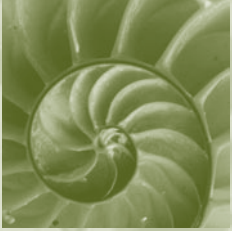
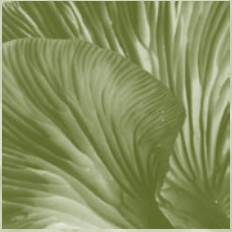
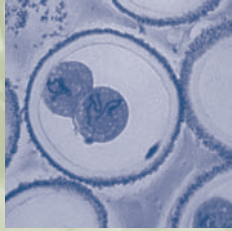


Part 3

How Evolution Works



The Nature of Natural Selection

Douglas J. Futuyma

Evolution as such was not original with Charles Darwin, but his theory of how evolution happens was. The concept of natural selection was Darwin's (and Alfred Russel Wallace's, independently) wholly original idea, and it is the centerpiece of *The Origin of Species*. This is the theory that accounts for the complexity of organisms and for their adaptations, those features that so wonderfully equip them for survival and reproduction; this is the theory that accounts for the divergence of species and thus for the boundless diversity of life. It is one of the most important ideas in biology, and one of the most important in the history of thought. The philosopher Daniel Dennett (1995) calls it "Darwin's dangerous idea," because it replaces an entire worldview. It accounts for the appearance of design in living things.

Design in organisms had previously been imagined to be the product of an intelligent, omnipotent creator, and indeed was one of the most important arguments for the existence of such a being. Today's antievolutionists rally to the idea of intelligent design, arguing, as had their pre-Darwinian forebears, that the features of organisms are too complex, and too well fitted for their functions, to be explained by natural causes; they must, instead, have been caused by miracles. But natural selection (together with the origin of genetic variation) is indeed a sufficient explanation for organisms' complex adaptations—and for a good many other features of living things as well. So this is a concept with immense philosophical implications, and it is at the center of the creation-versus-evolution battle.

Given the importance of the concept, it is critical that it be conveyed as clearly and as accurately as possible in teaching students science. It is a simple concept, but it nevertheless works in many and sometimes subtle ways. Moreover, many people (even some biologists) carry misconceptions that make it all the more difficult for them to understand natural selection clearly. I will cite what I think are the most important points to understand when coming to

grips with natural selection. Much of what follows has been clearly explicated by George Williams (1966), Richard Dawkins (1986, 1989), and others, and draws on passages in *Evolution* (Futuyma, 2005).

Natural Selection Is a Consistent Difference in the Rate of Increase of Different Genotypes or Genes (and No More Than That)

Natural selection is not "caused by" differences in rates of survival or reproduction: it *is* a difference of this kind. If the average rate of increase of one genotype (or gene) is consistently greater than that of others, natural selection exists. Such a genotype (or gene) is likely to increase in *frequency* (i.e., its proportion in the population) and may replace all others (i.e., become *fixed*).

The simplest example of such a process is an increase or decrease in frequency of a mutation in a laboratory culture of a species of bacteria; for example, mutations in the gene encoding galactosidase (the enzyme that provides energy by metabolizing lactose) have been studied in cultures of *Escherichia coli* (Dean, Dykhuizen, & Hartl, 1986). Mutations have been found that either reduce or enhance enzyme activity; these result in slower or faster cell division and thus growth in numbers compared with the wild type allele (figure 1). This is the very essence of natural selection. A mutation that enhances galactosidase activity would improve the level of adaptation of an *E. coli* population to a lactose-rich environment. There is nothing intelligent or thoughtful about the process; *it is nothing more than a statistical difference in reproductive rate*, that is, in *reproductive success*.

The Slogan "Survival of the Fittest" Should be Discarded, Abolished

This slogan, often used as a definition of natural selection, is wrong and misleading on several grounds. First, natural selection is differential reproductive success, not merely survival. Survival to reproductive age is

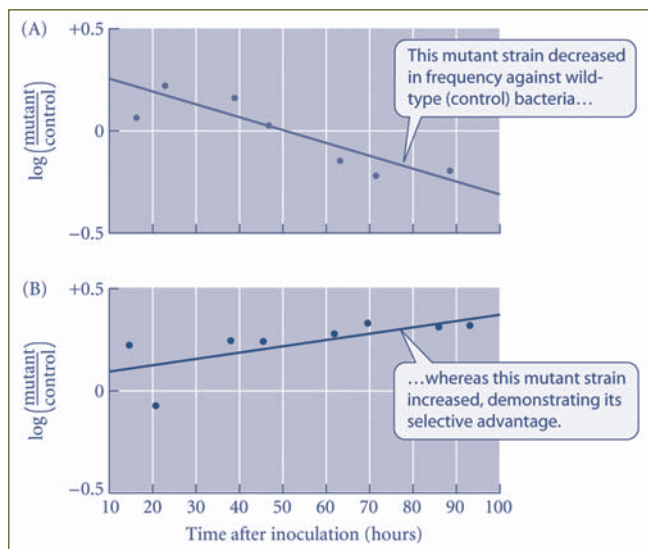


Figure 1. Natural selection illustrated by changes in the frequency of two mutations of the β -galactosidase gene of *Escherichia coli*, in separate laboratory cultures with the control (wild-type) allele. One mutation decreased in frequency, and the other increased, because of their effects on the rate of cell division. (From Futuyma 2005, after Dean et al. 1986.)

clearly a prerequisite for reproductive success, but a sterile genotype, however great its survival, has no future (except by virtue of kin selection, as in social insects, but that is another topic.) A great deal of natural selection consists of genetic differences in reproductive rate, by both sexes.

Second, there is not always a “fittest”: there can be stable coexistence of several genotypes, for any of several reasons. For example, each of several genotypes may be better adapted than the others to a different microhabitat, or to using a different resource, and all of them may be able to persist in a suitably variable environment.

Third, this slogan has been used to claim, falsely, that natural selection is an empty tautology. (Which type is the fittest? Answer: Why, the one that survives.) But this claim of tautology is false for two reasons:

1. We often can specify, or predict, which allele or phenotype will be the fittest, based on information other than simply seeing which takes over a population. I will explain this in the next section.
2. The allele that becomes fixed may not be the fittest: it may just have been “lucky.” It may have been fixed by genetic drift, which is simply random fluctuations in the frequency of alleles or genotypes, owing to sampling error. Two alleles may not differ at all in their effect on the organism (i.e., they are neutral), but it is a mathematical certainty that their frequencies will fluctuate

from generation to generation, and that one of them will eventually be fixed, purely by chance (figure 2). In another population, the other allele may well be fixed instead. We can calculate the probability that one or the other allele will be fixed, just as we can calculate the chance of drawing four aces from a randomly shuffled deck of cards. Thus evolutionary change can occur by chance (genetic drift) *or* by natural selection (or both). We must distinguish chance from natural selection!

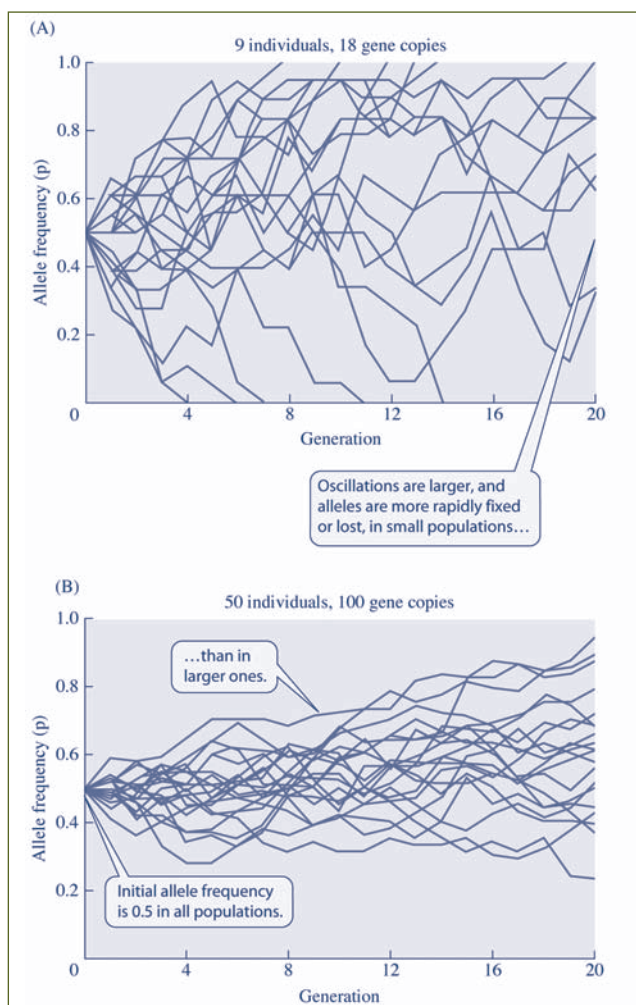


Figure 2. Computer simulations of random genetic drift in small (nine) versus larger (50) populations. In each case, 20 populations begin with identical allele frequencies (50 percent of each of two alleles, say *A* and *a*), and the frequency of one (say, *A*) is followed for 20 generations. The allele’s frequency fluctuates at random toward zero and one, and ultimately will end at one of those boundaries. (From Futuyma 2005, after D. L. Hartl and A. G. Clark, *Principles of population genetics*, Sinauer 1997.)

Natural Selection Is the Antithesis of Chance

The distinctive property of natural selection is that in a given environment there is a consistent difference among genotypes, and therefore consistency of the pattern of evolutionary change (given those genotypes and that environment). Consistency

implies that a nonrandom cause is at work. For example, replicate experimental populations, if initiated with the same set of genotypes, typically show similar patterns of change in genotype frequencies. (Note that “chance” in science refers to unpredictability, not to lack of purpose, as it sometimes means in everyday discourse. Scientists do not invoke purpose in any natural phenomenon (outside of human behavior), but nevertheless, they do not say that all natural events happen by chance.)

Chance means unpredictability, but we can often make rough predictions of the evolution of a characteristic, at least in the short term, if we know enough about the function of the character and about the environment in which the organism must function. For instance, we know that in many birds and insects, the effectiveness with which an individual feeds depends on the fit between its beak (or mouthparts in general) and the size or location of its food. (A famous example is provided by studies of the adaptive fit of beak size to seed size and hardness in the Galápagos ground finches [Grant, 1986].) The soapberry bug feeds most effectively on seeds if its beak is the right length to reach the seed through the enveloping fruit wall. Its native host plants are now much less common than several Asian species that have either larger or smaller fruits, depending on the

species. Within the last few decades, the bugs’ beak length has independently evolved in Texas and Florida to match the fruit radius of different Asian plants that are now abundant (figure 3; Carroll & Boyd, 1992). Beak length has evolved, *predictably*, toward a new optimum that differs, depending on the ecological situation. This is not a matter of chance!

Natural Selection Makes the Improbable Probable

The frequency distribution of beak length in soapberry bug populations now has shifted mostly beyond the range of variation that the populations had before new food plants were introduced (figure 3). This is a very common observation for characteristics in which alleles at several or many different gene loci contribute to variation. For a “quantitative character,” such as size, there may be at each locus “plus” alleles that increase size and “minus” alleles that decrease it; a genotype’s size then depends on how many + and – alleles are in its genetic makeup. (If, for instance, there were four loci, A–D, the largest and smallest genotypes might be denoted + + + + and – – – –, respectively. Intermediates have various mixtures of + and – alleles. If the population consists mostly of fairly small individuals, the + allele at each locus is quite uncommon. Then the probability that both a sperm and an egg

will have many + alleles is very low, so the production of an extremely large offspring is very improbable. (That is, extremely few gametes would have a ++++ set of alleles, i.e., the + allele at every locus.)

If we were to breed mostly the largest individuals (those with more than the average number of + alleles at these loci), we would produce F_1

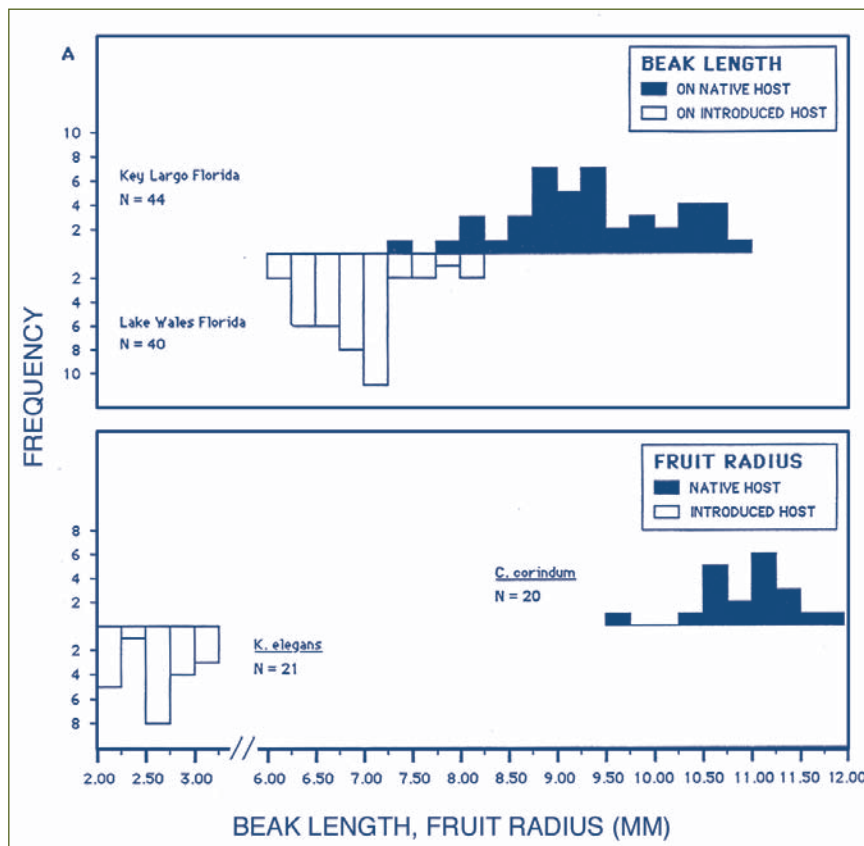


Figure 3. Rapid evolution of beak length in the soapberry bug in Florida. The bottom panel shows the frequency distribution of the radius of the fruit of the native host (*C. corindum*, black histogram at right) and of the much smaller fruits of an introduced host (*Koelerutaria elegans*) that is now abundant in a different region of Florida (white histogram at left, flipped upside down). The top panel shows that the beak length of bugs that feed on the introduced host is much shorter than that of bugs associated with the native host (black histogram). The average beak length is shorter than any that were measured in the population that still feeds on the native plant, and which represents the ancestral condition. (After Carroll & Boyd, 1992.)

offspring in which the frequency of + alleles is higher than it was in the general population in the previous generation. Then the “concentration” of + alleles would be higher in the gametes of these individuals than it had been in the previous generation—and it would be higher still if only the largest members of the F_1 generation bred. So the probability of gametes, and therefore F_2 offspring, with many + alleles (and therefore larger size), would be increased. The selection process acts as a distiller or sieve for + alleles, making formerly improbable gene combinations (such as +A+A+B+B+C+C+D+D) more probable.

This is exactly what has occurred when plant or animal breeders, or researchers, have deliberately selected for characteristics in domesticated organisms or in experimental subjects such as fruit flies. Within a few generations, extreme phenotypes that were never seen in the base population become abundant, based on selection of genetic variation that was already present in the base population. The breeders have used selection to make the improbable probable. Darwin did not know about genes, but he was very familiar with this process, and he saw that natural environmental agents of selection could have exactly the same effects. If the reproductive success of the longest- (or shortest-) beaked bugs is greatest because they have better access to a new kind of seed, the frequency of relevant alleles will increase, and unlikely gene combinations become more likely.

This principle explains, very simply, how features with the appearance of design—including complex features based on the input of many genes—are formed by a natural process. Natural selection is the creative factor in evolution. However...

Natural Selection Is Not Another Name for God

Natural selection is not even a name for Luther Burbank, a 19th-century horticulturist who used deliberate selection to develop stunningly novel strains of plants. That is, natural selection isn't intelligent; it isn't even a being, much less an intelligent one with goals and foresight. So there is no guarantee that it will produce optimally designed organisms.

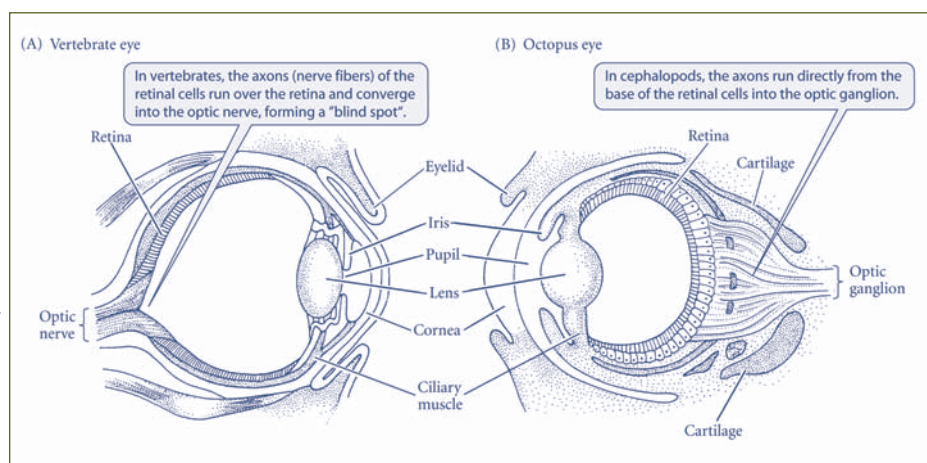


Figure 4. Sections through the eye of a vertebrate (a) and a squid or other cephalopod (b). In the vertebrate eye, the optic nerve forms a blind spot, the kind of design flaw that is common in organisms and which the mindless processes of mutation and natural selection can be expected to produce. (From Futuyma 2005, after R. C. Brusca and G. J. Brusca, *Invertebrates*, Sinauer Associates, 1990.)

Examples of suboptimal design are legion (as anyone who suffers from wisdom teeth or lower back pain will agree). For example, the axons of the retina cells in a vertebrate eye arise from the front of the cell and trail over the surface of the retina, converging into the optic nerve, which creates a blind spot where it plunges back through the retina and out the rear side of the eye as it extends to the brain (figure 4). There is no logical necessity for a blind spot, especially since cephalopods (e.g., squid) have evolved a very similar eye in which the axons sensibly arise from the rear of the retinal cells, and which therefore doesn't have a blind spot.

Such examples seem to speak of unintelligent design. The unintelligent designer, natural selection, is limited by the availability of the right genetic variations (which the mutation process may not have supplied), by historical legacies (for selection can act only on variations of whatever features an organism already has), and by trade-offs that limit adaptation. (For example, the elements of the male vocalization of the túngara frog that most appeal to females also attract frog-eating bats [Ryan, 1985].)

Moreover, because natural selection has no forethought (or any other thought), it cannot prepare organisms for future contingencies that differ from the regular pattern of environmental change that a species has experienced in the past. Arctic geese prepare for winter by flying south, because goose genotypes that didn't do that in the past have been eliminated. But natural selection cannot build features that are useless now but might prevent extinction in the future. For example, some parasites thrive by castrating

their host, redirecting host energy and materials from host reproduction to parasite reproduction. The possibility that the host population may go extinct in the future, by failure to reproduce adequately, cannot prevent the parasite from evolving the habit of castration. Likewise, many species produce great numbers of offspring not for the sake of the survival of the species population, but because under many circumstances, highly fecund (fertile) genotypes leave more descendants than less fecund genotypes.

Conversely, features that are advantageous here and now may evolve by natural selection even if they enhance the risk of future extinction. Many species have evolved specialized ecological requirements, such as the Kirtland's warbler, which is on the brink of extinction because it will nest only in stands of jack pine of the right age, with just the right shape. In a species with a 1:1 sex ratio, asexual (parthenogenetic) females have twice the rate of increase as sexual genotypes, because all the offspring of an asexual female are daughters that make more daughters, whereas only half of a sexual female's offspring are daughters. Quite often, therefore, a mutant genotype that is asexual will take over the species. (A familiar example is the common dandelion.) We know that the vast majority of these asexual species become extinct before very long, probably because they do not have the genetic flexibility that recombination in a sexually reproducing species provides. But that does not prevent populations from evolving asexual reproduction.

Natural Selection Is neither Moral nor Immoral

Since it is nothing more than a statistical process of differences in reproductive success, natural selection cannot be said to be either moral or immoral: it is *amoral*.

