

1 The Nature of Evolution

Introduction

In 1859 Charles Darwin finished his masterpiece, *The origin of species by means of natural selection*, as follows:

It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Darwin's daring message was that we can understand life by studying contemporary processes that we can observe and test. He thought evolution through natural selection was as magnificent as Newtonian physics. Events have proven him right. Evolution is now a well-established science with impressive explanatory power.

This book describes our current understanding of evolution. It starts with the mechanisms that cause evolutionary change—natural selection, inheritance, and gene expression—then moves through the evolution of sex, life histories, and sex ratios to sexual selection. After discussing multilevel selection and genetic conflict, it uses speciation to make the transition to phylogenetics and the history of life. The key events in evolution are then assessed, followed with insights from molecular analysis and the comparative method. We finish with thoughts on the status and prospects of evolutionary biology.

This chapter gives a brief overview of the whole subject.

A brief description of evolutionary biology

Evolutionary biology is a rich collection of well-developed approaches to the interpretation of biological diversity and organismal design. Part of it studies how **natural selection** produces **adaptations**. Another part studies what **genealogies** and **phylogenies** tell us about relationship and history. Some methods used to reconstruct history use the observation that much of the variation in DNA sequences is neutral with respect to selection—that part of evolutionary biology is not about natural selection. Evolutionary biology is also the study of conflicts, conflicts between hosts and parasites, between parents and offspring, among brothers and sisters, between genes with different transmission patterns. Participants in conflicts must make the best of a bad situation that they often cannot escape. Another part studies genetic and phenotypic dynamics, regardless of whether they lead to adaptation or not. Sometimes they do not, and sometimes they cannot. Other parts of the field study the relationships of organisms and patterns in the fossil record that reveal the history of life. No ideological monolith, evolutionary biology is rich in alternatives that can be played off against each other to provide a self-critical, well-tested, and reliable interpretation of the natural world.

How evolutionary biologists think

Evolutionary biologists want to understand how variation in reproductive success arises, what causes the correlation of traits with reproductive success and thus natural selection, how the genetic variation that enables a response to selection originates and is maintained, and how that response is constrained by geography, time, inheritance, conflicts, development, and history. They want to unravel the history of life and understand the relationships among all living things. They investigate all organisms, from viruses to humans, from fungi to trees.

Evolutionary biologists ask many types of questions and use several approaches to answer them. Here are some of the more important ways of thinking about evolution.

Population and quantitative geneticists think about **microevolution**, which occurs within populations over relatively short periods of time; about the effects of changing the frequency of the different forms that one gene can take (its **alleles**) or of

holding these frequencies at a stable, intermediate level. Their classical problem is to understand what maintains genetic variation. Among the candidate explanations are a balance between natural selection and **mutation, gene flow**, and the **drift** of neutral genes. **Population geneticists** tend not to worry about the design of phenotypes.

Evolutionary ecologists think about the design of **phenotypes** for **reproductive success**. This involves traits such as age and size at maturity, number and size of offspring, life span and aging, strategies for investing in sons or daughters, and the consequences of competition for mates and of choosing mates. They tend to avoid genetic details.

Molecular evolutionists think about history recorded in DNA sequences. Some examine parts of the genome that are not transcribed into RNA or translated into proteins, parts that have little influence on the phenotype. They view adaptive change against a background of history that they can best infer from the parts of the genome that have not adapted, for adaptation can obscure history.

Systematists-many of whom are also molecular evolutionists-think in terms of evolutionary trees, give great weight to history, and focus on variation among species. For them, the major problem is to infer relationships among species reliably, so that they can reconstruct the history of life on the planet, not to understand why gene frequencies change or how phenotypes are designed for reproductive success.

Paleontologists are also historians of life. They think in deep time and concentrate on largescale trends and major events, such as adaptive radiations, mass extinctions, and irregularities in the rate of evolution. They often cannot see processes occurring within periods of less than 100 000 years, but they see the big picture-**macroevolution**-with particular clarity. Paleontology, for example, tells us that rates of evolution in many lineages are irregular, with long periods of little or no change-**stasis**-interrupted by short periods of rapid change-**punctuation**. Paleontology also connects evolutionary history to continental drift and to ancient climates, often with fascinating insights.

Each approach is a different way of thinking about evolution, with its own advocates, its own school, and its own focus. Good evolutionary biologists are not constrained by these categories. They have the background and flexibility to use whatever methods are needed to answer a question. They know that these approaches all legitimately simplify a complex process, and that none of them retains all the important features of that process. Therefore, when adopting one approach, they check the consistency of assumptions, interpretations, and predictions against those made by other approaches.

Evolutionary change: adaptive and neutral

Microevolution describes how populations change in the relative abundance of genes or of phenotypes. The logical conditions necessary for microevolutionary change are described below.

Two concepts and a link between them explain microevolution. The two concepts are heritable variation in traits and variation in reproductive success among individuals within a population. The link is the correlation between the two types of variation. These three elements explain both adaptive and neutral evolution. When the correlation between reproductive success and a trait is positive or negative, natural selection is operating on that trait, for natural selection consists precisely of variation in reproductive success correlated with variation in a trait. When that correlation is zero, natural selection disappears, even though variation in reproductive success may remain, and what is left is neutral evolution.

You may have heard that evolution is concerned with the survival of the fittest. That is a misleading half-truth. Survival is important, but only in so far as it contributes to reproductive success, to the number of offspring produced per lifetime that survive to reproduce. And to express the central process as the survival of the fittest is to think in a circle and beg the question, for if fitness is defined by survival, the statement is empty. The action of selection is located in the many mechanisms that connect variation in reproductive success to variation in traits and genes. There is no logical circularity in tracing such connections.

