has resulted in a great diversity of forms among living organisms.

31. Explain what is meant by convergent evolution. Distinguish between analogous and homologous structures, recognizing that analogous structures may arise as a result of convergence. Appreciate that some biologists also recognize parallel evolution (as distinct from convergence) to indicate evolution along similar lines in closely related groups.

32. Distinguish between the two models for the pace of evolutionary change: punctuated equilibrium and gradualism. Discuss the evidence for each model.

33. Describe the role of extinction in the process of evolution. Identify some of the major mass extinctions and state when they occurred. Discuss some of the theories for the causes of these extinctions.


The Sixth Extinction Nat Geographic, 195(2) Feb. 1999, pp. 42-68. High rates of extinction have occurred five times in the past. The sixth extinction is on its way, driven by human impact.

Listen, we're Different New Scientist, 17 July 1999, pp. 32-35. Speciation in decades as a result of behavioral and morphological mechanisms.

How the Species Became New Scientist, 11 Oct. 2003, pp. 32-35. Stability in species and new ideas on speciation. Species are stable if changes in form or behavior are damped down, but unstable if the changes escalate as new generations shuffle parental genes and natural selection discards the allele combinations that do not work well.

Live and Let Live New Scientist, 3 July 1999, pp. 32-36. Recent research suggests that hybrids are intact entities subject to the same evolutionary pressures as pure species.

The American Biology Teacher contains many excellent articles covering the teaching of basic evolutionary principles. A list of recent articles in this topic area is provided on the Teacher Resource CD-ROM. In addition, access to a searchable database for this and other periods will soon be available from Bing.com's web site.

TEACHER'S REFERENCE


Fair Enough New Scientist, 12 Oct. 2002, pp. 54-57. Skin color in humans: this article examines the argument for there being a selective benefit to being dark or pale in different environments.

Skin Deep Scientific American, October 2002, pp. 50-57. This article presents powerful evidence for skin color ("Tanor") being the end result of opposing selection forces. Clearly written and of high interest, this is a perfect vehicle for student discussion and for examining natural selection.

Evolution: Five Big Questions New Scientist, 14 June 2003, pp. 52-58, 48-51. A discussion of the most covered points regarding evolution and the mechanisms by which it occurs.

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See the "Textbook Reference Grid" on pages 8-9 for textbook reference pages relating to material in this topic.

See page 6 for details of publishers of periodicals:

STUDENT'S REFERENCE


Optimality Biol. Sci. Rev., 17(4), April 2006, pp. 2-5. Environmental stability and optimality of structure and function can explain evolutionary stasis in animals. Examples are described.

Presentation Media to support this topic:


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GENETICS: Population Genetics: Introduction to evolutionary biology Micro-evolution and population genetics Random genetic drift
In 1859, Darwin and Wallace jointly proposed that new species could develop by a process of natural selection. Natural selection is the term given to the mechanism by which better adapted organisms survive to produce a greater number of viable offspring. This has the effect of increasing their proportion in the population so that they become more common. It is Darwin who is best remembered for the theory of evolution by natural selection through his famous book: 'On the origin of species by means of natural selection', written 23 years after returning from his voyage on the Beagle, from which much of the evidence for his theory was accumulated. Although Darwin could not explain the origin of variation nor the mechanism of its transmission (this was provided later by Mendel's work), his basic theory of evolution by natural selection (outlined below) is widely accepted today. The study of population genetics has greatly improved our understanding of evolutionary processes, which are now seen largely as a (frequently gradual) change in allele frequencies within a population. Students should be aware that scientific debate on the subject of evolution centers around the relative merits of various alternative hypotheses about the nature of evolutionary processes. The debate is not about the existence of the phenomenon of evolution itself.

**Darwin's Theory of Evolution by Natural Selection**

**Overproduction**
Populations produce too many young; many must die

Populations tend to produce more offspring than are needed to replace the parents. Natural populations normally maintain constant numbers. There must therefore be a certain number dying.

**Variation**
Individuals show variation; some are more favorable than others

Individuals in a population vary in their phenotype and therefore, their genotype. Some variants are better suited to the current conditions than others and find it easier to survive and reproduce.

**Natural Selection**
Natural selection favors the best suited at the time

The struggle for survival amongst overcrowded individuals will favor those variations which have the best advantage. This does not necessarily mean that those struggling die, but they will be in a poorer condition.

**Inherited**
Variations are inherited. The best suited variants leave more offspring.

The variations (both favorable and unfavorable) are passed on to offspring. Each new generation will contain proportionately more descendants from individuals with favorable characters than those with unfavorable.