If a designer were to equip species with a way to survive environmental changes, it might make sense to devise a Lamarckian mechanism, whereby genetic changes would occur in response to an individual's need. Instead, adaptation is based on the combination of a random process (mutation) that cannot be trusted to produce the needed genetic variation (and often does not) and a process that is the epitome of waste and seeming cruelty: natural selection, in which the increase of an advantageous allele requires the demise or reproductive failure of vast numbers of organisms with different genotypes. Some African human populations have a high frequency of the sickle-cell hemoglobin allele because heterozygotes are more resistant to malaria than normal homozygotes. Sickle-cell homozygotes usually die before they reach reproductive

age. It would be hard to imagine a crueler instance of natural selection, whereby part of the population is protected against malaria at the expense of hundreds of thousands of people who are condemned to die because they are homozygous for a gene that happens to be worse for the malarial parasite than for heterozygous carriers.

Any property that enhances the reproductive success of one genotype compared with others can enable that genotype to become fixed—to take over a population. This, as Richard Dawkins (1989) made clear in his book *The Selfish Gene*, is also true of one gene (allele) compared with others.

As my colleague George Williams (1989) has said, “natural selection is a mechanism for maximizing short-sighted selfishness.” This intrinsic “selfishness” of genes and genotypes has many consequences that are repugnant from a moral point of view. For example, cannibalism can be advantageous to an individual. Flour beetles (*Tribolium*) eat eggs and pupae, and this tendency has been observed to increase in experimental populations, even though it reduces the growth rate of the population and could increase the chance of extinction (Wade, 1977). Male lions and langurs that take over a group of females kill the nursing offspring of the previous male, since this brings the mother back into reproductive condition and the male can father his own offspring faster. The seminal fluid of *Drosophila melanogaster* fruit flies is toxic to females (Chapman, Arnqvist, Bangham, & Rowe, 2003). They live long enough to lay the eggs that the male has fertilized, but they may not live long enough to mate again and lay other males' offspring. There is conflict between mammalian mothers and their fetuses: it is advantageous for the fetus to obtain as much nutrition from the mother as possible, but advantageous to the mother to withhold some, which can be used for her own subsequent reproduction. Accordingly, a paternally inherited gene in mice, encoding an insulin-like growth factor, enhances the fetus's ability to obtain nutrition from its mother, but a maternally inherited gene degrades this growth factor, opposing the paternal gene's effect (Haig, 1997).

This is an example of conflict between different genes in the same genome, of which many examples are coming to light (Hurst, Atlan, & Bengtsson, 1996). For example, mitochondria are transmitted only through female gametes in plants (and in most animals), so any mutation that can increase the production of eggs at the expense of pollen or sperm has an advantage. Almost all thyme plants carry a mitochondrial allele that prevents the development of

anthers and pollen; the resources that would go into their development are used instead for higher seed production. However, natural selection has favored a chromosomal gene that completely counteracts the male-sterility gene, so that most thyme plants have normal stamens and pollen. (It is advantageous for chromosomal genes if the plant has both male and female function, since these genes are spread through both pollen and seeds.) The result is a standoff between genes that cannot be called an adaptation, since the function of one gene is simply to nullify the effect of the other—but it is nevertheless an easily comprehended result of natural selection.

Discussion

Of course, natural selection can lead to the evolution of cooperation, not just conflict. I have focused on the results of “selfishness” to emphasize that natural selection can produce characteristics that are downright offensive to anyone’s sense of ethics (or at least would be, if humans were displaying these features). But, of course, infanticide by lions and toxic seminal fluid are no more unethical than volcanoes that erupt and kill, because there is neither morality nor immorality, neither ethical nor unethical behavior, outside the human realm. From these examples and this realization, we can draw two major consequences:

1. Organisms have many characteristics that you would not want to attribute to an intelligent, beneficent designer, and in fact they have many characteristics that make no sense at all from a design point of view—such as toxic semen, cub killing, or dueling genes that exactly counteract each other. But they make a great deal of sense if you understand evolution by natural selection.
2. Evolution provides no foundation at all for a code of human behavior. What is natural among other animals is totally irrelevant to ethics or morality. There is no foundation for the naturalistic fallacy, that what is natural is good.

The points I have emphasized concern the overall nature of natural selection and its implications. I have not treated the details of natural selection, such as the many forms it takes (kin selection, group selection, sexual selection, soft selection, hard selection, and so on). I have not discussed the evidence for natural selection (literally hundreds of studies, most of which have demonstrated selection in its many forms). Nor have I discussed the importance of natural selection

for human affairs. It is imperative that students understand that evolution by natural selection can sometimes occur rapidly, and that it can occur in organisms that really matter to us (Palumbi, 2001). The soapberry bug does not attack plants we care much about, but other insects have evolved to attack our crops (e.g., the apple maggot, which became a major pest of apples a little more than a century ago), and hundreds of insect pests have evolved resistance to chemical insecticides. Above all, probably the most serious crisis in medicine is the failure of antibiotics to control some of the pathogens they were designed to combat. This stems, of course, from the ongoing evolution of antibiotic resistance—in organisms ranging from HIV to the tuberculosis bacterium—due to natural selection that we impose by widespread (and often unnecessary) antibiotic use. Students simply must learn about evolution by natural selection, if for no other reason than self-protection. The applications of evolution are many, and they are steadily increasing. We cannot afford another 145 years of denial that Darwin was right.

References

- Carroll, S. P., & Boyd, C. (1992). Host race radiation in the soapberry bug: Natural history with the history. *Evolution*, 46, 1052–1069.
- Chapman, T., Arnqvist, G., Bangham, J., & Rowe, L. (2003). Sexual conflict. *Trends in Ecology and Evolution*, 18, 41–47.
- Dawkins, R. (1986). *The blind watchmaker*. New York: W.W. Norton.
- Dawkins, R. (1989). *The selfish gene* (New ed.). Oxford: Oxford University Press.
- Dean, A. M., Dykhuizen, D.E., & Hartl, D.L. (1986). Fitness as a function of galactosidase activity in *Escherichia coli*. *Genetical Research*, 48, 1–8.
- Dennett, D. C. (1995). *Darwin’s dangerous idea: Evolution and the meanings of life*. New York: Simon & Schuster.
- Futuyma, D. J. (2005). *Evolution*. Sunderland, MA: Sinauer Associates.
- Grant, P. R. (1986). *The ecology and evolution of Darwin’s finches*. Princeton, NJ: Princeton University Press.
- Haig, D. (1997). Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proceedings of the Royal Society of London Series B Biological Sciences*, 264, 1657–1662.
- Hurst, L. D., Atlan, A., & Bengtsson, B. O. (1996). Genetic conflicts. *Quarterly Review of Biology*, 71, 317–364.
- Palumbi, S. R. (2001). *The evolution explosion: How humans cause rapid evolutionary change*. New York: W. W. Norton.
- Ryan, M. J. (1985). *The túngara frog: A study in sexual selection and communication*. Chicago: University of Chicago Press.
- Wade, M. J. (1977). An experimental study of group selection. *Evolution*, 31, 134–153.
- Williams, G. C. (1989). A sociobiological expansion of evolution and ethics. In J. Paradis & G. C. Williams (Eds.), *Evolution and ethics: T. H. Huxley’s evolution and ethics with new essays on its Victorian and sociobiological context* (pp. 179–214). Princeton, NJ: Princeton University Press.

Evolution by Sexual Selection

Kerry L. Shaw, Tamra C. Mendelson, and Gerald Borgia

Charles Darwin's stunning insight was elegant in its simplicity. He observed that individuals vary in the traits they possess, that variation in these traits can be genetically inherited, and finally, that some individuals survive and reproduce better than others because they possess certain traits. These three simple conditions form the basis of Darwin's seminal theory of evolution by natural selection. His theory proposes that the makeup of a population will change over time, as traits that confer an advantage to the survival and reproduction, or fitness, of individuals increase in frequency. Thus, Darwin reasoned that organisms are adapted to the environment in which they live because they have inherited traits that enhanced survival and reproduction.

Darwin struggled, however, with the presence of showy, visible traits often expressed by males in many animal populations. Why would frogs, for example, reveal their location to predators with loud vocalizations or birds attract visual attention through vivid plumage coloration? How could such traits ever be advantageous, increase fitness, and evolve by natural selection, when they apparently put the bearer at predation risk? In his insightful but lesser-known work *Sexual Selection and the Descent of Man*, published in 1871, Darwin proposed the theory of evolution by sexual selection to explain the evolution of such traits. Sexual selection occurs when some individuals are more successful at attracting mates and obtaining fertilizations than others owing to the traits they possess, and consequently produce more offspring. Sexual selection can cause the evolution of the traits that enable individuals to attract more mates of the opposite sex. Darwin's great insight was explaining that these kinds of traits could evolve by sexual selection even when they hinder survival.

To see how selection for mating success might work in opposition to selection for survival, consider what it takes for an individual to contribute his or her genes to the next generation. Ultimately, what matters is the number of offspring an individual pro-

duces, but fitness is affected by three major components: survival, fecundity, and mating/fertilization success. Traits that cause some individuals to leave more offspring than others can be competitively superior in any of these fitness components. An individual that lives a long life should have many opportunities to produce offspring. An individual that has many eggs or sperm for fertilization also has much offspring potential. And, if an individual is able to attract many mating partners (called mating success), then the opportunity to produce many offspring should also exist. Obviously, however, if an individual lacks any one of these three components of fitness, the opportunity to produce offspring will be severely limited. An individual that lives a very long life will not have offspring if he or she lacks gametes to fertilize. Likewise, an individual that could attract many members of the opposite sex as mates because of the expression of traits, but that dies before having the chance to do so, will also have no offspring. Thus, survival, fecundity, and mating/fertilization success are all necessary to produce offspring. If a trait greatly enhances mating/fertilization success, even at the partial expense of survival, it has the potential to increase in a population because of sexual selection.

The insight that mating and fertilization success are very much a part of fitness as survival has led to a very powerful theory of sexual selection. Not only does sexual selection provide an explanation for traits that hinder survival, but it explains other observations in nature as well. For example, the traits that males use in attracting mates are often wildly exaggerated structures or behaviors. In addition, such traits are usually different between males and females within a species (a phenomenon known as sexual dimorphism). Furthermore, these traits are typically only expressed in sexually mature individuals, and frequently only during the breeding season (such as bright plumage in birds). In other words, the expression of traits that enhance mating success is often restricted to adult males in the breeding season. If

such traits were advantageous for survival, then we would expect that natural selection would lead females and juveniles to express them as well. Sexual selection can explain this discrepancy and can also explain behaviors such as the tendency of males to fight or defend territories.

The power of sexual selection in explaining this broad array of traits is perhaps matched only by the awesome diversity of ways in which males attempt to attract females. Animals have evolved sexual communication by the use of every sense. Visual, acoustic, and chemical signals displayed by males are very common. Brightly colored plumage in birds is a familiar example in the visual realm. The songs and calls of crickets, frogs, and birds (and many other animals as well; for a wonderful cricket song Web site, see <http://buzz.ifas.ufl.edu>; see also figure 1) are also familiar examples of acoustic signals typically produced only by males to attract mates. Males of some species produce chemical signals in courtship. The chemical signals produced by male terrestrial salamanders, for example, reduce the amount of time a pair spends in courtship (Rollmann, Houck, & Feldhoff, 1999; for a fantastic video clip of salamanders transferring pheromones, see (<http://oregon-state.edu/~houckl/>). Other ways in which males attract mating partners include the defense of territories (where males secure some area in the breeding habitat and have access to females who come to their nest), the possession of large body mass (in many species, females mate preferentially with larger males), or the offering of courtship feeding or gifts (as in the scorpion fly, where males provide a dead prey item to females during courtship). In all these varied circumstances, it is the adult male who displays exaggerated signals or expends energy to attract mates. Thus, these behaviors or morphologies are sexually dimorphic and context dependent in that they are expressed during the courting of females. Because they are conspicuous and can attract predators, or are demanding of energy that might be put into growth or maintenance of body condition, such traits may be costly in that they may reduce male survival. However, they add to male fitness by increasing mating success and the number of offspring a male sires.

Why Does Sexual Selection Occur?

To understand how the process of sexual selection leads to sexually dimorphic, exaggerated signals or costly behaviors often expressed only by males, we

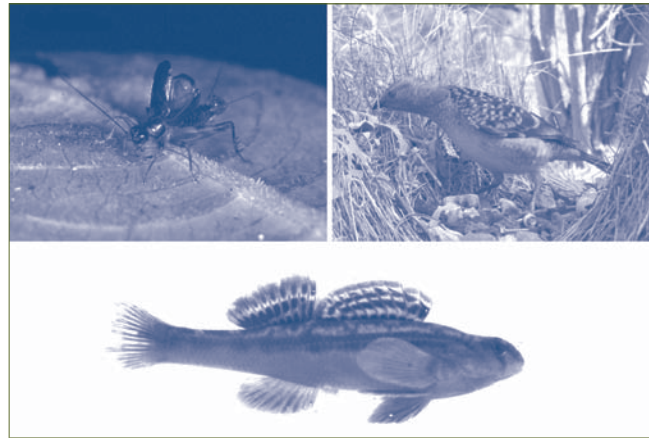


Figure 1. Study subjects of the authors. (a) Male crickets of the genus *Laupala* (studied by Kerry L. Shaw) produce songs that females are attracted to in their search for mates. Song is produced by the forewings, and both wing morphology and singing behavior are sexually dimorphic, expressed only by males. (b) Males of North American darters (studied by Tamra C. Mendelson) display bright breeding coloration with strong and highly visible contrast in the dorsal fin. Shown is *Etheostoma zonistum*. (c) Male spotted bowerbird, *Clamysdera maculate*, (studied by Gerald Borgia) arranging decorations on his bower. Males collect objects from the environment and use them as display objects to attract females for mating.

need to think more specifically about the different components of fitness (figure 2) and how they might differ between males and females (figure 3).

Returning to the three components of fitness discussed above, first consider survival. If an individual has normal mating success and fecundity, but lives a long life relative to others in the population, he or she will enjoy a relatively greater fitness than others. This will be true for both males and females. However, when we consider exceptional mating success in some species, we see a very different story. Males with a normal life span and fecundity but exceptional mating success can enjoy a much higher fitness than other males who obtain few (or no) matings. In contrast, in most (but not all) animal species, higher mating success does not appear to confer greater fitness to females.

This difference between males and females in the potential to achieve greater fitness through higher

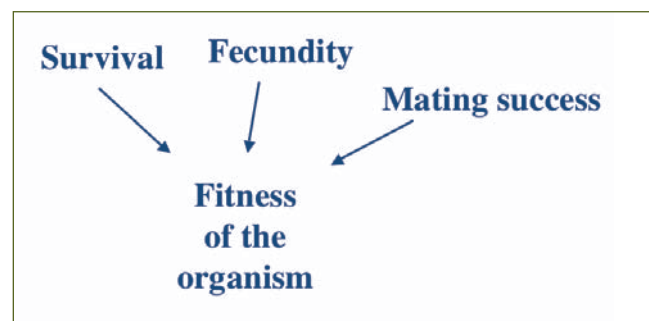


Figure 2. The three major components of fitness.

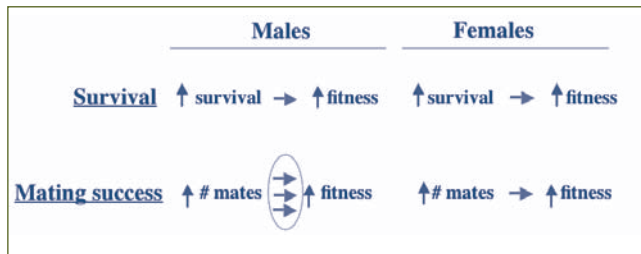


Figure 3. The effect of increased survival and increased mating success on the fitness of males relative to females.

mating success has been observed in natural as well as experimental populations, a perspective appreciated by Bateman (1948) as a result of an experiment conducted with the common fruit fly, *Drosophila melanogaster*. In his experiment, Bateman (1948) set up replicate populations including three males and three females, and the number of matings and the number of offspring, per individual, were counted. Eye color varied among the individuals in the experiment, and owing to the inheritance patterns of eye color, the parents of every offspring could be identified. These experimental conditions allowed Bateman to pose the question: Does reproductive success, measured as the number of offspring per individual, differ when an individual mated once, mated twice, or mated three times? The results of the experiment clearly showed that the more often a male mated, the more offspring he sired. This was not seen among females that differed in the number of mates they had (figure 4). Those females that mated three times did not produce any more offspring than females that mated only once or only twice. This and subsequent studies show that males can obtain greater fitness benefits from increased mating success than can females, and this has generally been shown to be true in species where males do not provide parental care to offspring. This phenomenon can lead to increased intensity of sexual selection on males, and thus the evolution of exaggerated, sexually dimorphic traits used by males to attract females.

The key to understanding why males gain greater fitness benefits from increased mating success than do females is in the asymmetries inherent in sexual reproduction. Parental investment in gametes is typically higher in eggs than in sperm. Eggs are larger than sperm and are fortified with energy and nutrients, and as a result, eggs are more expensive to produce than sperm. Consequently, there is a basic trade-off between the energy invested per gamete and the number of gametes produced. Males produce vastly more sperm than females produce eggs, but

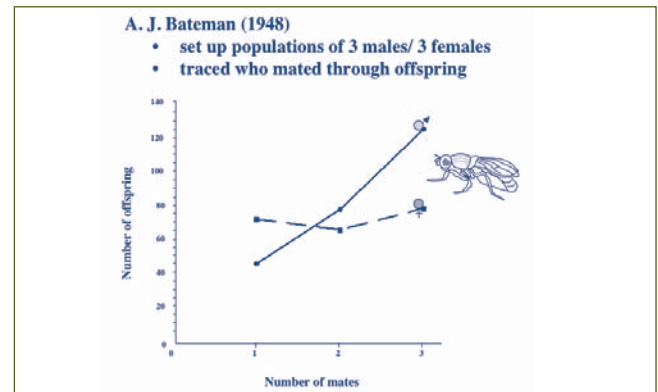


Figure 4. The number of offspring produced by males (solid line) and females (dashed line) in *Drosophila melanogaster* when they had one, two, or three mates. Offspring number goes up with increasing number of mates for males but stays roughly the same for females. (Drawn with data from Bateman, 1948.)

each sperm is much smaller and less costly to produce. In *D. melanogaster*, like most species, males produce large quantities of sperm whereas females produce far fewer eggs. With many more sperm than eggs available for fertilization, it follows that many sperm never find eggs to fertilize, while the reverse is not the case. In fact, in many species, one or two matings can result in an adequate number of sperm to fertilize all the eggs a female might produce in her lifetime, particularly when the female stores sperm for long periods of time (as in *D. melanogaster*). Thus, a female will not gain additional offspring by gaining additional matings because, once mated, she already has all the sperm necessary to fertilize her eggs. In contrast, the more females with which a male mates, the more offspring he can potentially sire. Putting all this together (figure 5), differences in the costs of reproduction will determine whether there are differences in mating success between males and females, and whether those differences translate into

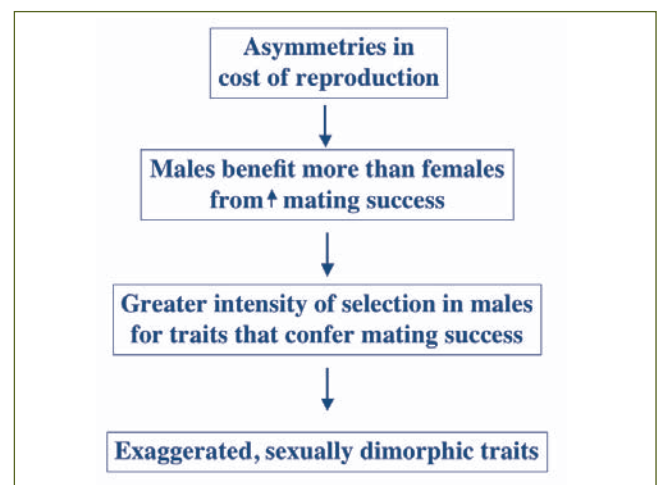


Figure 5. Flow diagram outlining the causes of sexual selection that lead to evolution in male traits.

bigger fitness payoffs for males than for females. In summary, evolutionary change will occur by sexual selection when three conditions are present: (1) males vary in their ability to acquire matings or fertilizations; (2) variation in the traits that allow males to achieve greater mating success are genetically inherited, and (3) some males reproduce better than others because they possess these traits. Evolutionary change by this process has resulted in an astounding array of sexual dimorphisms.

The Mechanisms of Sexual Selection

Two main types of selection on male traits were identified by Darwin in his seminal work on sexual selection, and these provide a solid foundation for the theory today: male-male competition (intersexual selection) and female choice (intrasexual selection). Male-male competition occurs when there is competition among males for access to females resulting in differential mating success among males, whereas female choice for particular traits in males results in differential mating success among males.