The production of surviving offspring is achieved through the number of offspring born, their survival, the survival of the parents to reproduce again, the number of offspring they have in their second and subsequent breeding attempts, the survival of those offspring, and so forth. Variation in reproductive success is made up out of variation in all these components.

On the one hand, if there were no variation in reproductive success, neither the distribution of genes nor the distribution of phenotypes would change. (This statement excludes mutations, which affect the variation in reproductive success of molecules.) Note that there is always some variation in reproductive success in natural populations. For example, in Newton's (1988) study of sparrowhawks in southern Scotland, 72% of the females that fledged died before they could breed, 4.5% tried to breed but produced no young, and the remaining 23.5% produced between 1 and 23 young apiece (Fig. 1.1).

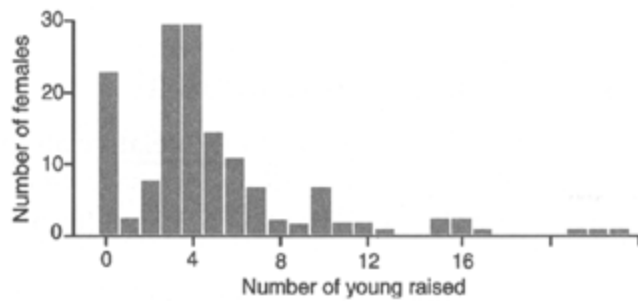


Fig. 1.1 Lifetime reproductive success measured as offspring that fledged for 142 female sparrowhawks from 1971 to 1984. Twenty-three females produced no fledglings, 1 produced 21, 1 produced 22, and 1 produced 23. The potential for natural selection was great. (From Newton 1988.)

On the other hand, if there is no heritable variation in a trait, there will also be no evolutionary change—even if there is variation in reproductive success—for the differences in performance exhibited by the parents will not be reflected in the offspring. Only if there is some variation both in the trait and in reproductive success can there be a correlation between the two producing natural selection. Both conditions are necessary for adaptive change. Both are also necessary for neutral change, in which case the correlation between the two must be near zero.

Many traits in natural populations display heritable variation. To determine whether variation is heritable we can see whether offspring resemble their parents. O’Neil (1997) did this in her study of an introduced plant, the purple loosestrife (*Lythrum salicaria*). She measured the number of seeds per capsule and found considerable variation in this trait among both parents and offspring. To see whether the variation was heritable, she plotted the values for the offspring against the average for the two parents (the midparent value) (Fig. 1.2). Parents that had above-average numbers of seeds per capsule had offspring that were above-average, and parents with below-average numbers of seeds per capsule had offspring that were below-average. The slope of the straight line that best described the relationship (the *heritability*), 0.44, was significantly greater than zero. Thus she found heritable variation on which selection could act.

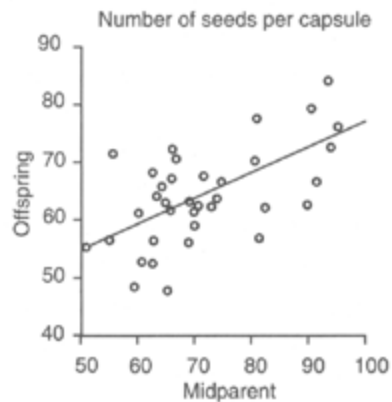


Fig. 1.2 The resemblance of offspring to parents for number of seeds per capsule in the purple loosestrife, an introduced plant that grows in wetlands. There is much heritable variation for this ecologically important trait in a population growing along the Kennebec River in Maine. Midparent = average of the two parents. The potential response to selection is great. (Data courtesy of Pamela O’Neil.)

When there is both heritable variation and variation in reproductive success, it is the correlation between them that determines the type of evolutionary change that occurs. If there is little or no correlation between heritable and reproductive variation, then the things that are inherited and that do vary, whether genes or traits, will fluctuate randomly in the population within the limits of the available variation. This is **neutral evolution**. If the correlation between reproductive success and heritable variation is strong, then evolutionary change in the gene or trait will not be random but will move in the direction of increasing adaptation. This is **adaptive evolution**. The engine of adaptive evolution, **natural selection**, consists of two of the three parts of the evolutionary mechanism: variation in reproductive success and the correlation between reproductive success and the trait under consideration. It does not include the heritable variation that enables a response to selection.

In natural selection, nothing consciously chooses what will be selected. Genes and traits increase or decrease in frequency because of their correlation with the reproductive success of the organisms that carry them. There is no long-term goal, for nothing is involved that could conceive of a goal. There is only short-term relative reproductive success, producing both short- and long-term change.

Note that both adaptive and neutral evolution require variation in reproductive success. The same variation in reproductive success that causes adaptive evolutionary change in one trait, where some genetic variation is correlated with reproductive success, will cause neutral drift in another trait, where none of its genetic variation is correlated with reproductive success. To see how this works, consider a neutral gene or trait in a large population in which there is a lot of variation in reproductive success, where some females have many surviving offspring whereas others have few or none. The neutral gene or trait increases or decreases erratically, depending on whether it occurs in a large or a small family. Because it is not correlated with family size, occurring in many different family sizes at random from generation to generation, it does not change steadily in any particular direction. Also central to neutral evolution is the fair segregation of alleles into gametes at meiosis, which resembles the flipping of a coin. Fair segregation combines with random variation in family size to cause neutral drift in populations of any size, large or small.

This way of distinguishing between adaptive and neutral evolution focuses attention on the correlation between a trait and reproductive success. The strength of that correlation determines whether a trait will undergo adaptation or perform a random walk through time. All three components of the evolutionary mechanism—heritable variation, variation in reproductive success, and the correlation between the two—are important. The generation and maintenance of heritable variability and the patterns that result from neutral evolution are just as much a part of evolutionary biology as is the study of natural selection and its resulting adaptations.