1. In your own words, describe how Darwin's theory of evolution by natural selection provides an explanation for the change in the appearance of a species over time:
Adaptations and Fitness

An adaptation is any heritable trait that suits an organism to its natural function in the environment (its niche). These traits may be structural, physiological, or behavioral. The idea is important for evolutionary theory because adaptive features promote fitness. Fitness is a measure of how well suited an organism is to survive in its habitat and its ability to maximize the numbers of offspring surviving to reproductive age. Adaptations are distinct from properties which, although they may be striking, cannot be described as adaptive unless they are shown to be functional in the organism’s natural habitat. Genetic adaptation must not be confused with physiological adjustment (acclimatization), which refers to an organism’s ability to adapt during its lifetime to changing environmental conditions. The physiological changes that occur when a person spends time at altitude provide a good example of acclimatization. Examples of adaptive features arising through evolution are illustrated below.

Ear Length in Rabbits and Hares

The external ears of many mammals are used as important organs to assist in thermoregulation (controlling loss and gain of body heat). The ears of rabbits and hares native to hot, dry climates, such as the jackrabbit of southwestern USA and northern Mexico, are relatively very large. The Arctic hare lives in the tundra zone of Alaska, northern Canada and Greenland, and has ears that are relatively short. This reduction in the size of the extremities (ears, limbs, and noses) is typical of cold-adapted species.

Body Size in Relation to Climate

Regulation of body temperature requires a large amount of energy and mammals exhibit a variety of structural and physiological adaptations to increase the effectiveness of this process. Heat production in any endotherm depends on body volume (heat generating metabolism), whereas the rate of heat loss depends on surface area. Increasing body size minimizes heat loss to the environment by reducing the surface area to volume ratio. Animals in colder regions therefore tend to be larger overall than those living in hot climates. This relationship is known as Bergman’s rule and it is well documented in many mammalian species. Cold-adapted species also tend to have more compact bodies and shorter extremities than related species in hot climates.

Number of Horns in Rhinoceroses

Not all differences between species can be convincingly interpreted as adaptations to particular environments. Rhinoceroses charge rival males and predators, and the horn(s), when combined with the head-down posture, add effectiveness to this behavior. Horns are obviously adaptive, but it is not clear that the possession of one (Indian rhino) or two (black rhino) horns is necessarily related directly to the environment in which those animals live.

1. Distinguish between adaptive features (genetic) and acclimatization:

2. Explain the nature of the relationship between the length of extremities (such as limbs and ears) and climate:

3. Explain the adaptive value of a larger body size at high altitude:
Natural selection operates on the phenotypes of individuals, produced by their particular combinations of alleles. In natural populations, the allele combinations of some individuals are perpetuated at the expense of other genotypes. This differential survival of some genotypes over others is called natural selection. The effect of natural selection can vary; it can act to maintain the genotype of a species or to change it. Stabilizing selection maintains the established favorable characteristics and is associated with stable environments. In contrast, directional selection favors phenotypes at one extreme of the phenotypic range and is associated with gradually changing environments. Disruptive selection is a much rarer form of selection favoring two phenotypic extremes, and is a feature of fluctuating environments.

Stabilizing Selection
Extreme variations are culled from the population (there is selection against them). Those with the established (middle range) adaptive phenotype are retained in greater numbers. This reduces the variation for the phenotypic character. In the example right, light and dark snails are eliminated, leaving medium colored snails. Stabilizing selection can be seen in the selection pressures on human birth weights.

Directional Selection
Directional selection is associated with gradually changing conditions, where the adaptive phenotype is shifted in one direction and one aspect of a trait becomes emphasized (e.g. coloration). In the example right, light colored snails are eliminated and the population becomes darker. Directional selection was observed in peppered moths in England during the Industrial Revolution. They responded to the air pollution of industrialization by increasing the frequency of darker, melanistic forms.

Disruptive or Diversifying Selection
Disruptive selection favors two extremes of a trait at the expense of intermediate forms. It is associated with a fluctuating environment and gives rise to balanced polymorphism in the population. In the example right, there is selection against medium colored snails, which are eliminated. There is considerable evidence that predators, such as insectivorous birds, are more likely to find and eat common morphs and ignore rare morphs. This enables the rarer forms to persist in the population.