One of the most conspicuous examples of male-male competition is straight-out combat, where males use some weapon to fight other males over access to mating with females. Some of the most elaborate examples of sexual dimorphism are male antlers, horns, and other weapons (figure 6). If traits have evolved by sexual selection through male-male competition, we would hypothesize that the male with the larger weapon (or the larger body size, or the more aggressive behavior) wins more fights, and thus wins a greater number of opportunities to mate with females.



Figure 6. Male-male combat in the elk, *Cervus elaphus*. A male uses the heavy, wide antlers in clashes with other males in an attempt to control a harem of females during the breeding season. Males grow a new set of antlers each breeding season. (Original drawing by Kerry Shaw.)

Another form of male-male competition is invisible to the eye (i.e., cryptic), but apparently quite common. Sperm competition occurs when females mate with more than one male over a short period of

time. At the biochemical level, sperm compete for access to eggs in the fertilization tract of the female. A male that produces sperm that can outcompete another male's sperm will achieve more fertilizations, and when this is possible, we expect selection on males for better fertilization ability. This process is thought to be common in many animals (Howard, 1999). The mechanism underlying this process is not well understood, but could be as simple as increasing the numbers of sperm transferred in a given mating. A recent example comes from the meadow vole, *Microtus pennsylvanicus* (delBarco-Trillo & Ferkin, 2004). The meadow vole is a small rodent with a widespread range across North America (for further reading, see Neuburger, 1999). Importantly, males and females both have many mating partners, and thus males regularly face the possibility of sperm competition. As is typical for studies that attempt to detect the presence of sperm competition, subject male meadow voles were mated to individual females under two conditions. First, a male was mated with a female in isolation of other social cues, and second, the same male was mated with a female in the presence of another male's odor. In mammals, much communication occurs by the sense of smell, so the authors manipulated the subject male by introducing into the mating chamber the cage bedding of another male, thus introducing cues that the female had previously mated (although under both treatments, females had not previously mated). The authors reasoned that if a male could detect the threat of sperm competition, he would increase the quantity of sperm he devoted to a particular mating in order to increase his chances of gaining fertilization opportunities (the probability of successful fertilization is often correlated to the number of sperm present). As predicted, delBarco-Trillo and Ferkin found a significant increase in the number of sperm invested by males in the presence of another male's odor when mated to these females.

As with male-male competition, there are many theories that explain how female choice can cause male sexual traits to evolve by altering the relative mating success of males in a population. Recently, much attention has focused on the material benefits model and the good genes model. Both ideas center on the fundamental argument that it is advantageous for a female to choose a male in order to obtain maximum benefit from the mating.

Females sometimes choose mates that will provide a superior resource, such as courtship feeding or better access to food for the female or her offspring (e.g., a good-quality territory that the male defends). Males that provide better material benefits are therefore chosen by females more often, and thus they achieve higher mating success. If variability in the male trait exists (for example, aggressive territorial behavior or foraging ability) and can be inherited, and females can associate the trait with superior male provisioning and choose them, then the trait should evolve by sexual selection. In effect, females are the agents of sexual selection because they choose which males mate most often and therefore leave the most offspring. But it is also important to realize that in this model, females who choose are favored by natural selection because by choosing they enjoy enhanced survival or fecundity due to receiving a better resource (e.g., by achieving a greater egg laying capacity).

The good genes model proposes that females choose males as mates that carry superior genes that lead to greater survivorship. Thus, in the context of mating, males may provide nothing to females other than sperm, but females benefit from choosing males with superior genes because their offspring will have higher fitness. For example, they may have faster growth rates, which in many organisms is associated with higher fitness. In this model, the fitness benefit is enjoyed by the *offspring* of the female who chooses the male with superior genes, rather than the female herself.

There are several challenges in the study of female choice and its importance in sexual selection, but there is widespread evidence for the fact that females are choosy in mating. In many systems, from insects to fish, amphibians, birds, mammals, and so on, females have been shown to have preferences for one value of a trait over another, leading them to choose some males over others as mates. But the observation that females choose begs the question, Do females choose a male for good material benefits or good genes? And if such an answer can be obtained, how does a female make a good choice? Establishing the links necessary to conclude evolution by sexual selection requires answering additional questions such as: Does female choice lead to greater mating success in males? Do females enjoy increased fitness from the choice? Determining whether the increased female fitness is due to material benefits or good genes is also very difficult.

At least in mating systems where males provide material benefits, females may have the opportunity to assess the quality of the benefit they are getting and respond to this information. One of the classic examples of a mating system under sexual selection is the scorpion fly, *Bittacus apicalis*. In this species, males attract females into mating with a nuptial offering in the form of a dead prey item (usually another insect). The male and female copulate while the female consumes the prey item. Thornhill (1976) demonstrated that the larger the prey item, the longer the female takes to consume it, and consequently the longer the copulation and the greater the sperm transfer from her mate, which translates to greater mating success for that male. Thornhill also demonstrated that females who choose males with larger prey items subsequently lay more eggs per unit time than females that are less choosy, suggesting that larger nuptial gifts translate into higher female fitness as well. Because of the immediacy of the resource, females can assess the benefit directly.

In other animal systems where females obtain a material benefit, such as occur in many bird species where males feed their mates, the quality of a benefit may not be apparent until after breeding has begun. For example, the great tit, *Parus major*, is a widespread and well-studied European bird. This species is socially monogamous, where the male and female nest together for the breeding season and males feed females during the egg laying and incubation period. Males also participate in the care of offspring and defense of the nest. It has been hypothesized that a female who chooses a male that is better able to feed her or her offspring will enjoy greater fitness, and so female choice should be favored by natural selection because choice will increase her reproductive output. But how does a female know whether a particular male will be a good provider? Male signals that may give females a clue as to the male's parenting prowess have been referred to as indicator traits, or traits that provide females with information about the male. Males of *P. major* are variable in the size of a striking black vertical breast stripe (figure 7), and Norris (1990a) found that females who paired with males with larger stripes lay larger clutches, leading to the conclusion that males with larger breast stripes achieve higher fertilization success. In addition, Norris (1990b) was able to show that males with larger stripes are more vigilant in defense of the nest and that their offspring have faster growth rates,

suggesting these males are better fathers. Norris concludes that males that have larger breast stripes have higher fertilization success because females choose them, and females that choose such males have higher fitness because their offspring have better fathers.



Figure 7. A male great tit, *Parus major*, with breast stripe. Females choose males with a larger breast stripe, and males with a larger stripe are better providers and defenders of the nest. (Original drawing by Kerry Shaw.)

Females also choose males in animal species where the male apparently gives only his sperm to the mating. This phenomenon has been documented many times (Kokko, Brooks, Jennions, & Moreley, 2003) but presents a puzzling situation because the benefit to females (the basis for their choice) is not obvious. However, in such systems, females do choose to mate with some males and not others, perhaps by selecting males that carry “good” genes, that is, genes that enhance the fitness of their offspring. One fascinating context for this behavior that has been demonstrated in some insects, frogs, and birds is known as the lek, where males assemble in an area for courtship display and to attract the attention of females. These male groups are thought to present opportunities for females to choose among males who engage in competition, for example, through vocalizations, acrobatic feats, or bouts of aggression. Yet in lekking species, females usually gain only sperm. These contests among males may reveal their competitive abilities, allowing a female to select a mate of superior genetic quality.

Especially prevalent in birds, extrapair copulation is another context in which females gain only sperm through a mating. In social species where the male and female are monogamous and form a pair-bond for the breeding season, males (the social mate) may provide food to the female or her young and assist in building or defense of the nest. Thus, as in *P. major*, the material benefits to female mate choice are clear. However, in such systems it has been shown repeatedly that females also sneak matings with other males

(the extrapair mate), in addition to their social mate. What benefit would a female have in mating and producing young with a second male who provides nothing but sperm? One answer has gained strength recently. It may be that females choose social mates for their superior foraging and feeding ability, but sneak extrapair sires for some of their young for the genetic benefits of disease resistance. Studying the bluethroat, *Luscinia svecica*, another socially monogamous European bird, Johnsen, Andersen, Sunding, & Lifjeld, 2000) found evidence of frequent extrapair copulations (29 percent of all young in their study were from extrapair matings). These investigators were able to assess the response to infection in offspring from the same nest that resulted from social as compared with extrapair matings (hence these offspring had the same mother but different fathers). They reached the exciting conclusion that extrapair young are more disease resistant and suggest that females may seek extrapair mates with immune-resistant genes more compatible with their own. What emerges from these results is the idea that females pair-bond to obtain male assistance with rearing young, but the process forces some females to mate with genetically less compatible or undistinguished males. Females can ameliorate these negative effects of pair-bonding by engaging in extrapair copulations with males that are genetically superior or more compatible with their own genes.

It is possible, of course, that a male could be chosen for both material benefits and the good genes he can contribute to offspring. Thus, these forces may act together in forming the mate choice behavior of females. As scientists, we are usually interested in establishing the validity of such hypothesized causes, however, and we therefore look for test systems in which one potential cause can be extricated from the other. Thus, mating systems where males contribute only sperm are particularly useful because the potential for material benefits to play a role are minimized.

Sex Role Reversal: Exceptions that Prove the Rule

As discussed above, the foundation on which sexual selection theory is built is that a male can achieve much higher fitness by increasing the number of matings he obtains, whereas multiple matings in females will increase her fitness only marginally, if at all. This disparity results because one gender, usually the female, is less available for mating than the male, owing to the scarcity of eggs a female has for

fertilization and the fact that a single male can usually provide enough sperm to fertilize the eggs of many females. However, in some species successful reproduction apparently requires a greater investment by males. Because of a limited supply of resources (such as energy the male needs to feed the female, or limited brood space, or nest size in situations where the male cares for the young), there may be more females than males available to mate at any given time. This reversal of roles has led to some of the most satisfying tests of sexual selection theory. Role-reversed species, where males and females swap the behavioral roles they typically display (for example, males, rather than females, raise and care for the offspring), have been documented in crustaceans, insects, fishes, frogs, and birds (Gwynne, 1991; see <http://www.zoo.utoronto.ca/dgwynne/labpage/> for active research in this area). This swapping of roles enables scientists to test predictions of sexual selection theory, such as, Do females compete for males? Do males choose among females? Does male choice result in higher fitness for males? Is there variance in mating success among females because of male choice?

Studies of the Australian *Kawanaphila* (figure 8) by Gwynne and Simmons (1990) have revealed that roles are reversed between males and females in this group. In katydids, males present females with edible gifts during mating that envelop the spermatophore, or the capsule that contains the sperm. This gift is technically known as the spermatophylax, but is casually referred to by Gwynne as the “mozzarella cheese of the insect world” (personal communication). Once the male has produced and transferred the spermatophore with attached spermatophylax to the female, the female begins to chew on the spermatophylax, which provides nutrients to the developing eggs of the female. *Kawanaphila* katydids live in the dry western desert of the Australian continent where food resources are limited. Under conditions of limited resources, females seek matings, as they are a source of nutrition. However, a male’s ability to produce a spermatophore and spermatophylax is limited by the available resources. Thus, Gwynne and Simmons have documented that under conditions of limited food availability, more females seek matings than there are males available, setting the stage for sex role reversal. They were also able to show that females compete for access to males, and that males choose to mate with larger females. As these females have more eggs to fertilize than smaller females,

males that choose larger females fertilize more eggs and enjoy greater fitness, and larger females have higher mating success than smaller females. Gwynne and Simmons hypothesized that if food were not the limiting factor, more males would be available for mating. They were able to provide support for this idea by supplementing food in a test population and witnessed the expected switch to the more typical roles where relatively fewer females and more males are available for mating. This increase in the number of available males relative to females was due to an increase in the number of males able to produce the spermatophore and spermatophylax.

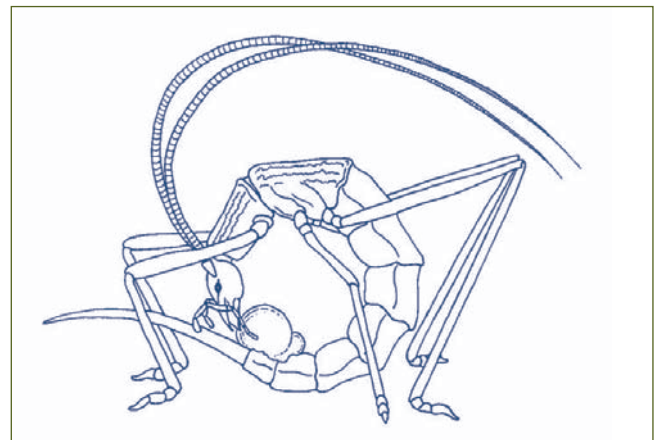


Figure 8. A female katydid of the genus *Kawanaphila* chewing on the spermatophylax. Her head is doubled back to reach the spermatophylax and spermatophore that are attached near the ovipositor. (Original drawing by Heather Proctor.)

Take-Home Messages

Regardless of the role that males or females take in a mating system, mating and fertilization success are an indispensable component of fitness. Over a century since Darwin’s lesser-known book on sexual selection, mounting evidence supports his original insight that selection can cause sexual dimorphism and exaggerated secondary sexual traits to evolve even when these features reduce survival. Typically, males gain a greater fitness advantage than females by increasing mating success. But these roles can be reversed when resource conditions lead to increased male investment in offspring, resulting in some of the best opportunities to test aspects of sexual selection theory. Genetically inherited traits that increase competitive success for mates among males (or among females in role-reversed species) will be favored by sexual selection.

Acknowledgments

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References

- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, 2, 349–368.
- Darwin, C. (1871). *Sexual selection and the descent of man*. London: John Murray.
- delBarco-Trillo, J., & Ferkin, M. H. (2004). Male mammals respond to a risk of sperm competition conveyed by odours of conspecific males. *Nature*, 431, 446–449.
- Gwynne, D. T. (1991). Sexual competition among females: What causes courtship-role reversal? *Trends in Ecology and Evolution*, 6, 118–121.
- Gwynne, D. T., & Simmons, L. W. (1990). Experimental reversal of courtship roles in an insect. *Nature*, 346, 172–174.
- Howard, D. J. (1999). Conspecific sperm and pollen precedence and speciation. *Annual Review of Ecology and Systematics*, 30, 109–132.
- Johnsen, A., Andersen, V., Sunding, C., & Lifjeld, J. T. (2000). Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature*, 406, 296–299.
- Kokko, H., Brooks, R., Jennions, M. D., + Moreley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London B*, 270, 653–664.
- Norris, K. J. (1990a). Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. *Behavioral Ecology and Sociobiology*, 26, 129–138.
- Norris, K. J. (1990b). Female choice and the quality of parental care in the great tit *Parus major*. *Behavioral Ecology and Sociobiology*, 26, 275–281.
- Neuburger, T. (1999). *Microtus pennsylvanicus*. Retrieved March 25, 2005, from University of Michigan Museum of Zoology, Animal Diversity Web site:
http://animaldiversity.ummz.umich.edu/site/accounts/information/Microtus_pennsylvanicus.html
- Rollmann, S. M., Houck, L. D., & Feldhoff, R. C. (1999). Proteinaceous pheromone affecting female receptivity in a terrestrial salamander. *Science*, 285, 1907–1909.
- Thornhill, R. (1976). Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *American Naturalist*, 110, 529–548.

Speciation: The Origin of Species

Robert M. Zink

Addressing this title, “Speciation: The Origin of Species,” seemingly carries with it a daunting task—to summarize the contributions of the most famous science book in western society, Charles Darwin’s (1859) *On the Origin of Species by Means of Natural Selection*. However, it has been apparent since the book’s publication that, in fact, Darwin dealt little with the origin of species in his famous book. Instead, he concentrated mostly on changes that occur within populations via natural selection. In this chapter, I will summarize what is known about the origin of species, known today as speciation. In beginning, I note two important points: (1) evolutionary biologists do not doubt that speciation occurs, although we argue about the details, and (2) different evolutionary biologists would write this chapter very differently, which does not change point one.

Speciation Defined, Natural History, and How to Study Speciation

Species originate from the splitting of preexisting species (figure 1). In a sense, species leave offspring in the form of new, descendant (referred to as daughter) species. During the 3.5 billion years of life on Earth, hundreds of millions of species have existed, each a product of the speciation, or splitting, process, so it is obvious that speciation is a frequent occurrence. Speciation is the way in which biodiversity is generated. It would seem that with so many speciation events having occurred during Earth’s history, speciation should be relatively easy to study and understand. But speciation occurs over evolutionary timescales. That is, unlike a chemical reaction occurring nearly instantaneously in a test tube, speciation might take thousands to a million years. It is therefore unlikely that we can observe the origin of a new species within a human lifetime. Thus, it requires that we use methods of inference to decipher the details of how species arise. In particular, it requires that we compare newly evolved species, or sister species, and study their geographic distributions, and genetic, morphological,

physiological, ecological, and behavioral differences. Simply put, sister species are each other’s nearest relatives. Because sister species share a common ancestor with each other more recently than either does with any other species, they are the most appropriate species to compare and represent the “signatures” of speciation that should be most legible to scientific investigation. That is, we can best infer what happened during speciation if we compare sister species. If the species being compared are too old and are separated by many speciation events, the differences due to speciation cannot be deciphered from those that occurred afterward. Just like any detective work, the trail gets colder with time since the event (speciation, in our case).

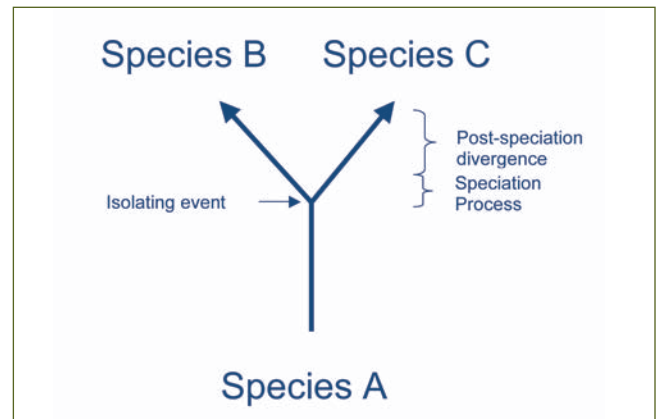


Figure 1. Simple model in which species A undergoes speciation, resulting in two daughter species, B and C. Note that the speciation process occurs over time; best estimates are from thousands of years to a million years, depending on the group and situation. Note also that when we compare sister species B and C, some of the differences are not directly associated with speciation, rather with being different species. That is, divergence in morphology, ecology, behavior, and genetics continues to occur after speciation. Therefore, it is difficult to know which of the differences between B and C are due to speciation and which occurred afterward.

Evolutionary biologists involved in deciphering the details of speciation infer aspects of two basic phenomena: what I will call the geography of speciation, and the mechanisms of speciation. The former entails changes in the geographic distribution of ancestral populations that facilitate speciation. The latter

includes the genetic, ecological, behavioral, physiological, and morphological changes that occur to make a species new and different from preexisting species. How these changes are related to speciation depends on what one considers a species, which is explored briefly here. Lastly, the types of changes that affect both premating and postmating isolation are also reviewed.

The Geography of Speciation

One of the fundamental steps in the origin of species is the physical isolation of ancestral populations. A typical scenario involves an ancestral population that is split by the formation of a mountain range, a river, a drifting island or continent, a land bridge, or an environmental change that makes an intermediate part of the range uninhabitable (figure 2). This process is termed vicariance. Populations isolated across geography are said to be allopatric. Allopatric populations also can be a result of dispersal to a new site (with no back or return dispersal). In many cases, it is thought that an especially conducive situation is a population that is not only allopatric, but small. Evolutionary changes can happen relatively quickly in small populations. However, observing species with small, isolated ranges is relatively rare because small populations are vulnerable to extinction. Thus, it is thought that speciation might quickly occur in small, allopatric populations, followed by an increase in the range of the new species. Nonetheless, the splitting of an ancestral population, isolating at least two groups of individuals formerly in contact, is the basic geographic step in the speciation process.