Distinguishing between adaptive and neutral evolution by using the correlation between a trait and reproductive success clarifies and unifies the basic evolutionary processes. The loose application of 'natural selection' to the entire process, including the response enabled by heritable variation, is confusing. We therefore use 'natural selection' to refer just to the correlation of reproductive success with a trait. When we want to refer to the complete process, including the genetic response to selection, we use the phrase 'adaptive evolution'.

Information replicators and material interactors

Most of what gets inherited is not matter but information, a set of instructions coded in genes that specify how to build an organism. The design of organisms for reproductive success can only be changed by changing the stored genetic instructions. Genetic instructions are changed by natural selection when organisms with different genetic instructions vary in their reproductive success. Thus evolution occurs both in information (in genotypes) and in matter (in phenotypes). Genes function as information **replicators** while organisms function as material **interactors**, interacting with their environments and with each other to survive, reproduce, and get their genes into the next generation (Dawkins 1982; Williams 1992).

Adaptation

A response to selection occurs whenever heritable variation in a trait is correlated with reproductive success. The result is improvement in reproductive performance. If this improvement continues for enough generations, a *process* called adaptation, it results in a *condition* in the trait that we also call an adaptation. Adaptation can be hard to demonstrate, but as a starting point we can define it as a condition that suggests to us that it evolved because it improved survival and reproductive performance. Here are a few examples of conditions that suggest adaptation.

The striking precision of adaptations is demonstrated by the accurate, coordinated timing of reproduction in marine organisms that rely on the predictability of the moon and the tides. For example, the palolo worm lives most of the year hidden on the sea floor in shallow water in the western Pacific. As the reproductive season approaches, it differentiates a special reproductive organ on the posterior part of its body that looks like an individual worm. Reproduction is triggered by a specific phase of the moon, detected by millions of individuals scattered across a large area. On just a few nights of the year, the reproductive organ splits off the worm and swims to the surface, where it encounters millions of others, forming a massive swarm that spawns and dies. If the timing were not precise, reproduction would often fail, for lack of synchrony would lead to lack of partners. Meanwhile, the adults survive and grow another reproductive organ for the next year.

Similarly, the grunion, a fish found along the coast of California, spawns with the highest tide of the month. It rushes in with the waves just as the tide is turning and throws itself out of the water, depositing eggs and sperm in pockets in the wet sand where the eggs will not be disturbed again by waves until a month later, at the time of the next spring tide. When that tide

arrives and the waves disturb the eggs, the young hatch explosively and swim out with the receding water. The timing of reproduction, development, and hatching are coordinated precisely with the rhythm of the tides.

The precision of adaptation is also illustrated by the ability of bats to find prey in the dark, using echolocation. The brilliant work of Spallanzani in the late eighteenth century on blinded bats that flew without difficulty was completely ignored by science, which waited for Griffin to rediscover bat echolocation in 1938. Bats produce high-frequency, short wavelength cries that are reflected by small objects. There is a physical constraint on this method of seeing'. Sound waves lose energy rapidly with distance. Lower-frequency waves penetrate further but can only detect large objects, and many bats use echolocation to detect small, rapidly moving, flying insects (Fig. 1.3). Griffin (1958) discovered that when a bat approaches to within 1 or 2 m of an obstacle, it increases the number and raises the frequency of the ultrasonic pulses that it emits. Griffin also tested the ability of bats to fly through grids of fine wires. They had no problem with wires that were 0.4 mm in diameter or larger and had some success with wires down to 0.2 mm in diameter, which reflect very little sound energy.



Fig. 1.3 A bat catching a moth in complete darkness. Bats have exquisite adaptations that help them to catch moths, and moths have equally exquisite adaptations that help them to avoid bats. (By Dafila K. Scott.)

Later experiments (Simmons 1973) demonstrated that a flying bat could discriminate target distances as small as 1 cm by detecting differences of as little as 60 microseconds in the pulseto-echo interval. It could also discriminate a stationary from a vibrating target where the vibration was as small as 0.2 microsecond, implying a difference in pulseto-echo interval of just 1 microsecond. For comparison, the duration of a single action potential in the bat's auditory nerve is about 1 millisecond, a thousand times as long as the interval being discriminated. These astounding abilities to discriminate the distance and nature of an object in complete darkness result from selection for ability to locate flying insect prey whose wing beats convey information on both distance and direction of movement.

Similarly impressive abilities to detect faint signals that carry critical information are found in the noses of migrating salmon, which can detect as little as a single molecule characteristic of their native stream, and in the darkadapted eyes of nocturnal mammals, which can detect as little as a single photon of light.

Thus natural selection evidently has great power to shape precise adaptations. It operates whenever there is variation in reproductive success and the variation in reproductive success is correlated with heritable variation in the trait. When these conditions are fulfilled, the process of adaptation begins. Whether or not it will ever result in the state we call adaptation, illustrated above, depends on whether other factors constrain the response to selection-whether it can occur at all, and whether only certain phenotypes can be produced and not others. Even if the response to selection can occur and if a certain phenotype can be produced, other factors, such as population size, gene flow, and the frequency with which selection occurs, affect the precision with which a trait can be shaped for reproductive success.

Because there is always some variation in reproductive success, and some trait is usually correlated with reproductive success, natural selection has almost always acted and is usually acting in all populations, including our own. Because natural selection acts on all variable traits that contribute to survival and reproduction, if such a trait is not in the state best for survival and reproduction, then something must be limiting its evolution. Three such limiting factors are particularly important: gene flow, sufficient time, and **tradeoffs**. Gene flow and sufficient time are discussed next. Tradeoffs are introduced later under Principles of phenotypic design (p. 22).