1. (a) Distinguish between directional selection and disruptive selection, identifying when each is likely to operate:

(b) Identify which of the three types of selection described above will lead to evolution, and explain why:

2. Explain how a change in environment may result in selection becoming directional rather than stabilizing:

3. Explain how, in a population of snails, through natural selection, shell color could change from light to dark over time:
Industrial Melanism

Natural selection may act on the frequencies of phenotypes (and hence genotypes) in populations in one of three different ways (through stabilizing, directional, or disruptive selection). Over time, natural selection may lead to a permanent change in the genetic makeup of a population. The increased prevalence of melanic forms of the peppered moth, *Biston betularia*, during the Industrial Revolution, is one of the best known examples of directional selection following a change in environmental conditions. Although the protocols used in the central experiments on Biston, and the conclusions drawn from them, have been queried, it remains one of the clearest documented examples of phenotypic change in a polymorphic population.

Industrial Melanism in Peppered Moths, *Biston betularia*

The peppered moth, *Biston betularia*, occurs in two forms (morphs): the gray mottled form, and a dark melanic form. Changes in the relative abundance of these two forms was hypothesized to be the result of selective predation by birds, with pale forms suffering higher mortality in industrial areas because they are more visible. The results of experiments by H.D. Kettlewell supported this hypothesis but did not confirm if, since selective predation by birds was observed but not quantified. Other research indicates that predation by birds is not the only factor determining the relative abundance of the different color morphs.

Museum collections of the peppered moth made over the last 150 years show a marked change in the frequency of the melanic form. Moths collected in 1840 (above left), prior to the major onset of the Industrial Revolution in England. Fifty years later (above right) the frequency of the darker melanic forms had greatly increased. Even as late as the mid 20th century, coal-based industries predominated in some centers, and the melanic form occurred in greater frequency in these areas (see map, right).

**Key to frequency graphs**

- **Gray or spotted form**
- **Melanic or carbonaria form**

**Industrial areas**

**Non-industrial areas**

A gray (mottled) form of *Biston* camouflaged against a lichen covered bark surface. In the absence of soot pollution, mottled forms appear to have the selective advantage.

A melanic form of *Biston*, resting on a dark branch, so that it appears as part of the branch. Note that the background has been faded out so that the moth can be seen.

Frequency of peppered moth forms in 1850

This map shows the relative frequencies of the two forms of peppered moth in the UK in 1850; a time when coal-based industries still predominated in some major centers.
Changes in frequency of melanic peppered moths

In the 1940s and 1950s, coal burning was still at intense levels around the industrial centers of Manchester and Liverpool. During this time, the melanic form of the moth was still very dominant. In the rural areas further south and west of these industrial centers, the gray or speckled forms increased dramatically. With the decline of coal burning factories and the Clean Air Acts in cities, the air quality improved between 1960 and 1980. Sulfur dioxide and smoke levels dropped to a fraction of their previous levels. This coincided with a sharp fall in the relative numbers of melanic moths.

1. The populations of peppered moth in England have undergone changes in the frequency of an obvious phenotypic character over the last 150 years. Describe the phenotypic character that changed in its frequency:

2. (a) Identify the (proposed) selective agent for phenotypic change in Blston:

(b) Describe how the selection pressure on the light colored morph has changed with changing environmental conditions over the last 150 years:

3. The industrial centers for England in 1950 were located around London, Birmingham, Liverpool, Manchester, and Leeds. Glasgow in Scotland also had a large industrial base. Comment on how the relative frequencies of the two forms of peppered moth were affected by the geographic location of industrial regions:


(a) State how much the pollution dropped by:

(b) Describe how the frequency of the darker melanic form changed during the period of reduced pollution:

5. In the example of the peppered moths, state whether the selection pressure is disruptive, stabilizing, or directional:

6. Outline the key difference between natural and artificial selection:

7. Discuss the statement “the environment directs natural selection”:

There are two mechanisms by which natural selection can affect allele frequencies. Firstly, there may be selection against one of the homozygotes. When one homozygous type (for example, $aa$), has a lower fitness than the other two genotypes (in this case, $Aa$ or $AA$), the frequency of the deleterious allele will tend to decrease until it is completely eliminated. In some situations, both homozygous conditions ($aa$ and $AA$) have lower fitness than the heterozygote; a situation that leads to heterozygous advantage and may result in the stable coexistence of both alleles in the population (balanced polymorphism). There are remarkably few well-documented examples in which the evidence for heterozygous advantage is conclusive. The maintenance of the sickle cell mutation in malaria-prone regions is one such example.