If it is the case that allopatry is the first step in speciation, then one ought to often note that sister species do not occur together, but have abutting

ranges. In many cases, it is obvious what the barriers are, such as mountain ranges. In other cases, the barrier is no longer apparent, but when one examines the distributions of sister species, they occur adjacent to one another. Shrimp that occur on opposite sides of the Isthmus of Panama provide an example of a barrier causing allopatry and setting the stage for speciation. Geologists have discovered that about 3 million years ago, a land bridge rose up to connect the two Western Hemisphere continents, North America and South America. This provided a corridor for terrestrial plants and animals, but presented a barrier to marine organisms. Organisms living in the ocean were thus isolated by this isthmus from what had been a continuously distributed population. Nancy Knowlton and her colleagues studied species of shrimp that occur on both sides of the isthmus of Panama, either in the Pacific or Caribbean oceans. It had been known that differently appearing populations occurred on either side of the Isthmus, but it was unclear whether they were sister taxa or even genetically different. Knowlton, Weight, Solorzano, Mills, & Bermingham (1993) found that more often than not, genetically distinct sister populations of each species occur on either side of the isthmus (figure 3). This is very strong evidence in support of the notion that the land bridge isolated marine environments in which the shrimp are found and provided the isolation necessary for them to undergo speciation. A moment's reflection reveals that if this were not true, and that species formed for some other reason, then one ought to find sister species in the Caribbean, sister species in the Pacific, and sister species on either side of the isthmus. Instead, there is a very strong pattern of sister species occurring on opposite sides of the land bridge.

As mentioned above, it is also possible for individuals from an ancestral population to disperse to a new area, start a new population, and, if there is no return dispersal, differentiate into a new species. An often-cited example of dispersal leading to speciation is that of fruit flies (genus *Drosophila*) in Hawaii. The flies are extremely diverse in Hawaii, with over 600 species recognized, showing a huge variety (for flies) of morphological and behavior divergence. There is even a species that lays its eggs in spiders. The geologic history of the islands provides a context in which we can see how dispersal could lead to allopatric speciation. We know that roughly under the island of Hawaii there is a stationary hot spot,

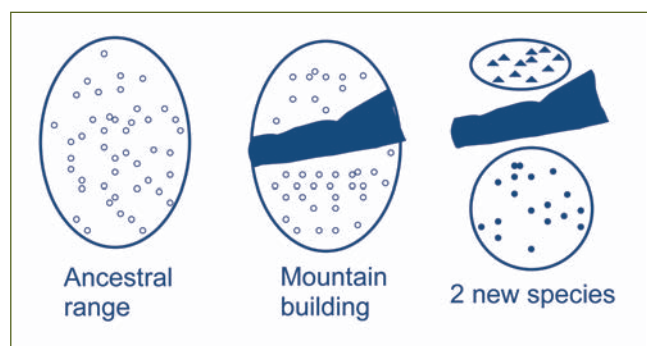


Figure 2. An ancestral population becomes divided over time by a barrier, in this case a mountain range. Because individuals are isolated geographically, they no longer exchange genes. If environments are different, they can adapt to local differences in temperature, humidity, and so on, and become different. If they become different enough (depending on your concept of species), they will be new species.

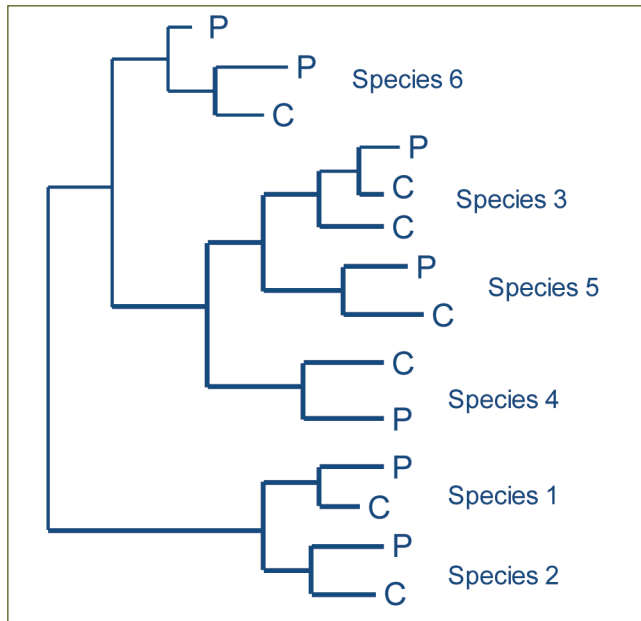


Figure 3. An evolutionary tree based on genetic differences for six species of shrimp found on either side of the Isthmus of Panama. The tree shows that sister groups occur on either side of the isthmus, supporting the notion that the formation of the isthmus isolated once-continuous marine populations, allowing them to differentiate and speciate in allopatry. (Knowlton, Weight, Solorzano, Mills, & Bermingham, 1993).

and that as the Pacific plate drifts over it, magma is periodically forced upward creating a volcanic island. The plate travels in a northwestward direction, meaning that the islands in the Hawaiian chain drift northwest as well, being eroded over time. Of the five main high islands, Kauai is the most northwestward, and hence the oldest (to the northwest of Kauai are very low atolls and sunken islands that have eroded away as they drifted over time), whereas Hawaii is the youngest (about 450,000 years old) and largest.

Given this established geologic history, we can predict that the most recently evolved species of *Drosophila* ought to be on the island of Hawaii, with successively older ones being on more northwestwardly islands. That is, after an island drifts northwest, individuals of species on it can disperse southeastward and colonize the next, newly formed island. Using comparisons of mitochondrial DNA, this is exactly what has been observed (figure 4). In particular, the oldest species is on Maui, and successively more recently evolved species are on younger islands, with a series of newly evolved species distributed allopatrically on Hawaii (DeSalle & Giddings, 1986). Thus, we made a testable scientific prediction based on the known geological history of the islands and tested it with comparisons of DNA. We were unable to falsify our hypothesis because the match between the phylogenetic relationships of species and the age of

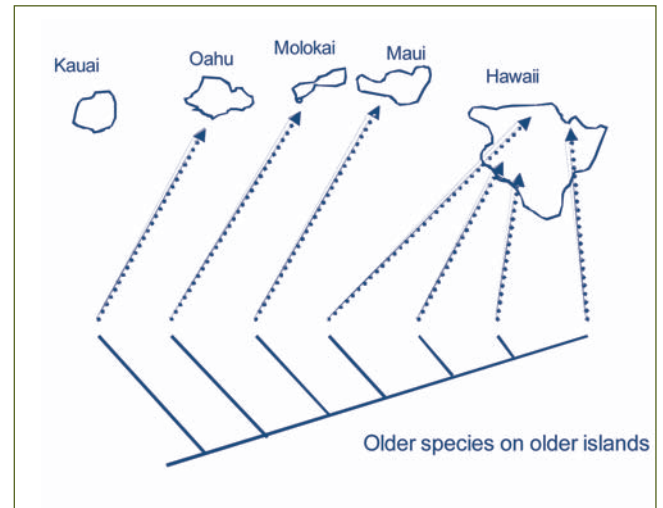


Figure 4. Speciation of fruit flies in Hawaii. An evolutionary tree (bottom) shows that relatively older species (toward the left of the tree) occur on the older islands, and newly evolved species occur on the youngest island, Hawaii (tree from DeSalle & Giddings, 1986). Geologists have discovered that as islands drift toward the Northwest and as new islands form to the Southeast the latter are then colonized by populations from older islands. From left to right on the tree: *Drosophila hemispiza*, *D. differens*, *D. planitibia*, *D. silvestris* (Hilo side), *D. silvestris* (Kona side), *D. heteroneura* (Kona side), and *D. heteroneura* (Hilo side) (after Freeman & Heron, 2004).

the islands on which they occur supports the concept of dispersal leading to allopatry and subsequent speciation.

As mentioned above, another factor promoting speciation is population size. If an allopatric population is small, it might speciate more quickly because there are few individuals that must acquire the new species-defining traits. A possible example is illustrated by kingfishers on and around the island of New Guinea (Mayr, 1942). On the main island, there are three allopatric populations, each relatively large, which differ subtly in their outward appearance. On five offshore islands, there are small populations, each of which has at one time been thought to be a distinct species. In effect, there are two kinds of allopatric populations of kingfishers: large, main-island populations and small, offshore island populations. Populations of each type are separated from others by approximately the same geographic distance. This is important because the farther away two populations are, the less likely it is for colonists to reach the other population. However, in the case of the kingfishers, it is only the small populations that have differentiated morphologically to species level, not the large, main island populations. Therefore, one can see that in allopatric populations separated by the same geographic distances, the small populations are more likely to undergo major morphological changes. It is important to note that, to my knowledge, these kingfishers have

not been studied with modern molecular genetic methods that could be decisive in showing the effects of small, isolated populations.

Numerous other examples have been discovered that support the generalization that speciation occurs in allopatric populations. For instance, one has only to look at bird species to see that newly evolved species do not live in the same area, but instead are allopatric. Breeding ranges of North American birds are freely available on the Web at: <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>. For example, examine the ranges of the western meadowlark (*Sturnella neglecta*) and eastern meadowlark (*S. magna*). These closely related species overlap slightly in the Great Plains of North America, but are essentially allopatric. The same can be said for the Baltimore oriole (*Icterus galbula*) and Bullock's oriole (*I. bullockii*), the myrtle warbler (*Dendroica coronata*), and Audubon's warbler (*D. auduboni*). There are hundreds of other such examples in all animal and plant groups. Although we have not observed the process of speciation, the clear pattern of sister-species distributions is strong verification of the principle of allopatric speciation. Otherwise, why would it be so common to find sister species with adjacent distributions?

The well-established fact that newly evolved species are allopatric has two interesting correlations. The first is that the ecological differences that would allow species to coexist in the same area must evolve more slowly than the differences that demarcate species. That is, although we think that newly evolved species have enlarged their new ranges, why haven't they invaded the homeland of their sister species? The reason is that they are likely too ecologically similar to permit coexistence—competition must keep them allopatric for a relatively long period to support our observation of the high frequency with which sister species are allopatric. Or, alternatively, it is possible that it just takes more time to elapse for sister species to invade each other's range.

A second, related prediction about the ranges of species is that the degree of range overlap should be correlated with evolutionary distance. Just think about the birds in a local area: there are many kinds present in the same park, for example. How or when did they become sympatric (living in the same area)? In theory, the longer it has been since speciation, the more likely it is for species to coexist in the same area. Another way of expressing this is to say that species that coexist are usually separated by two or

more speciation events (figure 5). We can measure a species' "age" by its DNA distance from its nearest relative. When ages of species pairs are plotted as a function of the degree to which their ranges overlap, we observe a positive correlation. This observation supports the notion that geographic isolation (allopatry) facilitates the origin of species from preexisting species and that for a period of time after speciation they are allopatric, because they are too ecologically similar to coexist.

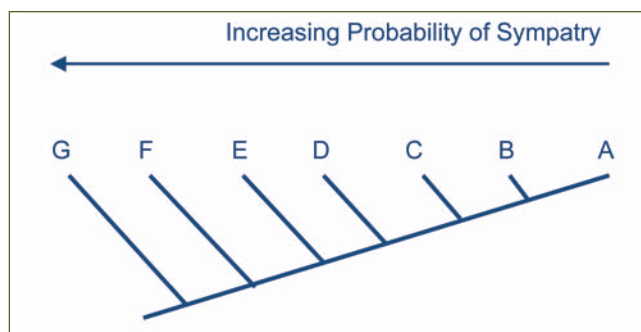


Figure 5. Hypothetical evolutionary tree. Species A and B are the most recently evolved (sister species), and species increase in relative age to the left. It is most likely to find the most-distant pairs of species sympatrically (A, G), whereas A and B are most likely to be allopatric. Intermediate pairs of species would have intermediate probabilities of being sympatric.

Let's look at a potential exception to the notion that geographic separation (allopatry) precedes speciation. In particular, some researchers have noticed that sister species occur sympatrically, albeit rarely. How could this occur? Perhaps they were allopatric, but quickly evolved different ecological habits and immediately invaded each other's range. Another possibility has been termed sympatric speciation. Requirements for this mode of speciation are that the new species arises from within the range of the sister species, and that individuals are in close proximity. The question is how the two groups became isolated and remained separate long enough for speciation to occur. It is possible to imagine a species that is found only on a single host plant in an area, in spite of many other plants occurring there as well. If an individual female insect makes a mistake and lays her eggs on a new host plant, and her babies survive on this host plant, remain on it for their lives, and mate with either siblings or others that were accidentally put there, then a new species could arise. This requires that once a new host is used, individuals remain true to this new host and there is no continual movement from the old host to the new host (which would prevent divergence).

A possible example of sympatric speciation involves flies that parasitize apples and hawthorns.

The flies (*Rhagoletis pomonella*) and hawthorns are native to North America, whereas apples were introduced a few hundred years ago. It is thought that flies (maybe only one?) laid eggs on apples, and that the young subsequently stayed on the apples for all reproductive activities. The flies are very similar in their appearance, but they have detectable genetic differences and prefer to mate with flies raised on the same host as themselves. Therefore, the isolation needed for speciation to occur is not provided by geographic isolation, rather, it is intense preference for different food resources. Adaptation to this new resource had the secondary consequence of resulting in at least some degree of reproductive isolation, likely that involved in mate choice. Despite the theoretical attractiveness of sympatric speciation, it is not thought to be very common in any group.

Plants and Hybridization

Speciation in the plant world adds at least a couple of new twists (Freeman & Heron, 2004). First, many botanists (scientists who study plants) think that new species arise from the hybridization of two species. Thus, unlike the flickers discussed below, two species might meet in an ecologically disturbed area and hybridize. If the hybrids are more fit in the intermediate habitat, they will be favored there and could become isolated from the parental species. Although the exact figure is under debate, perhaps even a majority of plants hybridize in this way. The reasons are speculative, but this appears to be an infrequent way that speciation occurs in animals.

Another aspect of plant speciation is the tendency to undergo polyploidy, or duplication of chromosome number. One can observe allopolyploidy, where two sets of chromosomes come from different parental species, or autopolyploidy, where a meiotic mistake results in gametes having (usually) a duplicate set of chromosomes. If offspring have different numbers of chromosomes from their nearest living relatives, they will be unable to breed with either parental species. If the hybrids can interbreed successfully, and remain separate from the parental species, speciation will have occurred.

Mechanisms of Divergence—Beyond Geography

Just because two populations are allopatric does not mean that they will automatically diverge and become new species. However, once allopatric, populations can diverge because of natural selection, sexual

selection, and chance (e.g., genetic drift). There are many examples of divergence as a result of natural selection (see chapter 8 by Douglas Futuyma). For example, it is often observed that individuals of populations of warm-blooded vertebrates living in cold places have larger body size relative to populations in warmer places, a phenomenon known as Bergmann's rule. Being bigger means that the surface to volume ratio favors heat retention (less surface area relative to volume), and this makes being larger in cold climates adaptive. A well-known example of this phenomenon is the house sparrow (*Passer domesticus*), which was introduced into eastern North America in the 1800s and spread across the continent. When Johnston and Selander (1964) studied this species, they found that birds were indeed larger in colder climates. Another example of how natural selection can cause geographically separated populations to diverge is called Gloger's rule. In this case, individuals in populations acquire coloration that helps match the ambient background. For example, in the song sparrow (*Melospiza melodia*), populations in arid areas have pale coloration whereas those in the coastal regions of the Pacific Northwest have sooty plumages (see the Provincial Museum of Alberta's Web site at <http://www.pma.edmonton.ab.ca/natural/birds/collects/collects.htm>). This illustrates how natural selection can modify the external appearance of these birds in an adaptive way.

Sexual selection is another way in which allopatric populations can diverge (see chapter 9 by Kerry Shaw, Tamra Mendelson, and Gerald Borgia). In this manner, individuals of one sex or another select for particular traits. For example, if a new trait arises in males that makes them more attractive to females, by choosing the new male phenotype, females can change the way males look. An example might be the peacock, in which the elaborate train of feathers (on the male's back—a common misperception is that this is the bird's tail) could have evolved if females selected males with larger and larger trains. A reason females might do this (after all, in nature females make choices for good biological reasons), is that by growing a big train, males might "signal" to females that they are good at getting resources, in good condition, free of parasites, or some other sign of their high genetic value. Through this process, females can drive males to have such elaborate plumage ornaments. Females get, theoretically, offspring that are genetically better than they would have obtained from mating with males with inferior trains. For our

purposes, this sort of sexual selection could cause males in allopatric populations to look differently.

In the Hawaiian *Drosophila*, sexual selection is thought to be very important in causing divergence among some allopatric populations. The species *D. heteroneura* has a very large head, relative to other closely related species, and it has been observed experimentally that males with large heads get more matings, and in contests between males with different-sized heads, males with bigger heads usually win (Boake, DeAngelis, & Andreadis, 1997). If females choose as mates the winners of physical combat among males, then head size could increase. Thus, it is likely that the speciation of *D. heteroneura* was coupled with sexual selection for large head size.

Another important aspect of sexually selected traits is that they can spread relatively quickly and across environmentally variable landscapes. The reason is that it is the females who are choosing the phenotypes, not the environment. Recall the discussion of plumage coloration in song sparrows. The pale plumages of the desert areas could not spread into a humid region with a lot of dense vegetation because it would not be adaptive to be so conspicuous. But for sexual selection, this is not a concern, and traits can spread quickly because females (or males, if it is male-male competition) do the choosing.

Genetic drift is also a way in which changes can accumulate between allopatric populations. For example, many DNA polymorphisms between species are likely the result of genetic drift rather than natural selection. When we measure DNA differences between closely related species, we often find that the diagnostic differences are transitions at third base positions in the codons. Recall that the third position in a codon can often wobble—meaning that more than one base can specify the same amino acid. Such changes are thought to be selectively neutral and accrue between allopatric populations as a result of genetic drift.

Speciation and Species Concepts

Natural selection, sexual selection, or chance events can yield allopatric populations that are recognizably different. However, it is important to ask the question: How much or what kind of divergence is enough for allopatric populations to be considered separate species? This requires having a concept of species, with a certain set of characteristics. One of the more popular definitions is the biological species concept

(BSC), which is often formulated as: “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr, 1963). In this view of species, it is not enough that changes occur in allopatric populations, because the new characteristics must function to keep daughter species reproductively isolated. Characteristics that keep populations isolated are termed either premating or postmating reproductive isolating mechanisms (RIMs).

Premating RIMs are features that influence whether or not two individuals from different populations intermate. For example, if a new color pattern evolves in members of an allopatric population, it might be that individuals from the other population would not recognize them as potential mates, and if given a choice, would prefer to mate with individuals having their own color pattern. An example comes to mind from the bird world. The northern flicker (*Colaptes auratus*) consists of two largely allopatric populations, an eastern population that has yellow shafts to the wing and tail feathers and a black “mustache” mark in males, and a western bird with red shafts to the wing and tail feathers and a red mustache mark (a quick Web search will locate images of these birds as well as their distributions). These populations have been considered separate species, the red-shafted flicker and the yellow-shafted flicker. However, the two groups meet in the Great Plains and individuals from each group hybridize. Therefore, according to the BSC, the two groups of flickers are considered the same species. That is, although there are morphological differences that likely evolved in allopatry, these plumage differences do not function as premating RIMs. Because the hybrids appear fit (they survive and reproduce), there are also no postmating RIMs. Speciation has not occurred because of hybridization and survival and reproduction of hybrids.

Many alternative species concepts exist. One alternative is the phylogenetic species concept (PSC). In this view of species (Cracraft, 1989), groups of individuals are species if they have a diagnostic trait that is genetically based (and that does not conflict with other traits). It is interesting but not a requirement that the groups are also reproductively isolated. This species concept is applicable to populations that are allopatric, as well as asexual organisms. (When populations are allopatric, it is necessary to make an educated guess whether they are reproductively isolated, which has long been acknowledged as a drawback

to the BSC). Under the PSC, the two groups of flickers discussed above would qualify as species because they are diagnosable groups. That is, under the PSC, speciation has occurred. Speciation under the PSC is the evolution of groups that exhibit evidence of their having had an independent evolutionary history. This view of species and speciation removes some of the mystery that often surrounds speciation, because the differences that qualify as speciation need not also function as RIMs, which can only be evaluated in sympatry.

There is much debate about species concepts. For the purposes of this essay, the two species concepts discussed above bring into perspective what we need to know about speciation. For both species concepts, allopatric populations diverge via natural selection, sexual selection, or genetic drift. The species concepts diverge because the kind of differences required for speciation in the BSC are more restrictive than those for the PSC. Changes that occur in allopatry must confer reproductive isolation for speciation to have occurred under the BSC viewpoint. For the PSC, speciation occurs if groups are diagnosable.

Isolating Mechanisms and Speciation

Even though the PSC (and other species concepts) does not require that speciation be accompanied by reproductive isolation, this is still an important evolutionary phenomenon. For example, if two phylogenetic species are ever to become sympatric, they have to acquire RIMs at some point. That is, phylogenetic species that are not also reproductively isolated probably cannot attain sympatry. Because of past emphasis on the BSC, much research has focused on the evolution of reproductive isolating mechanisms. Several questions have been asked: How many genes are involved, and how long does it take for either premating or postmating RIMs to evolve (i.e., speciation to occur)? Which type of RIM is most important? Does speciation always entail changes in the same genes? Might there be selection for isolating mechanisms? What causes isolating mechanisms to evolve? A recent book by two fly geneticists, Coyne and Orr (2004), reviews much of this material from the BSC perspective.

Speciation is not instantaneous (see figure 1). Once groups are isolated, it takes time for speciation to be completed, irrespective of species concept. That is, allopatric populations do not instantly acquire reproductive isolation (unless via ploidy; see the plant

discussion above) or diagnostic traits. The length of time is unclear, but estimates for the evolution of RIMs range from 100,000 years to 1 million years (Coyne & Orr, 2004), and we are not sure how long it takes for phylogenetic species to evolve. This explains why we rarely, if ever, observe speciation during a human lifetime. However, it has been observed that mating preferences can evolve in the laboratory in a relatively short time. For example, Dodd (1989) separated members of a single population of fruit flies (*Drosophila*) into two isolated groups (functionally allopatric), one group being fed starch, another only maltose. These two groups were kept on these food sources for about 10 generations. Then they were put into a situation where they could choose mates from either starch- or maltose-fed groups. If nothing had occurred during this brief period of “allopatry,” you would predict that individuals would choose mates irrespective of whether they were from the starch or maltose groups. The results showed that individuals, in fact, preferred individuals from the same medium: of 31 starch males, 22 chose starch females. Therefore, some degree of premating isolation had occurred in just a few generations, as a by-product of selection for a different food resource. This illustrates what many feel is typical of the evolution of RIMs—they evolve as by-products of natural selection for adaptation to differing environments, and not directly as isolating mechanisms per se. Because there would be no reason for RIMs to evolve in allopatry, it makes sense that RIMs would be a secondary consequence of genetic changes in allopatry.

It is thought that if, as a by-product of divergence, isolating mechanisms evolve that are not fully functional, the selection might sharpen premating mechanisms if two formerly allopatric groups come into secondary contact. The reason is that if there is some penalty for intermating, selection should act in a way that inhibits individuals from mating and making a mistake. This mechanism is termed reinforcement. Although it is controversial, some feel that it is an important part of the speciation process (under the BSC). A potential example involves fruit flies, *D. mojavensis* and *D. arizonae*. These two species occur in the southwestern United States and Mexico. In some areas, they are sympatric. If one does breeding experiments, one finds potential evidence for reinforcement. It was observed that if flies from allopatric populations were crossed, mating was relatively free between the two species. For flies taken from areas of

sympatry, however, individuals tended to choose mates of their own species. This suggests that selection has sharpened the mate choice behavior in the sympatric populations so as to prevent fitness penalties from mating with the wrong species. (Note that there are no apparent premating isolating mechanisms, yet these are considered species by fruit fly specialists.)

It was once thought that speciation involved changes in many genes of sister species (a genetic revolution). It is now known that relatively few genes underlie both phenotypic differences and reproductive isolation. For example, in the plant *Mimulus guttatus micranthus*, it is thought that a single gene is responsible for differences in flowering time. Thus, a premating isolating mechanism (flowering time) can be caused by a very small genetic difference. The reproductive isolation between *D. pseudoobscura* and *D. persimilis* is thought to be due to only three or more genes. Phenotypic divergence and reproductive isolation can be caused by relatively few genetic differences. In other cases, estimates of the number of genes causing phenotypic changes and reproductive isolation range up to 200.

Another finding from studies of the genetic basis of phenotypic differences and reproductive isolation is that there are no consistent genetic characteristics of speciation: different numbers of genes, and different genes themselves, are involved. Thus, speciation is a unique phenomenon each time it evolves. Another way of putting it is that reproductive isolation is an epiphenomenon—an inevitable but unpredictable by-product of genetic changes occurring in allopatry. The same can be said for speciation under the phylogenetic species concept—it is idiosyncratic.

Summary

Much progress has been made since Darwin's book in our understanding of speciation. We are confident that speciation occurs largely in allopatric populations, and the populations become different because of natural selection, sexual selection, and chance. How one views speciation depends on one's species concept, although the initial stages of allopatry and divergence are the same. Genetic differences underlying reproductive isolation are still under active study, as evolutionary biologists try to discover how many and which genes are responsible. At this point, it appears clear that speciation is best viewed as a stage in the evolutionary process, taking a variable amount of time depending on the group and circum-

stances. Although much remains to be learned about speciation, evolutionary biologists do not doubt the fact that this is the process by which the hundreds of millions of species that have existed over time came into being.

References

- Boake, C. R. B., DeAngelis, M. P., & Andreadis, D. K. (1997). Is sexual selection and species recognition a continuum? Mating behavior of the stalk-eyed fly *Drosophila heteroneura*. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 12442–12445.
- Coyne, J. A., & Orr, H. A. (2004). *Speciation*. Sunderland, MA: Sinauer Associates.
- Cracraft, J. (1989). Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In D. Otte & J. A. Endler (Eds.), *Speciation and its consequences*. (pp. 28–59). Sunderland, MA: Sinauer Associates.
- Darwin, C. R. (1859). *On the origin of species by means of natural selection*. London: John Murray.
- DeSalle, R., & Giddings, L. V. (1986). Discordance of nuclear and mitochondrial DNA phylogenies in Hawaiian *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 83, 6902–6906.
- Dodd, D. M. B. (1989). Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*. *Evolution*, 43, 1308–1311.
- Freeman, S., & Heron, J. C. (2004). *Evolutionary analysis*. Upper Saddle River, NJ: Prentice Hall.
- Johnston, R. F., & Selander, R. K. (1964). House sparrows: Rapid evolution of races in North America. *Science*, 144, 548–550.
- Knowlton, N., Weight, L. A., Solorzano, L. A., Mills, D. K., & Bermingham, E. (1993). Divergence in proteins, mitochondrial DNA, and reproductive incompatibility across the Isthmus of Panama. *Science*, 260, 1629–1632.
- Mayr, E. (1942). *Systematics and the origin of species*. New York: Columbia University Press.
- Mayr, E. (1963). *Animal species and evolution*. Cambridge, MA: Harvard University Press.
- Patuxent Wildlife Research Center, U.S. Geological Survey. (n.d.). *The North American breeding bird survey results and analysis, 1966–2003*. Retrieved May 3, 2003, from <http://www.mbr=pwrc.usgs.gov/bbs/bbs.html>.

Evolution of Animal Life: Perspectives from the Geological Record

Peter M. Sheehan

Introduction

Paleontology offers unique insights into the evolution of life that are not available to disciplines described in other chapters of this book. Because the fossils are long dead, the immediate interactions between organisms cannot be observed. However, the perspective of geologic time allows examination of the results of interactions over millions of years, rather than the decades or at most centuries of observations available to neontologists. Paleontological insights, therefore, focus on the results of long-term changes in evolutionary patterns.

The first part of this chapter presents a brief history of the expansion of animals from their origin about 543 million years ago to the present. The rest of this chapter examines recent findings that provide a new understanding of the importance that ecological interactions between species have on constraining evolution. The evolutionary patterns cover tens of millions of years during which groups of incumbent animals (those currently occupying ecological space) coevolve and dominate the ecosystem. Over time, incumbents were removed repeatedly by extinction events, which eliminated dominant animals and allowed new groups to evolve and become the incumbents that dominated the next interval.

These new ideas exemplify how science is always changing and increasing our understanding of evolutionary processes. Science is often thought of as a dull compendium of facts to be memorized. However, the excitement for scientists is in the research that provides an ever-improving understanding of our world. We must convey the excitement of new discoveries and changing paradigms to students if we hope to stimulate their interest in science. The new realization that extinction events, especially the extinction of dinosaurs, played an important role in the evolution of life may provide just the needed stimulant.

Geologic Time and the Fossil Record

Understanding the immensity of geologic time is a prerequisite to understanding the history of life. The fossil record is far from complete, and most of our knowledge comes from groups that have substantial hard skeletal parts. Fossils from shallow marine sediments have the best record, but the deeper oceanic rocks also have a good record of plankton, especially single-celled organisms with skeletons. The terrestrial record is much less well preserved than the marine. This is because erosion dominates sedimentary processes above the strandline, while marine sediments are deposited in environments where they are likely to be preserved.

Far more biologists are identifying and describing living species than there are paleontologists examining fossils. Furthermore, average species survive for only a few million years, meaning that, on average, a complete turnover of species occurred perhaps 100 times in the last 600 million years, leaving paleontologists with the daunting task of describing perhaps a hundred worldwide faunas with completely different species.

In spite of the problems, the basic features of the geologic record have been established. Information on such things as time of origin of a particular group is problematic, because early in their history, groups have low numbers of individuals, and these individuals may be in a very localized area. In either case, it is unlikely that these early members of a particular group will be found by paleontologists.

On the other hand, we have a very good record of when fossils with hard skeletons became abundant and dominated environments or when they declined in importance. This is because the abundant taxa will be the most numerous individuals in collections of fossils. Thus, for example, we have a good record of when ceratopsian dinosaurs became abundant in the Late Cretaceous, and the fact that they were no longer part of the fossil record after the end of the Cretaceous. It is entirely possible that in a refuge somewhere on Earth, ceratopsian dinosaurs survived

the end-Cretaceous extinction and lived for a while in the Tertiary. This is difficult to disprove. But we do know that large collections of Tertiary fossils have been examined and no ceratopsians have been found. Though it is possible a few survived, it is clear that ceratopsians were not an important part of the Tertiary fauna.

The Marine Fossil Record

One of the most ambitious summaries of the history of life in the oceans was done by Jack Sepkoski (1981), who produced a compendium of the duration in geologic time of all marine genera and families recorded by paleontologists in scientific publications. Michael Benton and his colleagues (1993) produced a parallel compendium of both marine and terrestrial families. Sepkoski's compendium allowed him to examine the standing diversity (numbers of taxa) of marine animals from their origin to the present (figure 1). Subsequent work, including Benton's compendium, has produced a similar history of animals in the terrestrial fossil record.

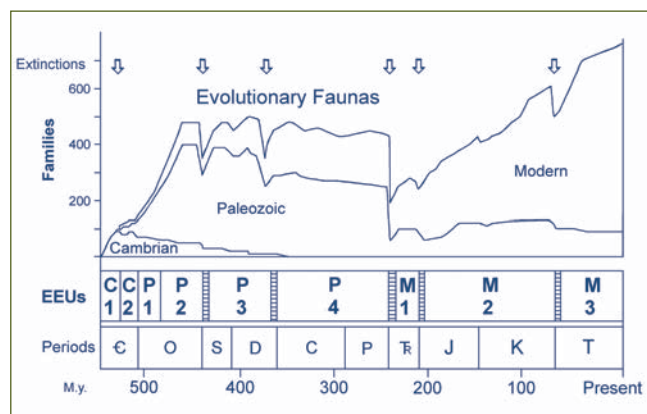


Figure 1. Marine families of animals with shells. Family diversity of marine animals through time compiled by Jack Sepkoski (1981). Intervals of rapid diversification (e.g., O = Ordovician), diversity plateaus (e.g., S = Silurian to P = Permian), and extinction events (e.g., arrows at end of P). Three evolutionary faunas (EF) are present. Nine marine EEUs (ecological evolutionary units) are shown; most end with extinction events. Five terrestrial EEUs begin in EEU P3, when animals first invade land, and have the same time intervals as the marine EEUs. Letters designate the standard geologic periods.

Prior to Sepkoski's compendium, paleontologists worked under a paradigm developed from Darwinian expectations that there would be a gradual, continuing increase in the complexity of life. As organisms competed, increasingly specialized species would appear, and ecospace would be increasingly more finely subdivided—increasing the number of taxa through time. Paleontologists assumed the pattern would be somewhat erratic, with intervals of extinctions or radiation coming into play through time. But the

expected pattern was quite different from what Sepkoski found.

Another revelation that came from the Sepkoski compendium was that there were three intervals, each dominated by different, progressively more diverse organisms. These intervals' distinctive assemblages of dominant animals are called evolutionary faunas (EFs).

For most of Earth's history, life consisted of single-celled organisms. About 543 million years ago, the first multicellular animals evolved in the oceans, and the complexity of life began to increase. The three successive evolutionary faunas are called the Cambrian (figure 2), Paleozoic (figure 3) and Modern (figure 4) EFs. More recently, paleontologists found a variety of enigmatic, soft-bodied, multicellular organisms, referred to as the Ediacaran evolutionary fauna, in beds slightly older than the Cambrian. Because the Ediacaran fauna's relationships with younger organisms is still being hotly debated, this chapter will concentrate on the final three EFs of marine animals.

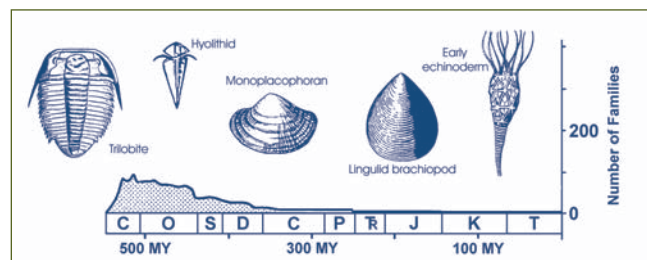


Figure 2. Diversity of Cambrian EF through time. Representatives of several significant groups are illustrated. (Adapted from Sheehan, 2001)

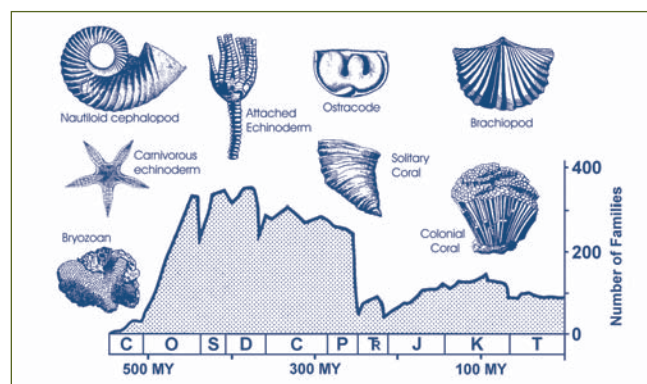


Figure 3. Diversity of Paleozoic EF through time. Representatives of several significant groups are illustrated. (Adapted from Sheehan, 2001)

The Cambrian evolutionary fauna (figure 2) appeared about 543 million years ago (Mya). Besides being the first multicellular animals, one of the most important innovations was the development of hard skeletons, which allowed organisms to increase greatly in size. Diversity of form, or disparity, increased along with diversity of taxa. However, both in terms

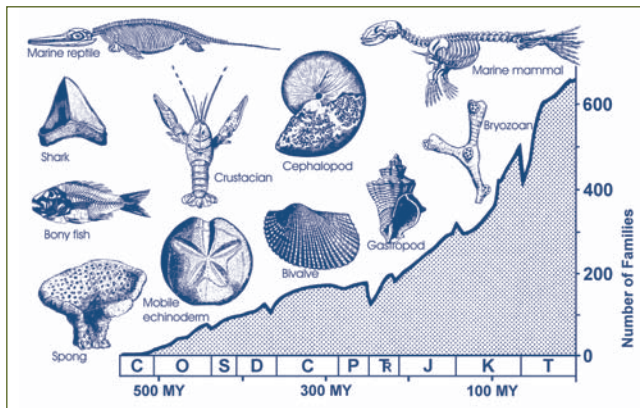


Figure 4. Diversity of Modern EF through time. Representatives of several significant groups are illustrated. (Adapted from Sheehan, 2001)

of the variety of forms and the variety of taxa, the Cambrian evolutionary fauna paled in comparison with younger assemblages. Mobile, attached, and free-living forms were present. Most organisms fed on microscopic organisms, and few predators were present.

Primitive arthropods called trilobites were common. Trilobites lacked mouthparts. In modern arthropods, the anterior limbs are modified as mouth structures that manipulate and chew food particles. Many modern groups have modified limbs that serve other functions, such as the claws of lobsters. In trilobites, however, all of the limbs were similar, and the mouth was a fleshy structure without jaws or other hard parts. Many trilobites fed on detritus (dead plant and animal material), but others fed on small animals. Also common at this time were lingulid brachiopods, simple bivalved organisms that fed by filtering food from water that was brought into their shells by currents the organisms created with cilia.

A second radiation of life began in the Ordovician period about 475 Mya, and led to the Paleozoic evolutionary fauna (figure 3), which had increased diversity and morphological variety (disparity). New predators, especially shelled cephalopods related to modern squid and octopuses, became abundant. Studies of modern communities have shown that the addition of predators to an ecosystem allows a greater variety of animals to coexist, because the predators feed on the most common organisms, which tend to be strong competitors that exclude other organisms. Eliminating individuals of these competitively dominant forms makes room for less competitive groups, thereby increasing diversity. Somewhat later, jawed fishes and predaceous snails appeared.

Colonial animals such as corals evolved in the Ordovician, paving the way for development of com-

plex reef systems. Other, less familiar groups were important, for example, the articulate brachiopods, which still live in the oceans today but have become insignificant members of the biota. Organisms living on top of the seafloor thrived.

Later, as predation increased, many of the organisms living on the seafloor either became extinct or evolved adaptations to burrow into the sediment on the seafloor to escape predators. Fish evolved and echinoderms, especially the attached filter-feeding crinoids, radiated.

The Paleozoic era closed with an enormous extinction on land and in the oceans. Survivors radiated, and the biota began to more closely resemble that of modern oceans. Marine predators still included many cephalopods and fish, and crustaceans such as crabs and lobsters radiated. Large terrestrial animals returned to the seas, and many, such as the mososaurs, were ferocious predators. Mollusks became dominant. As evolution continued, this fauna diversified into the biota that dominates the oceans today.

From the patterns of diversity through time established by Sepkoski, it became apparent that the evolution of life on Earth was unlike the orderly process of gradually increasing diversity and complexity paleontologists had inferred from their Darwinian paradigm. There were obviously long intervals when diversity remained relatively constant, for example, from about 450 to about 250 Myr (see figure 1).

There were three different evolutionary faunas, and there did not appear to be a simple gradual transition from one EF to the next. During the transition between EFs, many groups that became important players of the new EF initially evolved and diversified in shallow water, then moved gradually into deeper water as the earlier EF retreated to deeper water. Thus, new EFs developed in partial isolation from older EFs.

While Jack Sepkoski was working on his compendium of taxa from the published literature, Art Boucot (1983) was examining the changing patterns of marine communities through time. He documented a series of intervals beginning in the Cambrian and continuing to the Recent, during which communities were dominated by particular assemblages of animals. The intervals were given the unwieldy name of ecological evolutionary units, commonly abbreviated as EEU's. Each of the evolutionary faunas of Sepkoski had several of the shorter EEU's. The EEU's were recognized by long-lived, local community associations, rather than by the composition of the global marine fauna.

During an EEU, communities were dominated by groups of taxa, which, during their evolution, remained in a unique ecological setting throughout the interval. As the taxa evolved into new species and genera, the groups occupied the same niches (lifestyles) as their ancestors. Evolution occurred, but taxa only occasionally evolved the ability to live in new habitats. At the end of EEUs, new community associations developed and many taxa moved into new niches. This move to new niches is significant because it means that the organisms were undergoing major changes in their lifestyles.

Later it was realized that the EEUs were terminated by extinction events (Sheehan, 1996). And most of these extinction events were caused by outside forces that modified the environment so much that many groups became extinct and community structures were destroyed. The changes were not caused by competitive interactions between groups, but by an environmental perturbation. This was very different from the prevailing paradigm of Darwinian evolution, in which faunal interactions and competition governed the entire history of life. At these major changes in the composition of communities, outside events rather than faunal interactions were critical in eliminating the incumbent groups.

An Example of EEUs from the Terrestrial Fossil Record

At this point, moving from the marine to the terrestrial environment provides examples of EEUs that are easier to understand because the vertebrates are more familiar to students than are marine faunas. Consider a community of organisms that lived about 10 Mya in Nebraska (figure 5). Although none of the species is living today, it is quite easy to recognize the basic groups of animals. Two horned browsing deer lived much as they do today. An early horse browsed on grasses. An elephant and rhinoceros, though they have since died out in North America, are familiar herbivores. One animal, a chalicother, which belonged to a group related to horses, did not survive to the present. No mistake is made if you view the wolflike animal in the background as the main carnivore in this scene, though the small burrowing mammal in the foreground (unusual in being horned) was no doubt also wary of the hawk in the sky. The familiarity of the ecology of this scene, even though the animals are all extinct, rests on the continuity of life during the current EEU.



Figure 5. Nebraska about 10 Mya. The animals in this scene are familiar because they are from our current EEU, M3. The mammals dominated large body sizes for the last 65 Myr. (Mural at the Milwaukee Public Museum)

Now step further back in time, to eastern Montana 65 Mya (figure 6). The scene is very different. There is little doubt that *Tyrannosaurus rex* was a predator, but unrelated to any living predator with which we are familiar. The dead herbivore, *Triceratops horridus*, does not have descendants that dominate our EEU. The players in this community included carnivores, herbivores, and scavengers but they were part of an unfamiliar ecology. This EEU began early in the Mesozoic, approximately 200 Mya.



Figure 6. Montana 65 Myr. The animals are unlike those of the modern EEU. Large body sizes were dominated by dinosaurs for 135 Myr during EEU M2. (Diorama at the Milwaukee Public Museum)

In the terrestrial realm, animals evolved through a series of EEUs that correspond to those in the oceans (see figure 1). Animals did not move onto land until the Late Ordovician or Early Silurian, after plants invaded land, providing a food resource that animals could exploit. The earliest food pyramids during the Silurian and Early Devonian consisted of invertebrates, dominantly arthropods, such as spiders and centipedes, and mites, together with a few gastropods. Insects first appeared in the Early Devonian. Most of these animals fed on detritus or

dead plant matter. This assemblage was the first terrestrial EEUP3 (see figure 1). The first amphibian-like vertebrates evolved from fishes near the very end of this EEU, but they were extremely uncommon. The Late Devonian extinction event had little effect on terrestrial animals, perhaps because so few terrestrial vertebrates had evolved that the survivors were essentially just a subset of the previously dominant species, and no likely competitors for dominance had yet evolved.

Shortly after the Late Devonian extinction, amphibian-like tetrapods radiated and became abundant predators during the second terrestrial EEUP4. Insects radiated and began feeding on live plants. Reptiles, including one lineage leading to dinosaurs (including birds) and another leading to mammals, evolved and diversified in the Carboniferous. It was not until the Late Carboniferous that the first herbivorous tetrapods evolved. But by the end of the Permian, vertebrate food had abundant herbivores and lesser numbers of detritivores supporting much less common predators.

The end-Permian extinction was by far the most devastating extinction event. About 95 percent of all species on Earth disappeared. Only a few of the Permian reptiles survived, and new groups evolved to dominate the Early Triassic. Insects were also strongly affected, but rebounded quickly in the Triassic. This was a short-lived third EEUM1.

The Late Triassic extinction is poorly recorded in the terrestrial fossil record. Dinosaurs and mammals evolved during the Triassic but remained minor players in the ecosystem. Both survived into the Jurassic and quickly diversified. Dinosaurs radiated during the Jurassic and Cretaceous, but mammals, although they were common insectivores and omnivores, remained small and largely restricted to these lifestyles. This fourth terrestrial EEUM2, is often referred to as the age of dinosaurs. The EEU ended with an extinction event caused by an asteroid impact at the end of the Cretaceous period. Dinosaurs became extinct. Both mammals and insects were greatly reduced but they survived into the Tertiary period.

The final and current terrestrial EEUM3, saw the radiation of mammals into lifestyles that were previously occupied by the dinosaurs. About 5 million years after the extinction event, some mammals had evolved into large herbivores and others into predators. Of course, others remained omnivores and insectivores. Insects radiated once more.

Incumbency, Extinction, Radiation: A New View of the Fossil Record

The most interesting part of science is not what is known, but the search for answers to questions about what is unknown. While there is no doubt that evolution was a process that governed the development of life on Earth, many aspects of how evolution works are still being examined. An understanding of how evolution is being refined can be gained from recent changes in our view of patterns in the history of life.

Paleontology has always been an important contributor to our understanding of evolution. By the early 20th century, most paleontologists had accepted evolution as a paradigm that focused their understanding of the fossil record. This acceptance soon created expectations among paleontologists about how life evolved and how to interpret the fossil record.

One of the primary expectations among paleontologists was that evolution was a very gradual process of competitive interactions over the vast reaches of geologic time. However, the fossil record is far from perfect, and over geologic time intervals even the best-preserved sequences of fossils have numerous intervals when fossils are missing.

When abrupt morphological changes were found in the record, they were explained by inferring time gaps in the record during which gradual change occurred but was not preserved.

The expectation of gradual change permeated all fields of paleontology, from short-term studies of change within species through time to long-term studies of transitions between and within major groups of organisms and even large-scale changes in ecological associations.

The idea of gradual change within and between species was challenged in the latter 20th century by Niles Eldredge and Stephen Jay Gould (1972). By that time, Ernst Mayr had proposed that most speciation occurred not through gradual transitions from one species to the next, but by rapid changes in small, isolated populations of a species. Their small gene pools could evolve rapidly and develop morphologies or behaviors that would prevent them from breeding with the larger group. Once the populations were unable to interbreed, they were, in effect, separate species. Most of these new populations were very small and died out quickly. A few of the new fledgling species were successful and either competed with the original species or moved into other areas or lifestyles

sufficiently different from the original species that the two were not competing.

Applying Mayr's ideas to the fossil record, Eldredge and Gould reexamined the evidence for gradual speciation in the fossil record. What they found startled the paleontological community. There were very few examples of gradual change. Most species appeared suddenly in the geologic record and their morphology changed little during their life spans. Mayr's ideas of speciation provided a better explanation than gradualist explanations. A detailed study of Devonian trilobites by Eldredge provided a test of their new theory of punctuated equilibrium.

Another blow to the gradualist theories in paleontology came with the discovery by Louis and Walter Alvarez and their colleagues (1980) that an asteroid impact coincided with the extinction event at the end of the Cretaceous period.

Both marine and terrestrial ecosystems were devastated in the extinction event. Paleontologists long knew there was an extinction event at this time, but their explanations had always been based on gradual evolution. In the oceans, the event was thought to be quite gradual. The cause of the extinction had been uncertain—perhaps long-term climatic change, which favored some groups over others, allowing the newly superior competitors to prevail over previously dominant forms.

On land, the extinction of dinosaurs was such a fascinating subject that scores of possible causes were suggested. Most invoked some change in the environment. Examples include reasoned ideas such as when flowering plants evolved in the early Cretaceous, they contained chemicals that prevented dinosaurs from digesting them. Since there was a gap of more than 50 Myr between the origin of angiosperms and the extinction of dinosaurs, there was plenty of time for a gradual demise. The origin of angiosperms also drew less well-reasoned suggestions, such as the idea that new pollens caused hay fever-like allergies, which led to their demise. Most explanations involved competition with mammals, because mammals eventually replaced the dinosaurs. Mammals were seen as potent competitors because they are warm-blooded, have high activity levels, are relatively intelligent, and care for their young, which provides an opportunity for mammals to learn from their parents rather than having to be born with an ability to cope with the environment.

The Alvarez team provided a very different explanation of the transition: an asteroid impact destroyed

an ecosystem that was not in decline. An outside event suddenly changed the environment to such an extent that many organisms, including dinosaurs, were unable to survive. Mammals did not compete with dinosaurs but replaced them because they were able to survive the extinction. They radiated only after the dinosaurs disappeared. This idea necessitated a review of all EF and EEU transitions to see if they were caused by outside events that had nothing to do with gradual competitive interactions.

Boucot's examination of community patterns through the fossil record suddenly became an important way to frame the history of life. Most of the long intervals of community-level stability (EEUs) ended at extinction events caused by sudden physical changes in the environment.

The reaction by the gradualist community to the impact hypothesis was swift. One of the first, most-influential, and eloquent of a flood of rebuttals was by William Clemens and associates (1981), titled "Out With a Whimper Not a Bang." The long-standing contention that dinosaur extinction was gradual continues to this day. In subsequent years, three laborious field studies of the final 2 Myr of the reign of dinosaurs have independently found the dinosaur extinction was abrupt and the pattern of extinction fits the impact hypothesis. To date, no field study designed to test the hypothesis has found any evidence of gradual dinosaur extinction. In fact, proposals that dinosaurs were in decline during the Late Cretaceous, as in the example of angiosperm radiation cited above, have been refuted by studies that show dinosaurs reached the high point of their diversity in the Late Cretaceous.

Incumbency

Rather than a gradual process of change through time, the fossil record reveals a complex process of long periods of time when incumbent clades dominated their ecosystems. A clear pattern is that organisms that first move into a particular lifestyle tend to be successful, and other organisms have great difficulty displacing them.

For example, mammals and dinosaurs evolved at nearly the same time. At first, during the Triassic period, neither became particularly prominent forms. But both survived the Late Triassic extinction event, and dinosaurs rapidly evolved to become the dominant large-bodied animals on land for the next 135 Myr. Dinosaurs included both carnivores and herbivores.

Mammals, on the other hand, remained very small. Most were insectivores (a form of carnivore that focused on worms, insects, larvae, snails, and other invertebrates), some were omnivores, including fruit and high-energy plant food such as seeds in their diets. In fact, in these limited ecological settings the mammals were dominant incumbents.

Through 135 Myr mammals did not challenge the dinosaurs for dominance. There is every reason to believe the mammals were capable of evolving into the niches occupied by dinosaurs, for they rapidly replaced the dinosaurs after the end-Cretaceous extinction. One group of mammals even became small carnivores during the Early Cretaceous in China, and their prey included young dinosaurs. However, these mammals were unsuccessful, and they became extinct long before the dinosaurs.

Incumbents during the EEs evolved extensively. The earliest equids were small browsers of forested areas that eventually evolved into myriad larger horses capable of grazing on grasslands. There are many examples of arms races when carnivores increased their hunting abilities while prey species improved their defenses. During EEs, some incumbents were replaced by other animals, but in the broad perspective of the fossil record these were unusual events.

Animals that first evolve the ability to live in previously unoccupied habitat gain an advantage over organisms that try to move into these settings at a later time. As the first group evolves, it becomes progressively more capable of life in the new habitat. Animals trying to displace them have few adaptations for this new environment, putting them at a distinct disadvantage.

Another type of radiation took place when organisms evolved the ability to live in previously unoccupied habitats. An example is the movement of fish onto land. There, too, the first group to invade a new habitat commonly became dominant. In the marine realm, many habitats occupied by animals in today's oceans were unoccupied during the reign of the Cambrian evolutionary fauna. For example, during the Cambrian, deep burrowing animals such as today's long-necked clams or echinoids did not exist. In these cases, since the habitats were unoccupied, the habitats were there for the taking by the first animals to evolve the ability to live in them.

Extinction Events

Five major extinction events were apparent when

Sepkoski published his initial compendium. The first, near the end of the Ordovician period, was caused by glaciation. At that time, Africa was at the South Pole and the continents of Africa, South America, Australia, and Antarctica were assembled as the supercontinent Gondwanaland. A geologically very brief glaciation ended a long interval of very warm global climate. Glaciers covered much of Africa and South America. So much water was contained in the glaciers that sea level dropped nearly 100 meters, draining shallow seas that covered most of the continents. The deteriorating climate, together with the loss of extensive shallow seas, combined to cause an extinction event. Life had not yet radiated onto land, so the extinction was entirely marine. Another extinction event in the Late Devonian was much more drawn out than the Ordovician event. Causes of this event and the following two extinction events are still being debated (another example of how science is a work in progress).

The extinction at the end of the Permian period was far larger than any of the other extinctions. The cause may have been increasing carbon dioxide and falling oxygen levels, although this is still being debated.

The Late Triassic extinction occurred before a full recovery of the Permian extinction had taken place. The final great event, at the end of the Cretaceous, ended the age of dinosaurs and allowed the expansion of mammals, which have been a dominant incumbent ever since.

Each of the extinction events, together with a lesser extinction event during the Cambrian and still uncertain changes at the end of the Cambrian, ended an EE. Survivors radiated into the vacant niches and became dominant until the next extinction event.

Radiations

Following each extinction event, the ecological relationships of the previous EE were destroyed. Obviously, none of the events eliminated all animals because life on Earth continued. The extinction events had a variety of causes, and an animal's survival depended on having some part its life history that could protect it from extinction. The only feature that promoted survival in all the extinction events was having a very wide distribution over Earth, which increased the likelihood of at least some members of the group surviving the event.

Other animals had some feature of their lives that doomed them. For example, in the Late Ordovician, when the sea level declined and shallow seas were

drained, extinction was very severe among animals that lived in shallow seas that covered many continents.

The end-Cretaceous extinction provides an example of the way an extinction event proceeds. The asteroid had many devastating effects on the biosphere. At the Chicxulub impact site in Mexico, a crater 100 miles in diameter was emplaced in a matter of seconds. A magnitude 13 earthquake rang Earth like a bell. Debris buried everything for hundreds of miles around the crater. Giant tsunamis sped across the oceans. But the overriding cause of the extinction was a loss of sunlight. Dust and sunlight-blocking gases clogged the atmosphere for many months. Geochemical studies clearly show that photosynthesis both in the oceans and on land stopped for months. When the atmosphere cleared, the biota was changed forever. On land, green plant matter had disappeared. Many plants grew from seeds and root systems, but a significant number of plants became extinct. Interestingly, the first plants to return were opportunists such as ferns, which also are the first plants to return after forest fires.

But the recovery of plants was too late for the dinosaurs (figures 7–9). Herbivorous dinosaurs starved, and when they became extinct, the carnivorous dinosaurs succumbed also. In the aftermath of the extinction, there were no large animals on land for the first time in at least 135 Myr. Insects also suffered significant losses, but it is the absence of large animals that is most striking.

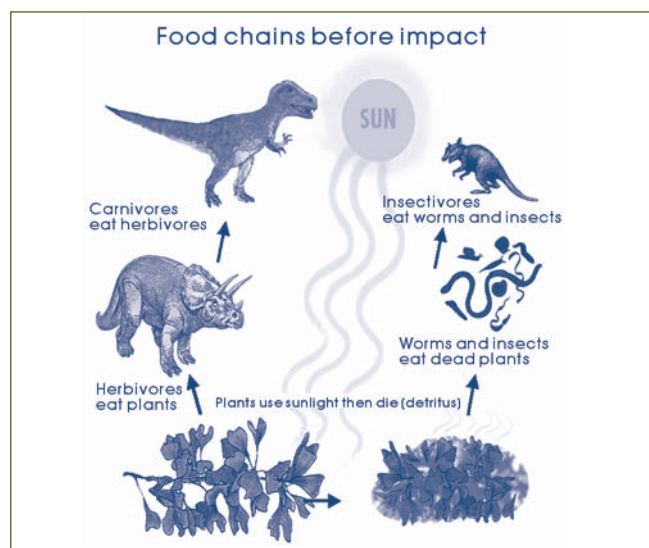


Figure 7. Late Cretaceous food chains before the asteroid impact. Sunlight is used by green plants during photosynthesis. Herbivorous dinosaurs fed on the green plants and were, in turn, fed on by predaceous dinosaurs. Mammals were in a food chain in which they fed on worms, insects, and other invertebrates, which in turn fed on dead plant matter.

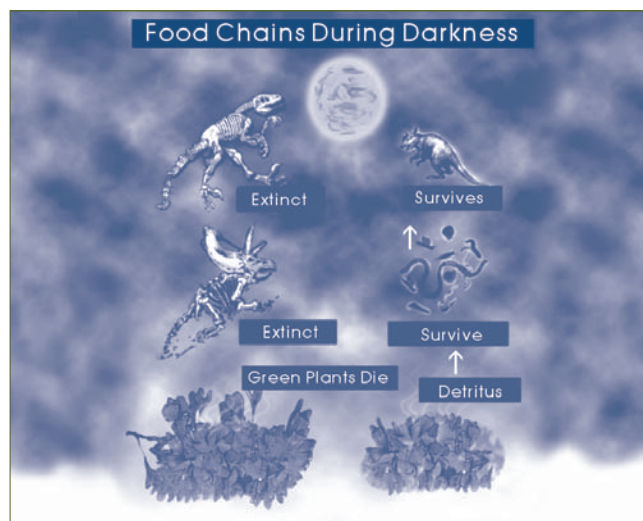


Figure 8. Immediately after the asteroid impact, dust and opaque gases blocked sunlight for many months. Green plants died and first herbivorous, then carnivorous, dinosaurs died. Detritus was still available, and the mammal's food chain survived.

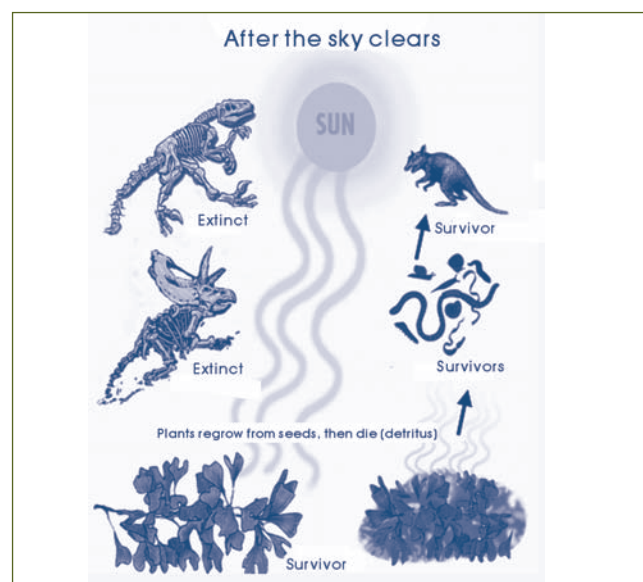


Figure 9. Months after the impact, dust settled and opaque gases dissipated. Sunlight returned and photosynthesis was once more possible. Some plants were able to survive as seed or root systems. No large terrestrial vertebrates, either carnivores or vertebrates, were present. The detritus-based food chain, including mammals, survived to radiate in the Tertiary.

Mammals obviously survived to repopulate the ecosystem, but how? Most likely they were saved by their lifestyle. The small, insectivorous mammals are the ones that eventually gave rise to the diversity of modern mammals. Insectivores feed on organisms such as those in dead logs and the soil—worms, insects, larvae, and other small invertebrates. Many of these animals feed on dead plant matter, and this appears to have allowed the mammals to survive.

Over the next few million years, mammals radiated into an enormous variety of lifestyles (figure 10). Some mammals evolved to replace the carnivorous

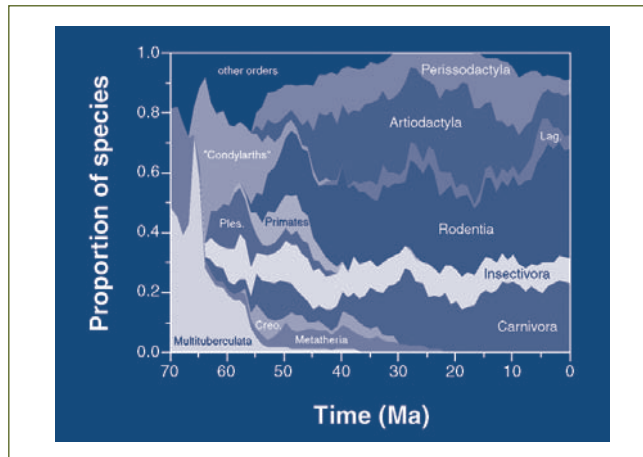


Figure 10. During the age of dinosaurs, mammal species belonged to only a few groups that were primarily insectivores, omnivores, and fruit and seed eaters, but they did not feed on green plants or large animals. The asteroid impact at 65 Myr eliminated the dinosaurs, and mammals quickly radiated into the immense variety of modern mammals, especially herbivores and carnivores. (Adapted from a figure on John Alroy's Web site: <http://www.nceas.ucsb.edu/~alroy/mammalorders.gif>)

dinosaurs, but this was probably not a very difficult transition for insectivores, which were already feeding on various kinds of invertebrates. The transition to digesting green plants was a much more difficult proposition (Sues, 2000). Tooth structures of insectivores are not suited for processing plants. The digestive tracts of herbivores are very specialized and need to process large amounts of plant matter, which has low nutritional value compared with food from animals. Symbiotic relationships with bacteria and protists living in the herbivores' intestinal tracts had to be developed before cellulose could be processed.

Within a few million years, mammals had begun to feed on green plants, because characteristic tooth structures had evolved in mammals. The presence of herbivores allowed the ecosystem to readjust. Herbivores are critical to our modern food pyramids, with large numbers of herbivores supporting smaller numbers of carnivores. Within a few million years, mammals were well along the road to replacing the dinosaurs.

Similar examples of changes can be found across every extinction event. A primary feature of this new view of evolution is that prior evolution does not prepare animals for the changes that cause the extinction. The animals with the finest adaptations for life in normal times may have nothing to save them during an extinction event.

The rapidity of evolution during these postextinction radiations was surprising. It now seems that during the EEU, animals evolve better ways to exploit the niches in which they live, but extinction events allow

survivors to rapidly invade newly vacated niches. Darwin actually found evidence that animals can radiate rapidly when he described the radiation of finches on the Galapagos Islands. After a group of narrowly adapted finches reached the islands, they rapidly evolved lifestyles that mimic many other kinds of birds.

Accepting a Revision of a Long-Held Scientific Theory

To accept the idea of incumbency, followed by disruption, followed by radiation requires a significant change in the mind-set of many paleontologists. Supporters of gradualist explanations of extinction events and evolution are still common. This is an ongoing debate that will not end soon. Interestingly, the mind-sets are so different between the two groups that it is difficult for the two groups to communicate rationally. Obviously, I am a supporter of the new interpretations of the fossil record. At this point, it would be difficult for me to logically explain the gradualists' ideas, just as it would be difficult for them to explain mine.

This is not an uncommon dilemma in science. Thomas Kuhn (1996), in a book I strongly recommend, points out that changes in a basic paradigm (conceptual worldview) are very difficult for longtime workers in a field to accept. They have, after all, framed all their research around the old paradigm. He notes that when changes do occur, they are commonly brought about by some new kinds of information. Those developing a new paradigm are often from the fringes of the field of study or they are graduate students who have not committed a great deal of effort to the old paradigm.

In this case, the new information was the discovery of an asteroid impact made by Louis Alvarez, a physicist, and his son Walter, a sedimentologist. The field studies of dinosaur diversity leading up to the extinctions that found no evidence of gradual decline among plants, insects, or dinosaurs were done by paleontologists who worked on much older rocks or were graduate students and amateur paleontologists when their studies began. Astronomers, experts on thermonuclear explosions, and geochemists have made important contributions. Scientists in fields outside paleontology are much more likely to accept the idea than are vertebrate paleontologists. But in truth, the controversy will not be settled until there is consensus.

Acknowledgments

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References

- Alvarez, L. W., Alvarez, W., Asaro, F., & Michel, H. V. (1980). Extraterrestrial cause for the Cretaceous-Tertiary Extinction. *Science*, 208, 1095–1108.
- Benton, M. (1993). *The fossil record 2*. London: Chapman & Hall.
- Boucot, A. J. (1983). Does evolution take place in an ecological vacuum? II. *Journal of Paleontology*, 57, 1–30.
- Clemens, W. A., Archibald, D. J., & Hickey, L. J. (1981). Out with a whimper not a bang. *Paleobiology*, 7, 292–298.
- Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology* (pp. 82–115). San Francisco: Freeman, Cooper & Co.
- Kuhn, T. S. (1996). *The structure of scientific revolutions*. Chicago: University of Chicago Press.
- McGhee, G. R. (1996). *The Late Devonian mass extinction*. New York: Columbia University Press.
- Powell, J. L. (1998). *Night comes to the Cretaceous*. New York: W.H. Freeman.
- Sepkoski, J. J. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7, 36–53.
- Sheehan, P. M. (1996). A new look at ecologic evolutionary units (EEUs). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127, 21–32.
- Sheehan, P. M. (2001). History of marine biodiversity. *Geological Journal*, 36, 231–249.
- Sues, H-D. (2000). *Evolution of herbivory in terrestrial vertebrates*. Cambridge, England: Cambridge University Press.
- Webby, B. D., Paris, F., Droser, M. L., & Percival, I. G. (2004). *The great Ordovician biodiversification event*. New York: Columbia University Press.
- Zhuravlev, A. Y., & Riding R. (Eds.). (2001). *The ecology of the Cambrian radiation*. New York: Columbia University Press.

More information on the various fossil groups considered here and many other paleontological topics are available at the Web site of the Museum of Paleontology at the University of California–Berkeley (<http://www.ucmp.berkeley.edu>). The Tree of Life Web Project has an extensive Web site detailing the evolutionary relationships of Earth's biota (<http://tolweb.org/tree>).

Teaching the Mechanisms of Evolution Education Panel F:

Exploratory Evolution Education: Engaging Students in Investigating Evolutionary Processes, Products, and Principles

John R. Jungck, Stacey Kiser, and Ethel D. Stanley

Evolution needs to be studied in the laboratory (in vivo, in vitro, and *in silico*) and in the field as we would any other field of biology, if not more so (Jungck, 1984). Whether the pedagogy is teacher directed or learner centered, students have a different commitment to work in which they are actively engaged. The performance of experiments, the exploration of simulations, or the interpretation of natural phenomena in the field requires students to examine their scientific worldviews in the context of their scientific experiences in hypothesis testing, data analysis, inference making, and work that they personally have performed. Lectures, textbooks, WebQuests, exams, discussions, debates, and term papers on evolution are extensively used in evolution courses as well as in the evolution section in general biology. If, however, we wish to provide learning experiences that engage students in asking their own questions and testing hypotheses, activities requiring experimental design, data collection, manipulation of parameters in simulations, analysis of complex data, original observations, fossil interpretation, and construction of apparatuses should be included in our instructional design.

If evolution is the only subject that is “covered” without laboratory and field activities, then what conclusions can students draw about their interactions with this area of science? If teaching about evolution consists entirely of a declarative description of facts, or worse yet, shifts suddenly into an interrogative examination of students’ beliefs, do educators understand that this connotes a hidden curriculum that students must grapple with? Despite good intentions, some educators remain convinced that students cannot “do” evolution and cite reasons such as “evolution occurs over a time period that is too long to observe”; “the data require sophisticated analyses using multivariate statistics, linear algebra, differential equations, or integral calculus that students haven’t had”; or that “there aren’t a variety of lab, computer, and field activities that they could easily use in their courses.” Herein we illustrate that this perspective is simply uninformed and introduce a variety of available resources for educators who wish to actively engage students in their own evolution education.

Finally, if we consider evolution as an essential problem-solving tool of contemporary biology, then why not provide multiple opportunities for our students to participate in its application and use evolution as a lens of analysis? We need to incorporate evolutionary themes in every biology instead of isolating evolution in a separate course (which students may avoid if they choose) or to a special section within our general courses. For example, students could be routinely introduced to scientific literature that explores evolutionary questions in cellular structure, human physiology, or neuroanatomy as part of those courses. If students are introduced to evolution only at the organismal and population levels, they cannot understand the underlying bases of comparative studies that attempt to solve scientific problems within the breadth of the discipline.

Wet Labs

It would be challenging to find an area of modern biological research where the interpretation of data is not influenced by an understanding of evolutionary theory. —Sam Donovan, personal communication, November 12, 2004

If you examine almost any issue of a current research journal in evolutionary biology, you will find a fine representation of laboratory work:

- Darwinian investigations of comparative anatomy, physiology, embryology, and ethology continue and are supplemented by 20th- and 21st-century examinations of comparative genomics including proteins (primary, secondary, tertiary, and quaternary structures), nucleic acids, chromosomes (cytogenetics), metabolic pathways, and gene expression (Hox boxes) as well as immunocompetence and immunoprecipitation to measure association, foreignness, and cross-reactivity.
- Early 20th-century work in population genetics is sustained through population cage experiments of *Drosophila*, *Tribolium*, and cockroaches (e.g., S. C. Johnson Wax breeds them to improve their formulation of pesticides), serial chemostat experiments of bacterial and viral populations, and associated measurements of heterozygosity, polymorphism, linkage disequilibrium, and genetic distance. Quantitative geneticists explore selection of traits such as chemotaxis, phototaxis, geotaxis, and other behaviors as well as yield, protein content, and weight gain. The analysis of QTLs (quantitative trait loci) has become almost an industry unto itself.
- Molecular evolutionists explore the molecular basis of mutation (transitions, transversions, deletions, insertions, translocations, transposable elements, etc.), recombination, repair, construction of new metabolic pathways, and selection. One famous experiment by Sol Spiegelman and colleagues explored the rate of replication and the length of the Q-Beta RNA genome.
- Medical applications are numerous, such as the isolation and sequencing of clones of HIV sequences over the course of infection to the development of AIDS. A recent pathogen chip promises to identify an infectious agent down to a very specific level by the use of phylogenetic probes. Such phylogenetic probes are also used extensively to examine environmental remediation, food contamination (not only for pathogens but also in such cases as examining whether tuna cans contain whale meat), import of endangered species, epidemiological spread, and forensics.
- Origin of life investigators not only investigate the formation of organic materials (amino acids, sugars, lipids, nucleobases, porphyrins) from inorganic chemicals but the development of macromolecules (proteins, nucleic acids, starches, triglycerides) and protocells (coacervates, proteinoid microspheres, micelles with lipid bilayers). They study protein-nucleic acid interactions to understand the evolution of specificity and genetic coding. The RNA World scenario has stimulated in vitro experiments with the evolution of ribozymes and their specificity.

- Astrobiology has been responsible for lab work investigating meteorites from Mars for molecular evidence of living systems, if amino acids are contained in moon rocks and carbonaceous chondrites, and if organics are formed in freshly cooled lava.
- Paleontologists section fossils in the lab, isolate DNA from amber-enclosed specimens and bone fragments, count and examine rings in fossilized trees, measure ages with radioisotope decay and conversion of optical isomers (such as L-isoleucine to D-alloisoleucine), and examine the process of fossilization itself.

Obviously, any list is woefully incomplete, but each kind of laboratory research affords opportunities for students to engage in evolutionary analysis in much the same way as researchers in medicine, agriculture, and environmental science do.

Experiment	Phenomenon investigated	Reference
Allozyme electrophoresis	Measuring genetic variability	Bader (1998)
Ampicillin resistance in <i>Serratia marcescens</i> -21.	Selection	Haddix, Paulsen, & Werner (2000)
Antibiotic resistance of <i>Staphylococcus</i>	Natural selection	Omoto & Malm (2003)
Cellulose acetate electrophoresis of zebra mussels	Genetic variability	Goldman (1998)
Evolution lab with <i>Drosophila</i>	Multiple aspects	Salata (2002)
Luria-Delbrück fluctuation test	Rate of mutation; selection of (Darwin) rather than selection for (Lamarck)	Glover (1968); Green & Bozzone (2000)
Magnetotactic bacteria	Natural selection	Culp (1995)
Miller apparatus followed by paper chromatography	Chemical evolution	Jasien, Miller, Levy, & Dworkin (2002)
Proteinoid thermal synthesis and proteinoid microspheres	Chemical evolution	DeWitt & Brown (1977)
Quantitative selection of hairs on Wisconsin Fast Plants	Heritability, variance, power of positive and negative artificial selection	Fell & Fifeld (1999)
Sunflower seed stripes	Variance, variation	Available from several

Table 1. A variety of classroom laboratory activities that illustrate several research areas used by educators. **See a more extensive appendix on the BioQUEST Curriculum Consortium Web page at <http://www.bioquest.org/evolution>. We urge readers to share more.

Field Explorations

Contemporary fieldwork in evolutionary biological research both reflects the pioneering work of Charles Darwin during his circumnavigation of Earth and his famous observations on speciation within the Galápagos finches, yet extends into many new areas:

- Evolutionary biologists investigate biogeographic patterns and their relationship to continental drift, vicariance, dispersal, colonization, invasion, epidemiology, and catastrophic events.
- Paleontologists regularly find fossils of previously unknown species that help better appreciate biodiversity in previous eras. As Bates (1862) and Müller (1879) studied mimicry in exotic places with beautiful butterflies, fieldworkers extend this work by working in the tops of 100-meter-high tree canopies or in deep valleys of Nepal.
- Microbiologists now explore extremophiles growing in the hot springs of Yellowstone Park, the ice crevices of Antarctica, the geysers of Iceland, and the black smoker geothermal vents in deep ocean bottoms near the Galápagos.
- Virologists regularly track the spread of new strains that affect humans, domesticated livestock and pets, and crops.
- Agricultural workers continue artificial selection in the development of livestock and crops—commercial seed companies developing a new strain of corn may grow plants in three seasons in one year in North Dakota, Hawaii, and Argentina and select heavily by throwing everything in the book at these plants: drowning, desiccation, nematode infection, caterpillar predation, and so on.
- The natural history museums of the world continue to maintain field collectors engaged in the active classification of life on Earth.

Field evolutionary biology is alive and well in the 21st century! Students similarly will benefit from the ability to participate in the exploration, collection, analysis, and interpretation of field observations.



Figure 1. Educators may use a variety of technological resources for evolutionary problem solving.

Computer Simulations, Tools, and Databases

In “Studying the Processes and Effects of Evolution with *Evolutionlab*,” Judith T. Parmelee of Manchester Community College in Connecticut, cites some misconceptions about students’ ability to perform evolutionary investigations in the lab and field and then moves beyond them:

Teaching and learning about evolution has always been difficult because one cannot do an exercise showing natural selection over time or examine hypotheses prospectively. Labs usually last three hours, not 300 years!! As a result, beginning undergraduate education in this area has been necessarily limited to presentation of retrospective studies based on fossil records or review of long-term observational research done by others. With the

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capabilities of the modern computer, however, all this changes. A good program can extrapolate results into the future given parameters that are known to affect survival, hardiness and adaptations of a species.

Fieldwork	Phenomenon	Reference
Animal behavior	Phylogeny	Yasukawa (2003)
Dinosaur tracks	Visualization (infer height, weight, mode of locomotion)	Buehler & Quillen (1995)
Fossil hunting in quarries, road cuts, and outcroppings	Morphology, population, (each new fossil adds to data), life history (ubiquitousness of ancient life)	Any field manual on local fossil hunting
Information theory analysis of biodiversity in neighborhood	Island biogeography	Green & Bozzzone (1999)
Measuring selection in natural populations of crown gall	Directional, stabilizing, and disruptive selection	Brown (2004)
Natural selection in the wild using the common dandelion	Open genetic systems	Hilbish et al. (1994)

Table 2. An abbreviated list of published educational activities designed to investigate evolutionary phenomena in the field

Students can explore mechanisms of evolution through collaborative modeling and simulation. There are many undergraduate classrooms where students actively engage in testing their own and others' ideas regarding evolution. Valerie Banschbach and Patricia Peroni at Davidson College in North Carolina use modeling and simulation in their classrooms since "all active areas of research involve this type of interplay between theoretical and empirical research, and our understanding of how the world operates depends upon both types of investigations," (Banschbach & Peroni, 2004).

Two classroom examples of the use of the modeling and simulation software Evolve (see figures 2 and 3), in which students examine evolution interactively, follow:

- Students enrolled in Evolution at Howard University in Washington, D.C., use the program Evolve to look at changes in the genotypes of populations over time under various evolutionary parameters. Muriel Poston, their instructor, wanted to "take evolution out of the 'talking head' format of lecturing" and provide an opportunity for students "to engage and do inquiry at the bench level," (Poston, 2004). She claims that "computer simulations provided the answer, allowing the students to visually track changes in population demographics over time." She asks them to explain when they don't get their predicted results and asks them to "dig deeper" with questions such as, What happened? Where does this lead us? What would be the next question here?
- At Westfield State College in Massachusetts, introductory students model microevolution using Evolve to analyze the effects of variables on the changes in genotype and allele

frequencies. Buzz Hoagland, their instructor, provides questions such as, How do allele and genotype frequencies change over 50 generations when the recessive allele has a selective advantage? and Is the effect of selection different in a large population compared to a small population? (Hoagland, 2004) Students predict results of a population crash and then simulate crashes. They continue predicting and modeling until they feel they can explain their data.

Figure 2. An example of the Evolve (Price & Vaughan, 2003) parameter screen.

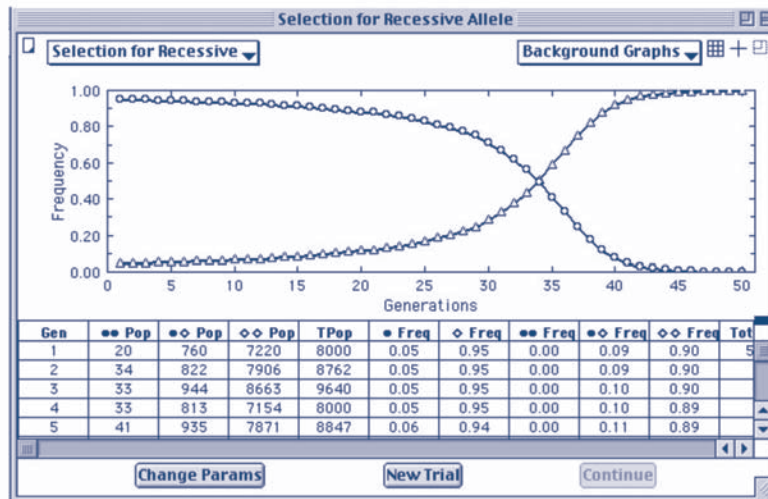


Figure 3. An example of simulation results for Evolve.

Introductory undergraduate education in evolution was necessarily limited to presentation of retrospective studies based on fossil records or review of long-term observational research done by others before the capabilities of modern computational tools and database access. Not only can a good program extrapolate results into the future given parameters that are known to affect survival, hardiness, and adaptations of a species, but bioinformatics tools can be used to look at sequence data in multiple ways.

The use of online computational tools such as BLAST, ClustalW, and Boxshade and access to online databases such as GenBank and Swiss-Prot is rapidly becoming part of biology curricula. These molecular approaches are not limited to advanced biology courses, but are in introductory biology courses. Biological Inquiry: A Workbook of Investigative Case Studies (Waterman & Stanley, 2005) includes cases for introductory biology students such as "Donor's Dilemma" with West Nile virus sequence data and "Tree Thinking"

with whale sequence data that students are encouraged to explore and interpret. In optional extended activities, the students are further encouraged to use newly published sequence data to explore their own questions. Access to bioinformatics tools on Web sites like Biology WorkBench (<http://workbench.sdsc.edu>) and problem sets like those of the BEDROCK project (Bioinformatics Education Dissemination: Reaching Out, Connecting, and Knitting-together, (<http://www.bioquest.org/bedrock>)) allows students to explore questions of evolution in all undergraduate biology courses including cell biology and comparative anatomy/physiology courses.

Since evolutionary biologists have explored the use of computers almost since the beginning of computing (see extensive annotated bibliography in Jungck & Friedman, 1984) and computer scientists have developed whole fields within their discipline that employ evolutionary reasoning and behavior such as evolutionary programming and genetic algorithms, the public is being exposed to modeling and simulation in evolution as well. Two popularizations follow:

- A recent cover of the popular magazine Discover touted: “Testing Darwin: Scientists at Michigan State Prove Evolution Works” (Zimmer, 2005) and reported on the use of an artificial life simulation named Avida. Some of the questions that they address are: Why sex? Why does a forest have more than one kind of plant? What good is half an eye? and What will life on Earth look like in the future?
- Richard Dawkins’s *Blind Watchmaker* (1986) describes software of the same name and was the winner of the Royal Society of Literature’s Heinemann Prize and the Los Angeles Times book award. Dawkins’s “biomorphs” became one of the icons of artificial life and the use of simulations to explore the power of artificial selection. It enjoys widespread international use in classrooms and has been the subject of thousands of Web pages.

All three authors of this chapter have been active in the use of computer simulations, tools, and databases to stimulate student investigations in biology. In particular, peer-reviewed, field-tested, and published modules in Quality Undergraduate Educational Simulations and Tools in Biology useful for evolutionary problem solving have been available to us since the publication of The BioQUEST Library (Jungck, 1993). From The BioQUEST Library VI (Jungck, 2002) and other sources, we list a few of our favorites. We also refer you to our Web site www.bioquest.org, and the BEDROCK project, and we invite you to look at the evolutionary labs in Microbes Count! (Jungck, Fass, & Stanley, 2002) and investigative cases in Biological Inquiry: A Workbook of Investigative Case Studies (Waterman & Stanley, 2005).

Conclusion

Why do we care? We contend that students will develop a much deeper understanding of biological systems by using evolutionary problem solving. Their ability to make better-informed decisions, examine current practices, and design new systems will be enhanced as they tackle issues of conservation, biodiversity, and extinction; determine consequences of selection, mutation; drift, and migration, or struggle with new biotechnological approaches to drugs, medical diagnostics, and agricultural needs.

What is our motivation? Much of our own evolution education was treated as philosophy rather than as a science. We wish to instill a view of working evolutionary scientists using a Darwinian approach rather than repeat these same Platonic and Aristotelian assumptions with our own students.

Platonic	Darwinian
Discovery	Constructivism
Abstract	Material
Individual	Collaborative
Invariant	Contextual
“Pure”	Utilitarian or relevant
“Truth”	Peer review
Received	Human activity
Closure	Open ended

Table 3. Comparison of views of the activities of the scientist

The active construction of new knowledge illustrated in peer-reviewed scientific journals (such as *Evolution*, *Journal of Molecular Evolution*, *Paleobiology*, *American Naturalist*, *Molecular Phylogenetics*, *Development and Evolution*, as well as regularly in *Science*, *Nature*, and *PNAS* [Proceedings of the National Academy of Sciences of the United States of America]) that is based on experiments, observations, and statistical analyses of data, is an important part of evolutionary biology that students will be screened from if they don't have opportunities for doing what evolutionary researchers do. The power of practice is far stronger than that of rhetoric! Students who engage in careful hypothesis testing based on empirical data are more likely to be able to make informed conclusions about the nature and application of evolutionary thinking.

Our students could understand evolutionary issues better if they were given many more opportunities for actively participating in evolutionary science. If we want them to be able to determine how data are to be collected, analyzed, interpreted, communicated, and peer-reviewed in evolutionary problem solving, then we must engage them through practical experiences that include hypothesis testing, rejection of ideas based upon data, and careful integration with prior knowledge. A wealth of such experiences exists for both educators and students.

Brief Description of the Resources

The following are examples of software, tools, and databases that are useful for investigating evolution.

Details of the Resources

Title	Author	Medium	Grade Level	Publisher	Copyright	Cost/Ordering Information
BIRDD (Beagle Investigations Return with Darwinian Data)	Price, Donovan, Stewart, & Jungck (2002)	Online database with activities	High school through university	BioQUEST Curriculum Consortium	2001	Free at http://bioquest.org/birdd/index.php Additional data found in the BioQUEST Library VI, available for purchase at http://bioquest.org/indexlib.html (will be available at no cost beginning in December of 2005 at http://bioquest.org).
Description: Original research data on Galápagos finches: morphology, songs, breeding on various islands, protein and nucleic acid sequences, etc.						
Evolve	Price & Vaughan (2002); see Soderberg & Price (2003); Price, Vaughan, Umezaki, & Jungck (2005)	Software simulation	High school through university	BioQUEST Curriculum Consortium	2002	Found in the BioQUEST Library VI, available for purchase at http://bioquest.org/indexlib.html (will be available at no cost beginning on December 20 th at http://bioquest.org).
Description: Selection, drift, and migration.						
DeFinetti	Barman, Collins, Louis, & Jungck (1985); Weisstein, Jungck, Johnson, & Louis (2004)	Online software tool	University	BioQUEST Curriculum Consortium	1985	Free Online-adapted version available at http://bioquest.org/bedrock/search_tools.php
Description: Adaptive landscape, selection on 1 locus with 3 alleles, 6 genotypes.						
Phylogenetic Investigator	Brewer	Online simulation	University	BioQuest Curriculum Consortium	2002	Found in the BioQUEST Library VI, available for purchase at http://bioquest.org/indexlib.html This will be available at no cost beginning in December 2005 at http://bioquest.org
Description: Cladistics						

Developmental Selection	Buckley	Software Simulation	High school to University	BioQUEST Curriculum Consortium	2002	Found in the BioQUEST Library VI, available for purchase at http://bioquest.org/indexlib.html This will be available at no cost beginning in December 2005 at http://bioquest.org
Description: Testing seed abortion and pollen tube competition theories						
Populus models of ecology	Alstad	Book and software	High school to University	Prentice Hall	2000	Software available at no cost http://www.cbs.umn.edu/populus/Download/Versions.html ISBN: 0-1302-1289-X Book is approximately \$20 used/ \$37 new
Description: Inbreeding, linkage disequilibrium, many others						
Excel – spreadsheet exercises in ecology and evolution	Donovan & Welden	Book	High school to University	Sinauer Associate	2001	\$29.95 http://www.sinauer.com/detail.php?id=1597 ISBN 0-87893-159-7
Description: Evolutionary stable strategies, game theory						
Fundamental Methods of Evolutionary Ecology Laboratory Exercises with Maple	Rogers	Mathematics software	High school to University	University of Utah	2003	Retrieved October 21, 2004 from http://www.anthro.utah.edu/~rogers/ant4471/kinseln.pdf
Description: Kin selection						
Testing evolutionary hypotheses in the classroom with MacClade software.	Cordella	Article	High school to University	Journal of Biological Education	2002	<i>Vol. 36</i> , pages 94–98
Description: Phylogenetic systematics						
BEDROCK Problem Spaces	BioQUEST Curriculum Consortium	Access to data, tools, contemporary problems in science	High school to University	BioQUEST Curriculum Consortium	2004	See: http://www.bioquest.org/bedrock
Description: Evolutionary bioinformatics						
Biology WorkBench	Musante	Online interface for access to multiple databases, tools, and visualization	High school to University	San Diego Super Computer Center	2004	Freely available at: http://workbench.sdsc.edu/
Description: Evolutionary bioinformatics; a web-based tool for biologists. The WorkBench allows biologists to search many popular protein and nucleic acid sequence databases.						
TB Lab	Reiser	Software simulation	High school to University	BioQUEST Curriculum Consortium	2003	Found in the BioQUEST Library VI, available for purchase at http://bioquest.org/indexlib.html (will be available at no cost beginning in December 2005 at http://bioquest.org).
Description: Antibiotic resistance in tuberculosis						

Luria-Delbrück	Green & Bozzone	Software tool	High school to University	BioQUEST Curriculum Consortium	2000	Free http://bioquest.org/bedrock/search_tools.php
Description: Fluctuation test, estimate of mutation rates						
EvolSeq	Weisstein	Software tool	High school to University	BioQUEST Curriculum Consortium	2004	Free http://bioquest.org/bedrock/search_tools.php
Description: Ultrametric and additive trees						
Dynamic Programming	Lockhart	Software Tool	University	BioQUEST Curriculum Consortium	2004	Free http://bioquest.org/bedrock/search_tools.php
Description: Pairwise sequence alignment						

References

- Alstad, D. (2000). *Populus models of ecology*. Englewood, NJ: Prentice Hall. [ISBN: 0-1302-1289-X, Web site: Populus 5.3, released on September 5, 2003, supercedes version 5.2.1 of March 2003; <http://www.cbs.umn.edu/populus/Download/Versions.html>].
- Altman, R. B. (1998). A curriculum for bioinformatics: The time is ripe. *Bioinformatics*, 14(7), 549–550.
- Atkins, J. F., Ellington, A., Friedman, B. E., Gesteland, R. F., Noller, H. F., Pasquale, et al. (2000). *Bringing RNA into view: RNA and its roles in biology*. Colorado Springs, CO: BSCS.
- Bader, J. M. (1998). Measuring genetic variability in natural populations by allozyme electrophoresis. In J. Karcher (Ed.), *Tested studies for laboratory teaching: Vol. 19. Proceedings of the 19th Workshop/Conference of the Association for Biology Laboratory Education* (pages 25–42).
- Banschbach, V., & Peroni, P. (2000). *Evolutionary Mechanisms*. Retrieved October 21, 2004 from <http://www.bio.davidson.edu/Courses/bio112/Bio112LabMan/Section%206.html>
- Barman, C. R., Collins, A., L.C. Louis, E. J., & Jungck, J. R. (1985). Sickle cell anemia: “Interesting pathology” and “rarely told stories.” *American Biology Teacher*, 47(3), 183–187.
- Bates, H. W. (1862). Contributions to an insect fauna on the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, 23, 495–566.
- Bornstein, S. (1999). *Modeling the mitochondrial DNA “clock” underlying the Eve hypothesis*. Retrieved October 21, 2004, from Access Excellence Web site: <http://www.accessexcellence.org/AE/ATG/data/released/0489-SandyBornstein/index.html>
- Brewer, S. (2002). Phylogenetic investigator. In J. R. Jungck (Ed.), *The BioQUEST Library VI*. San Diego, CA: Academic Press.
- Bright, K. (n.d.). *EvolNet*. Retrieved October 21, 2004, from <http://evonet.sdsc.edu/ROADS/subject-listing/labexk12.html>.
- Brown, J. (2004). *Measuring selection in natural populations of crown gall*. Retrieved October 21, 2004 from http://web.grinnell.edu/individuals/brownj/edu/136_lab6.html
- Buckley, D. (2002). Developmental selection: Seed abortion and pollen tube competition. In J. R. Jungck (Ed.), *The BioQuest Library VI*. San Diego, CA: Academic Press.
- Buehler, M., & Quillen, A., (1995). *Dinosaur tracks: From stride to leg length to speed*. Retrieved October 21, 2004, from Access Excellence Web site: <http://www.accessexcellence.org/AE/AEPC/WWC/1995/dinotracks.html>
- Camin, J. (2002). Caminacules. In J. R. Jungck (Ed.), *The BioQUEST Library VI* (p. 165). San Diego, CA: Academic Press.
- Carrapiço, F., Lourenço, A., Fernandes, L., & Rodrigue, T. (2002). A journey to the origins: The astrobiology paradigm in education. In R. B. Hoover, G. V. Levin, R. R. Paepe, & A. Y. Rozanov, *Proceedings of SPIE, Vol. 4495. SPIE Astrobiology Conference. Instruments, Methods, and Missions for Astrobiology IV* (pp. 295–300). Bellingham, WA: The International Society for Optical Engineering.
- Cordella, S. G. (2002). Testing evolutionary hypotheses in the classroom with MacClade software. *Journal of Biological Education*, 36, 94–98.
- Culp, T. (1995). *Using magnetotactic bacteria to study natural selection*. Retrieved October 21, 2004, from Access Excellence Web site: <http://www.accessexcellence.org/AE/AEPC/WWC/1995/bacteria.html>
- Dawkins, R. (1986, 1996). *The blind watchmaker: Why the evidence of evolution reveals a universe without design*. New York: W.W. Norton.
- DeWitt, W., & Brown, E. R. (1977). *Biology of the cell: Laboratory explorations*. Philadelphia, W.B. Saunders Company.

- Donovan, S. (2002, Fall). Bioinformatics Education Dissemination: Reaching Out, Connecting, and Knitting-together (BEDROCK). *BioQUEST Notes*, 12(1), 6–7.
- Donovan, T., & Welden, C. W. (2001). *Spreadsheet exercises in ecology and evolution*. Sunderland, MA: Sinauer Associates.
- Fall, B. A., & Fifield, S. (1999). Artificial selection and evolution: A laboratory exercise using *Brassica rapa*. In B. Fall, S. Fifield, & M. Decker, *Biology 1001 laboratory manual, Fall 1999, College of Biological Sciences, University of Minnesota, Minneapolis, MN*: Burgess International Group. [A nice adaptation of this experiment by C. Brewer, M. Poss, and P. Spruell at the University of Montana in *Artificial selection in Wisconsin fast plants (Brassica rapa) Part IV* is available online at http://ibscore.dbs.umt.edu/biol101_99/lab12.htm].
- Gabric, K. M. (2003, May). *Bioinformatics in the Biology Classroom*. Retrieved October 21, 2004, from <http://actionbioscience.org>
- Ginzburg, L. R., Soucy, S. L., & Carroll, S. D. (2002). Endangered species laboratory. In J. R. Jungck (Ed.), *The BioQUEST library VI*. San Diego, CA: Academic Press.
- Glover, B. W. (1968). Luria & Delbrück fluctuation test. In R. C. Clowes & W. Hayes (Eds.), *Experiments in microbial genetics* (pp. 22–26). Malden, MA: Blackwell Scientific Publishers.
- Goldman, C. A. (1998, June). *Measuring genetic variation in zebra mussels using cellulose acetate electrophoresis* [ABLE mini-workshop]. Presented at the 20th Annual Workshop/Conference of the Association for Biology Laboratory Education (ABLE), Florida State University, Tallahassee.
- Green, D. S., & Bozzone, D. M. (1999). Island biogeography and the design of natural preserves. In S. Kuntz, A. Hessler, + G. Bauer (Eds.), *Making meaning: Integrating science through the case study approach to teaching and learning* (pp. 15–33). New York: McGraw-Hill Primis.
- Green, D. S., & Bozzone, D. M. (2000). A test of hypotheses about random mutation: Using classic experiments to teach experimental design. *American Biology Teacher*, 63(1), 54–58.
- Haddix, P. L., Paulsen, E. T., & Werner, T. F. (2000). Measurement of mutation to antibiotic resistance: Ampicillin resistance in *Serratia marcescens*. *Bioscene*, 26(1), 17–21.
- Hilbish, T. J., et al. (1994). A simple demonstration of natural selection in the wild using the common dandelion. *American Biology Teacher*, 56, 86–90.
- Hoagland, B. (2004, March 4). *Modeling Microevolutionary Process*. Retrieved October 21, 2004, from <http://biology.wsc.ma.edu/biology/courses/concepts/labs/evolution/>
- Holtzclaw, T. (n.d.). *Biodiversity vs patch size and type*. Retrieved October 21, 2004, from the Access Excellence Web site: <http://www.accessexcellence.org/AE/ATG/data/released/0328-TrumanHoltzclaw/index.html>
- Jasien, P. G., Miller, S. L., Levy, M., & Dworkin, J. (2002). How could life have arisen on Earth? In J. L. Stewart & V. L. Wilkerson (Eds.), *ChemConnections: Series Guide to Teaching with Modules & CD-ROM*. New York, W. W. Norton.
- Jungck, J. R. (1984, January). Creation of the evolution laboratory. *Bioscene: Journal of College Biology Teaching*, 10(1), 16–20.
- Jungck, J. R. (1997, May). Ten equations that changed biology: Mathematics in problem-solving biology curricula. *Bioscene: Journal of College Biology Teaching*, 23(1), 11–36. Retrieved October 21, 2004, from http://papa.indstate.edu/amcvt/volume_23/
- Jungck, J. R. (1998, February). Evolutionary problem solving. *BioQUEST Notes*, 8(2), 4–5.
- Jungck, J. R. (1991). Ten questions for creationist policy makers. *Bioscene: Journal of College Biology Teaching*, 17(2), 33. Retrieved October 21, 2004, from http://papa.indstate.edu/amcvt/volume_17/v17-2p33.pdf
- Jungck, J. R. (Ed.). (1993). *The BioQuest Library I*. College Park, MD: University of Maryland Press.
- Jungck, J. R. (Ed.). (2002). *The BioQUEST library VI* (2003). San Diego, CA: Academic Press.
- Jungck, J. R., & Dyke, C. (1985). Evolution, economics and education: Understanding the consequences of natural selection in health and disease. *American Biology Teacher*, 47(3), 138–141.
- Jungck, J. R., & Friedman, R. M. (1984). Mathematical tools for molecular genetics data: An annotated bibliography. *Bulletin of Mathematical Biology*, 46(4), 699–744.
- Jungck, J. R., Fass, M. F., & Stanley, E. D. (Eds.). (2002). *Microbes count! Problem posing, problem solving, and peer persuasion in microbiology*. Washington, DC: American Society for Microbiology Press.
- Lockhart, P. (2004). *Dynamic programming—pairwise sequence alignment*. Retrieved October 21, 2004, from BEDROCK website: http://bioquest.org/bedrock/tool_details.php?item_id=16.
- Maddison, D., & Maddison, W. (2000). *MacClade 4: Analysis of phylogeny and character evolution* [CD-ROM]. Sunderland, MA: Sinauer Associates.
- Mankiewicz, C. (1998a). A laboratory exercise in experimental bioimmuration. *Journal of Geoscience Education*, 46, 182–186.
- Mankiewicz, C. (1998b). A laboratory exercise for studying borings. *Journal of Geoscience Education*, 46, 452–455.

- Mankiewicz, C., & Mendelson, C. V. (1993). Trace fossils. In S. G. Stover, & R. H. Macdonald (Eds.), *On the rocks: Earth science activities for grades 1–8* (pp. 99–101). Tulsa, OK: SEPM (Society for Sedimentary Geology). Retrieved October 21, 2004, from http://www.beloit.edu/~SEPM/Fossil_Explorations/Trace_Fossils.html
- Mertons, T. R. (1972, January–February). Student investigations of speciation in *Tragopogon*, *Journal of Heredity*, (1), 39–42.
- Mills, D. R., Peterson, R. L., & Spiegelman, S. (1967, July 15). An extracellular Darwinian experiment with a self-duplicating nucleic acid molecule. *Proceedings of the National Academy of the United States of America*, 58(1), 217–224.
- Muller, F. (1879). Ituna and Thyridia; a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, 1879, xx–xxix.
- Musante, S. (2004, July). Using bioinformatics in the undergraduate classroom. *BioScience*, 54(7), 625.
- Ogram, A. (1998). Teaching soil bacterial diversity from a phylogenetic perspective: A term project utilizing the Ribosomal Database Project. *Journal of Natural Resources and Life Sciences Education*, 27, 93–96.
- Omoto, C. K., & Malm, K. (2003). Assessing antibiotic resistance of *Staphylococcus*: Students use their own microbial flora to explore antibiotic resistance. *American Biology Teacher*, 65, 133–135.
- Parmelee, J. T. (2004). *Studying the processes and effects of evolution with EvolutionLab*. Retrieved October 21, 2004, from the Manchester Community College Web site: <http://www.faculty.virginia.edu/evolutionlabs/Studying%20the%20Processes%20and%20Effects%20of%20Evolution%20with%20Evolution%20Lab.htm>
- Platt, J. E. (1999). Putting together fossil collections for “hands-on” evolution laboratories. *American Biology Teacher*, 61, 275–81.
- Poston, M. (2004). *Using BioQUEST simulations to bring evolution into the lab*. Retrieved October 21, 2004, from Learning through Technology (LT²) Web site: <http://www.wcer.wisc.edu/archive/c11/ilt/solution/postonm2.htm>
- Price, F. (2002). Data collection and organization. In J. R. Jungck (Ed.), *The BioQUEST Library VI*. San Diego, CA: Academic Press.
- Price, F., Donovan, S., Stewart, J., & Jungck, J. R. (2002). BIRDD: Beagle Investigations Return with Darwinian Data. In J. R. Jungck (Ed.), *The BioQUEST Library VI*. San Diego, CA: Academic Press.
- Price, F., & Vaughan, V. (2002). Evolve. In J. R. Jungck (Ed.), *The BioQUEST Library VI*. San Diego, CA: Academic Press.
- Price, F., Vaughan, V., Umezaki, K., & Jungck, J. R. (2005). Evolve II. Retrieved October 21, 2004, from *The BioQUEST library resource center* Web site: http://bioquest.org/bedrock/tools_result.php
- Reiser, B. (2003). The Galápagos Finches [computer software]. Biology Guided Inquiry Learning Environments (BGulLE). Retrieved October 21, 2004, from <http://www.letus.org/bguile/tb/tb-overview.html>
- Reiser, B. (2003). *The trouble with tuberculosis* [computer software]. Biology Guided Inquiry Learning Environments (BGulLE). Retrieved October 21, 2004, from <http://www.letus.org/Software%20Descriptions/swfinches.htm>
- Rogers, A. R. (2003). *Fundamental methods of evolutionary ecology laboratory exercises with maple*. Retrieved October 21, 2004, from <http://www.anthro.utah.edu/~rogers/ant4471/kinseln.pdf>
- Salata, M. (2002). Evolution lab with *Drosophila*. *Bioscene*, 28(2), 3–6.
- Soderberg, P., & Price, F. (2003, January). An examination of problem-based teaching and learning in population genetics and evolution using EVOLVE, a computer simulation. *International Journal of Science Education*, 25(1), 35–55(21).
- Thomson, J. D., Rigney, L. P., Karoly, K., & Thomson, B. A. (1994). Pollen viability, vigor, and competitive ability in *Erythronium grandiflorum* (Liliaceae). *American Journal of Botany*, 81, 1257–1266.
- Waterman, M., & Stanley, E. (2005). *Biological inquiry: A workbook of investigative case studies*. San Francisco: Pearson/Benjamin-Cummings.
- Weinstein, A., & Jungck, J. R. (2004). *EvolSeq*. Retrieved October 21, 2004, from http://bioquest.org/bedrock/tool_details.php?item_id=7
- Weinstein, A., Jungck, J. R., Johnson, T., & DeFinetti, E. L. (2004). *DeFinetti: Population genetics of a one locus, three allele model in a diploid organism*. Retrieved October 21, 2004, from http://bioquest.org/bedrock/tool_details.php?item_id=19
- Welden, C. W., & Hossler, R. A. (2003). Evolution in the lab: Biocide resistance in *E. coli*. *American Biology Teacher*, 65, 56–61.
- Yasukawa, K. (2003). The evolution of behavior: A phylogenetic approach. In B. J. Ploger & K. Yasukawa (Eds.), *Exploring animal behavior in laboratory and field: An hypothesis-testing approach to the development, causation, function, and evolution of animal behavior*. San Diego, CA: Academic Press/Elsevier Science.
- Zimmer, C. (2005). Testing Darwin: Scientists at Michigan State prove evolution works. *Discover*, 26(2), 28–35. [The software Avida is available at <http://dillab.caltech.edu/avida/>]