Limits to adaptation: gene flow

Genes 'flow' from one place to another when organisms born in one place reproduce in another, introducing their genes into the local gene pool. When natural selection favors different things in different places, organisms can transport genes that have been successful in one place to other places where they may not be so successful. Gene flow, like mutation, introduces new genetic variants into local populations, and it can produce local maladaptations. For example, in the south of France a small bird, the blue tit, breeds both in downy oak, which is deciduous, and in holm oak, which retains its leaves in winter (Fig. 1.4).

Birds breeding in holm oaks start to breed at the same time as birds breeding in downy oaks. They should start to breed later because the peak of insect abundance on holm oaks comes later in the season; but because more individuals are recruited into the population from downy oaks than from holm oaks, the response to selection reflects the greater frequency with which genes have been selected in the downy oak environment. The birds are maladapted on holm oaks, where clutches laid later in the season would result in more surviving offspring. Because adult birds move freely between downy and holm oaks, and because there are not enough nesting territories on downy oaks, forcing some birds to nest on holm oaks, gene flow is strong, leading blue tits in southern France to breed inappropriately early on holm oaks (Blondel *et al.* 1992).



Fig. 1.4 Blue tits nesting in downy and holm oaks in southern France have greater success on downy oaks and lay clutch sizes adapted to downy oaks in both habitats, even though they would do better with smaller clutches on holm oaks. (By Dafila K. Scott.)

Despite gene flow, local adaptations can evolve when selection is strong. A classic example is heavy metal tolerance in plants. Plants on mine tailings grow on toxic soil and rapidly evolve adaptations to deal with it. Antonovics and Bradshaw (1970) sampled plants from a transect across a zinc-mine tailing and into an uncontaminated pasture. Patterns of continuous changes in trait values or gene frequencies along a geographical transect are called **clines**, and the steepness of a cline measures geographic differentiation. Antonovics and Bradshaw found an extremely steep cline in zinc tolerance at the boundary between the mine tailing and the uncontaminated pasture. The index of tolerance changed from 75% to 5% in less than 10 m. The plants that were zinc tolerant flowered later and were smaller, meaning that tolerance had costs. They also suffered less from inbreeding than those that were not zinc tolerant, which suggests an evolutionary response to local mating with relatives. Even more rapid evolution and stronger selection was suggested by another study of plants growing near galvanized-steel power poles, for the power poles appeared much more recently than the mine. Plants growing within 10 cm of a power pole had significantly higher zinc tolerance than those just 20 cm from it (Fig. 1.5).

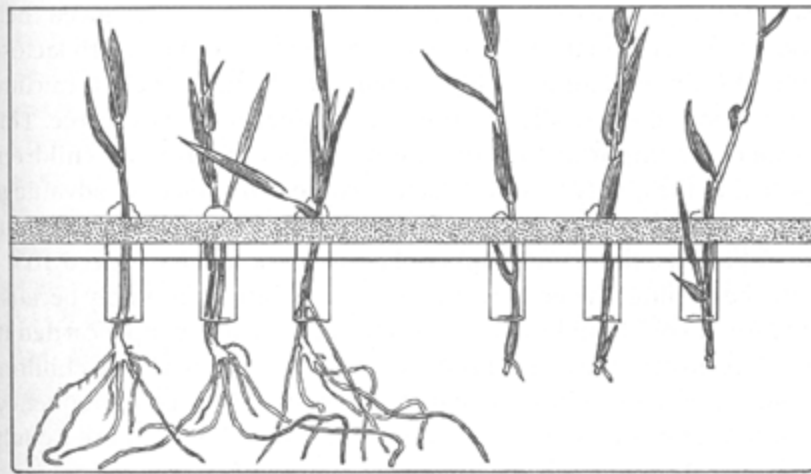


Fig. 1.5 Grass that has adapted to zinc from power poles (on the left) grows much more impressive roots in zinc solution than does grass grown from seed, collected from just a few meters away, that is not adapted to zinc (on the right). (By Dafila K. Scott from a photograph by A. D. Bradshaw.)

Thus strong selection can produce local adaptation despite gene flow, and species often consist of a patchwork of genetically different populations, each displaying different adaptations. For gene flow to prevent local adaptation, natural selection must be weak and the mean distance that genes move in each generation must be large (Endler 1977).

Limits to adaptation: sufficient time

Even without gene flow, it takes time for a population to adapt to an environmental change. Consider the absorption of the sugar in milk, lactose, by adult humans. Like other mammals, human children come equipped with the enzymes needed to digest milk, and most children lose that ability at the age at which they used to be weaned-at about 4 years. However, some humans retain the ability to digest fresh milk into adulthood, including the populations of northern Europe and some in western India and sub-Saharan Africa (Simoons 1978). This genetic difference may explain why dairy products are more prominent in French than in Chinese cooking. The ancestral condition was the inability to digest fresh milk after the age of four, and the recently evolved condition is that ability.

How long would it take that ability to evolve? The domestication of sheep and goats occurred about 10 000-12 000 years ago, the subsequent origin of dairying can be traced to 6000-9000 years ago, and the ability to digest fresh milk after the age of four has a simple genetic basis: it behaves as a single dominant allele on one of the normal chromosomes (an **autosome**), rather than on a sex chromosome. **Dominant alleles** increase in frequency under selection more rapidly than do **recessive alleles**, and knowing that the gene is on an autosome simplifies the prediction of how its frequency will change under selection. Imagine a stone-age human population in which goats and sheep had been domesticated and milk production had begun. In that population, a new mutation arose that allowed people to continue to utilize fresh milk after the age of four. It had an advantage over the ancestral state, for people who drank milk but could not absorb lactose suffered from flatulence, intestinal cramps, diarrhea, nausea, and vomiting, which reduced their reproductive performance. Moreover, those who could absorb lactose benefitted from an additional high-quality food source, rich in calcium and phosphorus, especially at times when other food was scarce. This was especially important to nursing mothers and growing children. Suppose that the ability to absorb lactose conferred a selective advantage of 5%, so that for every 100 surviving and reproducing children of nonabsorber parents, the same number of absorber parents produced 105.

At the beginning, the gene would have been rare, and simply because it was rare, it could only increase slowly, for very few people carried it, enjoyed its advantages, and produced a few more surviving children than did those who did not carry it. As the gene increased in frequency, and more and more people carried it, it began to spread more rapidly through the dairying culture. However, when it became common, its rate of spread decreased, for then most people carried it, and there were very few who suffered from the disadvantage of not having it. How long did it take to increase from a single new mutation to a frequency of 90%? The answer, which comes from genetic models, is 350-400 generations or 7000-8000 years. This estimate would increase dramatically if we assumed a weaker selective advantage. If the estimated age of adult milk-drinking is accurate, then milk-drinking would appear to have increased fitness substantially.

That argument assumes a causal connection between the ability to absorb lactose and individual fitness, an ability that arose with the origin of agriculture. As we will see in Chapter 15, agriculturists evidently had an advantage over hunter-gatherers for several reasons, not just dairying and the ability to absorb lactose. They spread not only their culture but their genes, including

the gene for lactose absorption, from the Near East over all of western Europe. Thus the rapid rise in frequency of the lactose absorption gene in Europe did not depend just on its digestive advantages; it may have hitch-hiked with a culture that expanded and dominated.

Even for a gene under strong selection, evolutionary change takes time.

Natural selection can rapidly produce highly improbable states

Mendelian populations are conservative when they are not under selection, but under strong selection they can rapidly produce combinations of genes that are, at first glance, extremely unlikely. We demonstrate this with two examples. The first, an analogy using the letters of the alphabet, exaggerates the power of selection because it pre-specifies the target. This is not how natural selection works, but the example makes an important principle clear. Because the second, more realistic example is more complicated, we approach it through the first example.

The 31 letters in THEREISGRANDEURINTHISVIEWOFLIFE can be compared to a sequence of 31 genes each with 26 different possible versions. If evolution assembled such sequences completely at random, it would have to sort through 26^{31} different possible combinations of letters to hit on this one. However, natural selection causes favored gene combinations to increase in frequency, and accurate replication in both molecules and populations preserves those increases-it remembers' what worked before. Here strong selection artificially retains the correct letter whenever it occurs. If we start with any random sequence of 31 letters and retain all the letters that happen to be correct, then repeat the process by generating new letters at random for the ones that are not yet correct, we get to the right sequence in about 100 trials, about 30 orders of magnitude faster than a random search (Dawkins 1986; Ewens 1993). For comparison, the age of the universe, about 10-20 billion years, is only 20 orders of magnitude longer than a millisecond.

That example is usefully clear but misleading because natural selection does not aim at any particular final state. It does not aim at anything. It just produces something that works better from among the variants currently available. The next example moves from letter-play to meaningful experimentation.

Ribonucleic acid (RNA), a macromolecule that stores genetic information, can evolve rapidly in test tubes. RNA seems to have originated before DNA, which only later became the common genetic molecule. RNA remains the genetic molecule in many viruses, and the fact that its mutation rate is much higher than that of DNA has important consequences. Human immunodeficiency virus (HIV), for example, is an RNA virus, and its high mutation rate is one reason that it is hard to find a vaccine against it. The high mutation rate of RNA is also one reason that the following experiment worked so quickly.

From a type of virus that infects bacteria (a **phage**), one can extract an enzyme that replicates RNA (an RNA replicase). Given an RNA molecule as substrate, an energy source, and a supply of the four necessary building blocks-the nucleotides-from which RNA is made, this enzyme rapidly produces a large population of RNA copies in solution in a test tube. By transferring a drop of the solution into a new test tube every 30 minutes, one selects the copies present at highest frequency, which are most likely to be transferred in the drop. The molecules that are copied most rapidly are at highest frequency and have a selection advantage. Replication is good but not exact: in about 1 in 10 000 cases the wrong nucleotide is substituted. Thus mutations occur, and some mutations are replicated faster than others-they have greater reproductive success.

Two types of molecules have an advantage: small ones, which can be replicated rapidly, and those that fit especially well to the replicating enzyme. After more than 100 transfers, a large, complex molecule dominates the population; which one depends on details. One that occurs frequently is 218 nucleotides long. Hitting on such a molecule at random has a probability of 4^{218} or 10^{131} . Since there are about 10^{16} molecules in a test tube just before transfer, the procedure screens about 10^{16} molecules every half hour. If it were random, it would take about 10^{110} years to find the best one. Instead, the procedure produces something very close to the best one in about 2 days. The response to selection is efficient because each step leads to a molecule that is better than the previous one, and because the improvements are inherited, they accumulate (Maynard Smith 1998).

Remember this example if you encounter the argument that natural selection cannot work because it starts with random variation. That argument is false. Natural selection can produce highly adapted states rapidly. They only *appear* to be improbable. The efficiency of natural selection makes them probable.

Population genetics answers important questions

Population geneticists study the consequences of genetic information transmission for populations. Some of their important discoveries are listed above: evolution is usually faster in sexual populations, Mendelian populations are conservative, and

natural selection can produce improbable states rapidly. Population genetics also answers other important questions, including:

1. When is inbreeding a problem (why avoid incest)?
2. Is evolution faster in small or in large populations?
3. What are the chances that the children of a given couple will have an inherited disease?
4. What can the geographical distribution of gene frequencies in a population tell us about its history?

Principles of phenotypic design for reproductive success

Fitness is relative reproductive success

Population genetics, which reduces the evolutionary process to the analysis of the factors that change the number of copies of a gene in a population from one generation to the next, has great simplicity and power. However, if we only think about changes in gene frequencies, we cannot explain phenotypic evolution. To understand why organisms are designed in some particular way for reproduction and survival, we must analyze both the replication of the genes that the organism carries and the organism as an interactor that manages to reproduce while overcoming problems posed by the environment.

An allele that increases the lifetime reproductive performance of the organisms in which it is found, relative to other alleles of the same gene, will increase in frequency in the population. We say that it has a higher fitness than the other alleles because it increases in frequency at their expense and because it improves the relative reproductive performance of the organisms that carry it. The allele that wins is only fitter, not necessarily fittest, for another mutant could come along and displace it.

After this process has continued for a long time in a large population in a stable environment, the probability of finding fitter mutants decreases, for most of the single mutations have already occurred many times. The versions that have survived are in some sense 'close to fittest', and most single mutations have become detrimental. This argument does not apply to double or triple mutations, which are much rarer. Traits for which several simultaneous mutations are necessary have not been 'saturated' by mutations and can still be improved. The same effect can be accomplished by reorganizations of the genome, such as chromosomal inversions, that 'freeze' beneficial combinations of genes that previously recombined independently.

Components of natural selection: individual, sexual, and kin selection

The analysis of reproductive success begins with the factors determining the number of surviving and reproducing offspring produced by a single individual over its lifetime. This is the most basic and general component of reproductive success, individual fitness. Selection driven by variation in offspring number per lifetime is called individual selection. It occurs in both asexual and sexual organisms, and it is often all that is needed to account for many adaptations. When parental state affects offspring performance, then the measurement of fitness involves the next generation as well, and reproductive success is the number of surviving and reproducing grandchildren.

In sexually reproducing organisms, reproductive success depends on success in interacting with a partner of the opposite sex to produce offspring. This component of natural selection is called **sexual selection**. Sexual selection can improve mating success so much that lifetime reproductive success increases although survival decreases. For example, the male peacock's large and beautifully colored tail improves his reproductive success by making him attractive to females, but it reduces his chances for survival by making it harder for him to fly-and tigers do eat peacocks.

Sexual selection involves the two sexes in a complex interaction, with surprising results. When females have preferences for certain male traits and by mating with such males transfer the preferred traits to their sons and their preferences to their daughters, a complex coevolutionary interaction between the sexes is generated.

Organisms that interact regularly with relatives experience a third kind of selection. Because an allele's reproductive success consists of the number of copies that exist in the next generation, relative to the copies of other alleles, it does not matter through whose reproductive activities those copies were replicated-directly, by the individual that carries it, or indirectly, by relatives that also carry that allele. Thus if an individual can influence the reproductive success of its kin, it should do so if the benefits exceed the costs-if the increase in its indirect fitness through the increased reproductive success of relatives exceeds the reduction in its direct fitness through the reduction of its own reproduction (Hamilton 1964). This is **kin selection**, a powerful tool for understanding the evolution of apparently altruistic behavior. Its success, and the success of the evolutionary theory of aging and sexual selection, which also emphasize the success of genes at the cost of the organisms that carry them, have convinced many evolutionary biologists that much of evolution is gene centered (Williams 1966; Dawkins 1976).

Traits do not evolve for the good of the species

People unfamiliar with evolution sometimes still say that things evolve for the 'good' of species, so that species can avoid extinction. This explanation is fundamentally wrong. Traits evolve because they improve the reproductive success of individuals and their kin, and if the species to which those individuals belong happens to survive longer because of those changes, this is a by-product of the essential process and not the reason for it.

This insight was achieved in a fascinating episode that can be summarized in three words: selfish mutants invade. If a trait arose that benefitted the species at the cost of the individual, a mutant that was selfish, profiting at the expense of the altruistic individuals, would invade and take over the population. Selection on individuals is much stronger than selection on species. Individuals have much shorter generation times than species, and there is much greater variation in reproductive success among individuals within a species than there is among species within a lineage. In the time that it takes for new species to form and go extinct, a process spanning thousands of individual generations, hundreds of millions of the individuals that form those species have lived and died, giving selection much greater opportunity to sort among individuals than to sort among species. That is why selfish mutants can invade.

Species selection cannot shape adaptations (Maynard Smith 1964; Williams 1966), whose precision is inexplicable by a process that happens infrequently and is poorly correlated with individual reproductive performance. The reproductive timing of palolo worms and grunion, or the ability of bats to fly in the dark, can only be explained plausibly by individual selection. However, species selection can affect large-scale patterns, such as the phylogenetic distribution of sexual species and asexual populations: sex appears to reduce the probability of extinction. The extinction of major groups, such as trilobites, ammonites, and dinosaurs, also affected the subsequent course of evolution of the groups that survived, by providing individual selection with a scope of action that would otherwise not have been available.

Trade-offs

A trade-off exists when a change in one trait that increases reproductive success is linked to changes in other traits that decrease reproductive success. The reasons for such linkages are not always well understood, but we know they are frequent. If there were no trade-offs, then natural selection would drive all traits correlated with reproductive success to limits imposed by constraints. Because we find many traits that are clearly correlated with reproductive success varying well within such limits, trade-offs must exist. A common trade-off is that between reproduction and survival. For example, fruit flies selected to lay many eggs early in life have shorter life spans (Rose 1991). They cannot both reproduce a lot early in life and have a long life, a trade-off that shapes the evolution of life span.

Other important trade-offs occur between the ability to eat one thing and the ability to eat many things, and between mating success and survival. There are many others. Whenever one analyzes the costs and benefits of changes in traits, trade-offs are usually found. They limit how much fitness can be improved by changing traits, for when traits cannot be changed independently of one another, the benefits gained by changes in one trait are often rapidly balanced by costs incurred in others, causing the response to selection to stop.

Constraints

Organisms are not soft clay out of which adaptive evolution can sculpt arbitrary forms. Natural selection can only modify the variation currently present in the population, variation that is often strongly constrained by history, development, physiology, and the laws of physics and chemistry. Natural selection cannot anticipate future problems, nor can it redesign existing mechanisms and structures from the ground up. Evolution proceeds by tinkering with what is currently available, not by designing ideal solutions, and the variation currently available is often limited by constraints.

The constraints imposed by physics and chemistry are straightforward. The diameter of an organism without a circulatory or respiratory system cannot be much greater than 1 mm, a limit set by the rate at which oxygen diffuses through water. Water-breathers would have great difficulty being endotherms, for they have to pass large volumes of water across large gill surfaces to extract oxygen, and moving water rapidly strips heat from warm bodies. The limbs of terrestrial animals must be thicker in heavier organisms, for the strength of a limb is determined by its crosssectional area, whereas weight is determined by volume, which grows more rapidly (x^3) with the length of an organism (x) than does the crosssectional area (x^2) of one of its limbs. That is why the legs of rhinoceroses are thicker, in proportion to their body lengths, than the legs of antelopes. Physics cannot be avoided.

Just as interesting are constraints that have evolved. Past adaptations can become future constraints, placing the imprint of

history on a lineage. Here are four examples.

First, why are there no **parthenogenetic** (asexual) mammals? Early development in mammals requires one egg-derived and one sperm-derived haploid nucleus. The two types of nuclei are marked differently in the germ line of the parents by the attachment of methyl groups to the DNA molecules, a pattern known as **genetic imprinting**. Early development requires the expression of some genes derived from the father and some genes derived from the mother, which is determined by the sex-specific imprinting that occurs in the germ line of the parent. The parental patterns are erased later in development, allowing the offspring to imprint the genes that are appropriate to their own sex and making it possible to clone mammals from adult cells. If all the genes came from the mother, then some normally paternal genes would not be turned on at the right time, and early development would fail.

Second, why are there no parthenogenetic frogs? In a freshly inseminated frog egg, the sperm donates the **centrosome** that replicates to form the poles of the first mitotic **spindle**. Activated eggs that lack the paternal contribution-the sperm-derived centrosome-divide abortively (Elinson 1989).

In both mammals and frogs, the constraints on parthenogenesis appear to result from a conflict between nuclear genes and mitochondrial genes, won by the nuclear genes. A genetic conflict exists whenever two types of genes have different patterns of transmission. **Mitochondria** are usually transmitted only through eggs, whereas nuclear genes are transmitted through both eggs and sperm. Because cytoplasmic genes have zero fitness in males, cytoplasmic mutants that induce parthenogenesis would be selected. The barriers to parthenogenesis in mammals and frogs may have evolved because sexual reproduction is advantageous to nuclear genes; they appear to protect the interests of nuclear genes against the invasion of cytoplasmic elements that could feminize their hosts.

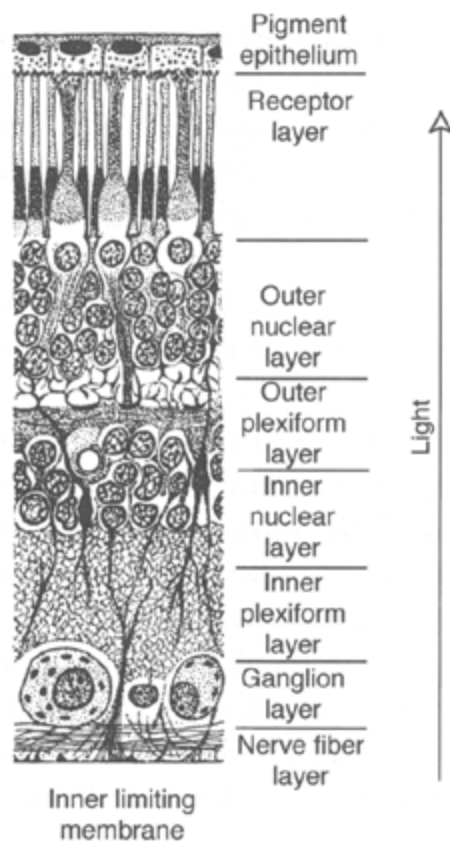


Fig. 1.7 The pigment epithelium of the vertebrate eye containing the light-sensitive cells develops inside the nerves and blood vessels through which light must pass, a design no engineer would approve. (From Romer 1962.)

Third, the vertebrate eye, admired for its precision and complexity, contains a basic flaw. The nerves and blood vessels of vertebrate eyes lie between the photosensitive cells and the light source (Goldsmith 1990), a design that no engineer would recommend, for it obscures the passage of photons into the photosensitive cells (Fig. 1.7). Long ago, vertebrate ancestors had simple, cup-shaped eyes that were probably originally used only to detect light, not to resolve fine images. Those simple eyes developed as an out-pocketing of the brain, and the position of their tissue layers determined where the nerves and blood vessels lay in relation to the photosensitive cells. If the layers had not maintained their correct positions, relative to one another, then the mechanisms that control differentiation, in which an inducing substance produced in one layer diffuses into the

neighboring layer, would not work. Once such a developmental mechanism evolved, it could not be changed without destroying sight in the intermediate forms that would have to be passed through on the way to a more rationally designed' eye.

The fourth example concerns the length and location of the tubes connecting the testicles to the penis in mammals. In the adult, cold-blooded ancestors of mammals, and in present-day mammalian embryos, the testicles are located in the body cavity, near the kidneys, like ovaries in adult females. Because mammalian sperm develop better at temperatures lower than those found in the body core, there was selection, during the evolutionary transition from cold- to warm-bloodedness, to move the testicles out of the high-temperature body core into the lower-temperature periphery and eventually into the scrotum. This evolutionary progression in adults is replayed in the developmental progression of the testes from the embryo to adult, and as they move from the body cavity towards the scrotum, they wrap the vas deferens around the ureters, like a person watering the lawn who gets the hose caught on a tree (Fig. 1.8). If it were not for the constraints of history and development, a much shorter vas deferens would have evolved, costing less to produce and perhaps doing a better job.

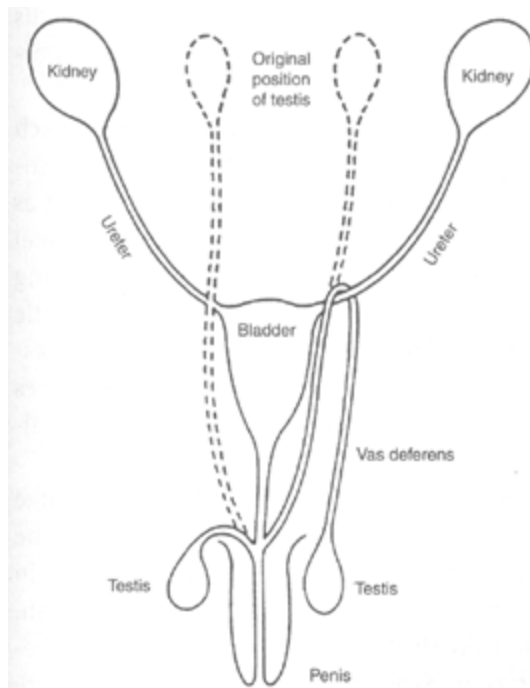


Fig. 1.8 The mammalian vas deferens is wrapped around the ureter like a hose wrapped around a tree by someone watering a garden. If the development of the testis were not constrained, the vas deferens could be much shorter (like the one on the left). (From Williams 1992.)

Speciation

The elementary processes in microevolution are genetic changes—first mutations, then changes in gene frequencies driven by selection, migration, and drift. Phenotypes with better reproductive success get more copies of the genes they carry into future generations, leading to inherited changes in the design of phenotypes. Adaptation occurs but perfection does not result because of constraints and the finite number of variants sorted by selection. Microevolution is, however, not the whole story, for the world is populated by organisms that form clusters of similar individuals, called **species**. Speciation, the splitting of populations into evolutionarily independent units, connects the microevolutionary processes occurring within populations to the macroevolutionary relationships and patterns of all living things. The species is the critical transition level between micro- and macroevolution.

Speciation does not result from just one mechanism. It is a by-product of several processes—isolation from neighboring populations caused by geography, local habitat selection, and mate selection—with diverse genetic consequences. Populations do not speciate to become better adapted. Individuals choose mates either because they are locally available and are geographically isolated from other mates, or because choosing those mates (or mates found in those habitats and not others) results in fitter offspring. Speciation is a by-product of selection and drift operating on individuals.

Species can be defined as sets of organisms that could mate with each other and produce viable grandchildren; or as sets of organisms resembling each other morphologically, or in their DNA sequences, that act as evolutionarily independent units. The first definition, the Biological Species Concept of Dobzhansky (1937) and Mayr (1942), was long thought to have decisive advantages, but some biologists now prefer the second definition, the Phylogenetic Species Concept, which also assumes that

common ancestry causes the similarity. This approach leaves open the mechanisms leading to speciation, allowing one to consider alternatives without prejudice (Mallet 1995).

No definition of species covers all known organisms. Species range from the relatively distinct and stable-as in birds and mammals-to the relatively indistinct and unstable, as in the hybrid complexes common in micro-organisms, plants, and some crustaceans, amphibians, and fish. Some bacteria exchange genetic information frequently enough to behave almost like sexual species (e.g. *Streptococcus*); others behave like asexual clones with nearly complete reproductive isolation (e.g. *Salmonella*).

Microevolution and macroevolution

Microevolution describes processes occurring within species and populations. We can do experiments on microevolution, and we can study its causes directly. Macroevolution describes patterns perceived in the comparison of species and larger groups-families, orders, and phyla-that are described in systematics and paleontology.

How microevolution connects to macroevolution is an important question that has not yet been answered satisfactorily. A promising approach suggests that the microevolution of developmental mechanisms produces constraints on the further evolution of the organisms containing those mechanisms. Different lineages evolve different developmental mechanisms. All the species sharing developmental mechanisms may therefore also share similar body plans and evolve under similar constraints. This is probably why we can recognize major groups of organisms by their body plans, what Darwin called Unity of Type.

Biological causation

Biologists want to understand everything about organisms. Some study the immediate causes, seeking the answers to questions such as 'How does photosynthesis work?', 'What determines the sex of an organism?', and 'What causes disease?', in physiology, genetics, biochemistry, development, and related fields. Here the aim is to identify what causes the trait or process within the lifetime of a single organism. This is the study of **proximate** (mechanical) **causation**. It constitutes much of biology.

Evolutionary biologists ask different questions and investigate different kinds of cause, in search of answers to questions such as: 'Why does photosynthesis occur in the plastids and not in the cell nucleus?', 'Why do most species have approximately equal numbers of males and females, and why are there dramatic exceptions?', 'Why do many animals senesce, but many plants and fungi hardly at all?', 'Why do some small organisms have large relatives?'. These are also questions about causation, but on a time scale of many generations and at the level of populations and species rather than individuals. This is the study of **ultimate** (evolutionary) **causation**. Whereas in mechanical analysis the causes can be described as biochemical and physical processes, in evolutionary analysis one describes the causes as how natural selection, chance events, or constraints shaped the trait under study.

All traits have both mechanical and evolutionary causes; a complete explanation requires understanding of both kinds of cause. Isolating the two kinds of analysis from each other is a strategic error because it reduces the number of interesting questions that can be asked. A biologist should be able to see the world both ways-from the bottom up (from molecules to species) and from the top down (from selection to molecules).