The Sickle Cell Allele ($Hb^s$)

Sickle cell disease is caused by a mutation to a gene that directs the production of the human blood protein called hemoglobin. The mutant allele is known as $Hb^s$ and produces a form of hemoglobin that differs from the normal form by just one amino acid in the $\beta$-chain. This minute change however causes a cascade of physiological problems in people with the allele. Some of the red blood cells containing mutated hemoglobin alter their shape to become irregular and spiky; the so-called sickle cells.

Sickle cells have a tendency to clump together and work less efficiently. In people with just one sickle cell allele plus a normal allele (the heterozygote condition $Hb^s/Hb^A$), there is a mixture of both red blood cell types and they are said to have the sickle cell trait. They are generally unaffected by the disease except in low oxygen environments (e.g. climbing at altitude). People with two $Hb^s$ genes ($Hb^s/Hb^s$) suffer severe illness and even death. For this reason $Hb^s$ is considered a lethal gene.

Heterozygous Advantage in Malarial Regions

Falciparum malaria is widely distributed throughout central Africa, the Mediterranean, Middle East, and tropical and semitropical Asia (Fig. 1). It is transmitted by the Anopheles mosquito, which spreads the protozoan Plasmodium falciparum from person to person as it feeds on blood.

SYMPTOMS: These appear 1-2 weeks after being bitten, and include headache, shaking, chills, and fever. Falciparum malaria is more severe than other forms of malaria, with high fever, convulsions, and coma. It can be fatal within days of the first symptoms appearing.

THE PARADOX: The $Hb^s$ allele offers considerable protection against malaria. Sickle cells have low potassium levels, which causes plasmodium parasites inside these cells to die. Those with a normal phenotype are very susceptible to malaria, but heterozygotes ($Hb^s/Hb^A$) are much less so. This situation, called heterozygous advantage, has resulted in the $Hb^s$ allele being present in moderately high frequencies in parts of Africa and Asia despite its harmful effects (Fig. 2). This is a special case of balanced polymorphism, called a balanced lethal system because neither of the homozygotes produces a phenotype that survives, but the heterozygote is viable.

1. With respect to the sickle cell allele, explain how heterozygous advantage can lead to balanced polymorphism:
Darwin's Finches

The Galapagos Islands, 920 km off the west coast of Ecuador, played a major role in shaping Darwin's thoughts about natural selection and evolution. While exploring the islands in 1835, he was struck by the unique and peculiar species he found there. In particular, he was intrigued by the island's finches. The Galapagos group is home to 13 species of finches in four genera. This variety has arisen as a result of evolution from one common ancestral species. Initially, a number of small finches, probably grassquits, made their way from South America across the Pacific to the Galapagos Islands. In the new environment, which was relatively free of competitors, the colonizers underwent an adaptive radiation, producing a range of species each with its own unique feeding niche. Although similar in their plumage, nest building techniques, and calls, the different species of finches can be distinguished by the size and shape of their beaks. The beak shape of each species is adapted for a different purpose, such as crushing seeds, peeling wood, or probing flowers for nectar. Between them, the 13 species of this endemic group fill the roles of seven different families of South American mainland birds. Modern methods of DNA (genetic) analysis have confirmed Darwin's insight and have shown that all 13 species evolved from a flock of about 30 birds arriving a million years ago.

The Evolution of Darwin's Finches

Vegetarian finch

Woodpecker finch

Large ground finch

Large ground finch

Large ground finch

Medium ground finch

Small ground finch

Sharp billed ground finch

Ground finches

Cactus finch

Cactus finch

Warbler finch

Warbler finch

Warbler-like finches

Tree finches

Large tree finch

Medium tree finch

Small tree finch

As the name implies, tree finches are largely arboreal and feed mainly on insects. The bill is sharper than in ground finches and better suited to grasp insects. Paler than ground or cactus finches, they also have streaked breasts.

Cactus finches

Probably descended from ground finches. Beak is probing. Males are mostly black, females are streaked, like ground finches. Found in arid areas on prickly pear cactus where they eat insects on the cactus, or the cactus itself.

Ground finches

Four species with crushing-type bills used for seed eating. On Wolf Island, they are called vampire finches because they peck the skin of animals to draw blood, which they then drink. Such behavior has evolved from eating parasitic insects off animals.

Warbler finches

Named for their resemblance to the unrelated warblers, the beak of the warbler finch is the thinnest of the Galapagos finches. It is the most widespread species, found throughout the archipelago. Warbler finches prey on flying and ground dwelling insects.

1. Outline the main factors that have contributed to the adaptive radiation of Darwin's finches: