Testing Natural Selection

Biologists working with the most sophisticated genetic tools are demonstrating that natural selection plays a greater role in the evolution of genes than even most evolutionists had thought • • • BY H. ALLEN ORR

Some ideas are discovered late in the history of a scientific discipline because they are subtle, complex or otherwise difficult. Natural selection was not one of these. Although compared with other revolutionary scientific ideas it was discovered fairly recently—Charles Darwin and Alfred Russel Wallace wrote on the subject in 1858, and Darwin's *On the Origin of Species* appeared in 1859—the idea of natural selection is simplicity itself. Some kinds of organisms survive better in certain conditions than others do; such organisms leave more progeny and so become more common with time. The environment thus "selects" those organisms best adapted to present conditions. If environmental conditions change, organisms that happen to possess the most adaptive characteristics for those new conditions will come to predominate. Darwinism was revolutionary not because it made arcane claims about biology but because it suggested that nature's underlying logic might be surprisingly simple.

In spite of this simplicity, the theory of natural selection has suffered a long and tortuous history. Darwin's claim that species evolve was rapidly accepted by biologists, but his separate claim that natural selection drives most of the change was not. Indeed, natural selection was not accepted as a key evolutionary force until well into the 20th century.

The status of natural selection is now secure, reflecting decades of detailed empirical work. But the study of natural selection is by no means complete. Rather—partly because new experi-

mental techniques have been developed and partly because the genetic mechanisms underlying natural selection are now the subject of meticulous empirical analysis—the study of natural selection is a more active area of biology than it was even two decades ago. Much of the recent experimental work on natural selection has focused on three goals: determining how common it is, identifying the precise genetic changes that give rise to the adaptations produced by natural selection, and assessing just how big a role natural selection plays in a key problem of evolutionary biology—the origin of new species.

Natural Selection: The Idea

The best way to appreciate evolution by natural selection is to consider organisms whose life cycle is short enough that many generations can be observed. Some bacteria can reproduce themselves every half an hour, so imagine a population of bacteria made up of two genetic types that are initially present in equal numbers. Assume, moreover, that both types breed true: type 1 bacteria produce only type 1 offspring, and type 2 bacteria produce only type 2s. Now suppose the environment suddenly changes: an antibiotic is introduced to which type 1s are resistant but to which type 2s are not. In the new environment,

ART OF the taxidermist and expertise of the scientist-curator combine to suggest the variety of life-forms to which evolution has given rise in the animal kingdom alone. The exhibit was photographed in the Hall of Biodiversity at the American Museum of Natural History in New York City.
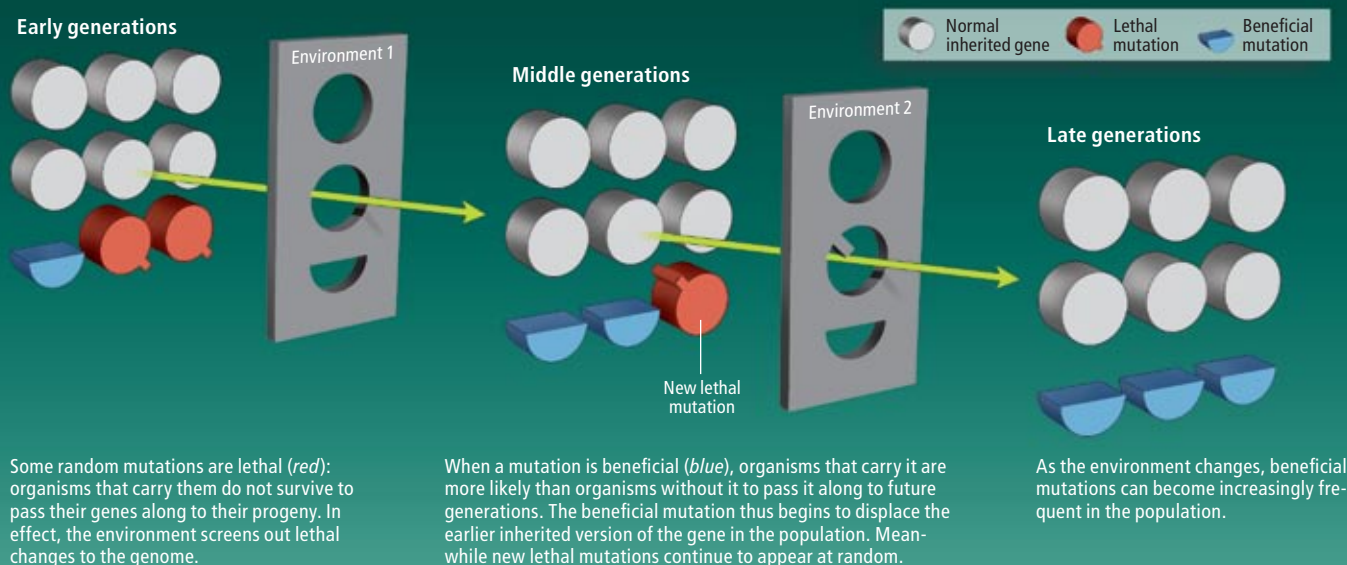
KEY CONCEPTS

- Charles Darwin's theory that evolution is driven by natural selection—by inherited changes that enhance survival—struggled against competing theories for the acceptance it has within biology today.

- Random genetic mutations having neither positive nor negative effects were once thought to drive most changes at the molecular level. But recent experiments show that natural selection of beneficial genetic mutations is quite common.

- Studies in plant genetics show that changes in a single gene sometimes have a large effect on adaptive differences between species.

—*The Editors*

○ ○ ○ Mutation and Natural Selection

Evolution by natural selection is a two-step process: first, random genetic mutations appear in a population; then the environment screens the organisms that carry them.

Early generations

Environment 1

Middle generations

Environment 2

Late generations

| Normal inherited gene | Lethal mutation | Beneficial mutation |

New lethal mutation

Some random mutations are lethal (*red*): organisms that carry them do not survive to pass their genes along to their progeny. In effect, the environment screens out lethal changes to the genome.

When a mutation is beneficial (*blue*), organisms that carry it are more likely than organisms without it to pass it along to future generations. The beneficial mutation thus begins to displace the earlier inherited version of the gene in the population. Meanwhile new lethal mutations continue to appear at random.

As the environment changes, beneficial mutations can become increasingly frequent in the population.

THE AUTHOR

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type 1s are fitter—that is, better adapted—than type 2s: they survive and so reproduce more often than type 2s do. The result is that type 1s produce more offspring than type 2s do.

"Fitness," as used in evolutionary biology, is a technical term for this idea: it is the probability of surviving or reproducing in a given environment. The outcome of this selection process, repeated numberless times in different contexts, is what we all see in nature: plants and animals (and bacteria) that fit their environments in intricate ways.

Evolutionary geneticists can flesh out the preceding argument in much richer biological detail. We know, for instance, that genetic types originate in mutations of DNA—random changes in the sequence of nucleotides (or string made up of the letters A, G, C and T) that constitutes the "language" of the genome. We also know a good deal about the rate at which a common kind of mutation—the change of one letter of DNA to another—appears: each nucleotide in each gamete in each generation has about one chance in a billion of mutating to another nucleotide. Most important, we know something about the effects of mutations on fitness. The overwhelming majority of random mutations are harmful—that is, they reduce fitness; only a tiny minority are beneficial, increasing fitness. Most mutations are bad for the same reason that most typos in com-
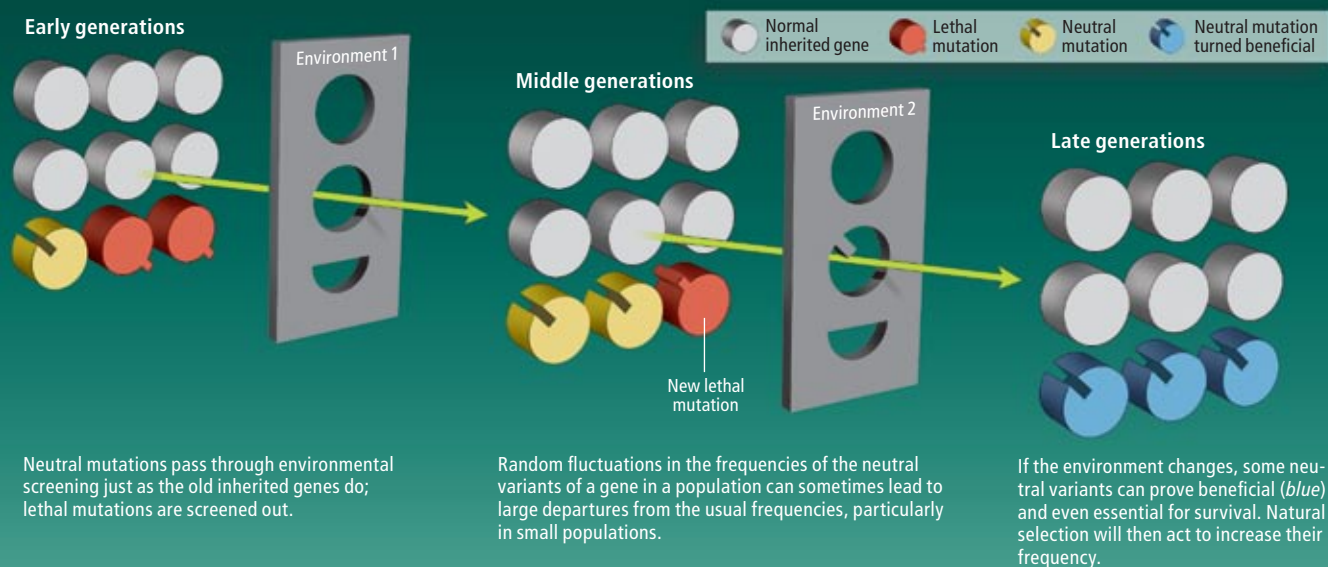
puter code are bad: in finely tuned systems, random tweaks are far more likely to disrupt function than to improve it.

Adaptive evolution is therefore a two-step process, with a strict division of labor between mutation and selection. In each generation, mutation brings new genetic variants into populations. Natural selection then screens them: the rigors of the environment reduce the frequency of "bad" (relatively unfit) variants and increase the frequency of "good" (relatively fit) ones. (It is worth noting that a population can store many genetic variants at once, and those variants can help it to meet changing conditions as they arise. The gene that protected the type 1 bacteria from the antibiotic may have been useless or even slightly harmful in the earlier, antibiotic-free environment, but its presence enabled the type 1s to survive when conditions changed.)

Population geneticists have also provided insight into natural selection by describing it mathematically. For example, geneticists have shown that the fitter a given type is within a population, the more rapidly it will increase in frequency; indeed, one can calculate just how quickly the increase will occur. Population geneticists have also discovered the surprising fact that natural selection has unimaginably keen "eyes," which can detect astonishingly small differences in fitness among genetic types. In a population of a

○ ○ ○ "Neutral" Evolution and Genetic Drift

Until recently, biologists believed that many of the changes in DNA that persist in a population for multiple generations were neutral (*yellow*), having no effect on survival or reproduction. The mix of such changes within a population can fluctuate randomly from generation to generation, a process known as genetic drift. The presumed abundance of neutral mutations led some geneticists to think that genetic drift, not natural selection, was the chief force driving change of DNA in populations. New experimental findings show that natural selection is also an important factor in such change.

Early generations

Environment 1

Normal inherited gene | Lethal mutation | Neutral mutation | Neutral mutation turned beneficial

Middle generations

Environment 2

Late generations

New lethal mutation

Neutral mutations pass through environmental screening just as the old inherited genes do; lethal mutations are screened out.

Random fluctuations in the frequencies of the neutral variants of a gene in a population can sometimes lead to large departures from the usual frequencies, particularly in small populations.

If the environment changes, some neutral variants can prove beneficial (*blue*) and even essential for survival. Natural selection will then act to increase their frequency.

million individuals, natural selection can operate on fitness differences as small as one part in a million.

One remarkable feature of the argument for natural selection is that its logic seems valid for any level of biological entity—from gene to species. Biologists since Darwin, of course, have considered differences in fitness between individual organisms, but in principle natural selection could act on differences in survival or reproduction between other entities. For example, one might reason that species with broad geographic ranges will survive—as species—longer than species whose geographic ranges are narrow. After all, broad-ranging species can tolerate the extinctions of a few local populations more readily than species with restricted ranges can. The logic of natural selection might predict, then, that the proportion of broad-ranging species should increase with time.

Yet though this argument is formally sound—and evolutionists do suspect higher-level selection does take place now and then [see "What's Good for the Group," on page 51]—most biologists agree that natural selection typically occurs at the level of individual organisms or genetic types. One reason is that the lifetimes of organisms are much shorter than the lifetimes of species. Thus, the natural selection of organisms typically overwhelms the natural selection of species.

How Common Is Natural Selection?

One of the simplest questions biologists can ask about natural selection has, surprisingly, been one of the hardest to answer: To what degree is it responsible for changes in the overall genetic makeup of a population? No one seriously doubts that natural selection drives the evolution of most physical traits in living creatures—there is no other plausible way to explain such large-scale features as beaks, biceps and brains. But there has been serious doubt about the extent of the role of natural selection in guiding change at the molecular level. Just what proportion of all evolutionary change in DNA is driven, over millions of years, by natural selection—as opposed to some other process?

Until the 1960s biologists had assumed that the answer was "almost all," but a group of population geneticists led by Japanese investigator Motoo Kimura sharply challenged that view. Kimura argued that molecular evolution is not usually driven by "positive" natural selection—in which the environment increases the frequency of a beneficial type that is initially rare. Rather, he said, nearly all the genetic mutations that persist or reach high frequencies in populations are selectively neutral—they have no appreciable effect on fitness one way or the other. (Of course, harmful mutations continue to appear at a high

TOMMY MOORMAN (*illustrations*)

rate, but they can never reach high frequencies in a population and thus are evolutionary dead ends.) Since neutral mutations are essentially invisible in the present environment, such changes can slip silently through a population, substantially altering its genetic composition over time. The process is called random genetic drift; it is the heart of the neutral theory of molecular evolution.

By the 1980s many evolutionary geneticists had accepted the neutral theory. But the data bearing on it were mostly indirect; more direct, critical tests were lacking. Two developments have helped fix that problem. First, population geneticists have devised simple statistical tests for distinguishing neutral changes in the genome from adaptive ones. Second, new technology has enabled entire genomes from many species to be sequenced, providing voluminous data on which these statistical tests can be applied. The new data suggest that the neutral theory underestimated the importance of natural selection.

In one study a team led by David J. Begun and Charles H. Langley, both at the University of California, Davis, compared the DNA sequences of two species of fruit fly in the genus *Drosophila*. They analyzed roughly 6,000 genes in each species, noting which genes had diverged since the two species had split off from a common ancestor. By applying a statistical test, they estimated that they could rule out neutral evolution in at least 19 percent of the 6,000 genes; in other words, natural selection drove the evolutionary divergence of a fifth of all genes studied. (Because the statistical test they employed was conservative, the actual proportion could be much larger.) The result does not suggest that neutral evolution is unimportant—after all, some of the remaining 81 percent of genes may have diverged by genetic drift. But it does prove that natural selection plays a bigger role in the divergence of species than most neutral theorists would have guessed. Similar studies have led most evolutionary geneticists to conclude that natural selection is a common driver of evolutionary change even in the sequences of nucleotides in DNA.

The Genetics of Natural Selection

Even when biologists turn to ordinary physical traits ("beaks, biceps and brains") and are confident that natural selection drove evolutionary change, they are often in the dark about just how it happened. Until recently, for instance, little was known about the genetic changes that un-

EVOLUTION IN ACTION

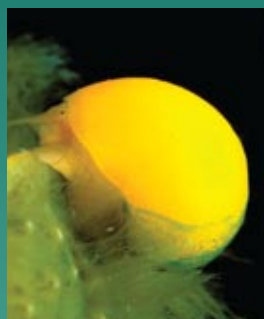In some animals, adaptive changes have unfolded fast enough to be observed:

Wild rabbit (Australia)
Animals brought from Europe changed in body size, weight and ear size as they adapted to the hot, dry Australian climate.

Scarlet honeycreeper (Hawaii)
As its favorite source of nectar began disappearing, the bird sought nectar elsewhere, and its bill became shorter.

Marine snail (New England)
Likely in response to being hunted by crabs, the snail's shell changed shape and became thicker.

derlie adaptive evolution. But with the new developments in genetics, biologists have been able to attack this problem head-on, and they are now attempting to answer several fundamental questions about selection. When organisms adapt by natural selection to a new environment, do they do so because of changes in a few genes or many? Can those genes be identified? And are the same genes involved in independent cases of adaptation to the same environment?

Answering those questions is not easy. The main difficulty is that the increase in fitness arising from a beneficial mutation can be very small, making evolutionary change quite slow. One way evolutionary biologists have coped with this problem is to place populations of rapidly reproducing organisms in artificial environments where fitness differences are larger and evolution is, therefore, faster. It also helps if the populations of the organisms are large enough to provide a steady stream of mutations. In microbial experimental evolution, a population of genetically identical microorganisms is typically placed in a novel environment to which they must adapt. Since all the individuals begin by sharing the same DNA sequence, natural selection must operate only on new mutations that arise during the experiment. The experimenter can then plot how the fitness of the population changes with time by measuring the rate of reproduction in the new environment.

Some of the most intriguing research in experimental evolution has been performed with bacteriophages, viruses so small that they infect bacteria. Bacteriophages have commensurately tiny genomes, and so it is practical for biologists to sequence their entire genomes at the beginning and end of experiments as well as at any time in between. That makes it possible to track every genetic change that natural selection "grabs" and then perpetuates over time.

K. Kichler Holder and James J. Bull, both at the University of Texas at Austin, performed such an experiment with two closely related species of bacteriophages: ΦX174 and G4. Both viruses infect the common gut bacterium *Escherichia coli*. The experimenters subjected the bacteriophages to an unusually high temperature and allowed them to adapt to the new, warm environment. In both species, fitness in the new environment increased dramatically during the experiment. Moreover, in both cases the experimenters saw the same pattern: fitness improved rapidly near the start of the experiment and then leveled off with time. Remarkably, Holder and

Bull were able to identify the exact DNA mutations underlying the increased fitness.

Natural Selection "in the Wild"

Although research in experimental evolution provides an unprecedented view of natural selection in action, the approach remains limited to simple organisms for which repeated sequencing of entire genomes is feasible. Some workers have also cautioned that experimental evolution might involve unnaturally harsh selective pressures—perhaps much harsher than the ones encountered in the wild. We would like, then, to study selection in higher organisms under more natural conditions—and so we must find another way to investigate the glacial pace of much evolutionary change.

To do so, evolutionists typically turn to populations or species that have been separated long enough that the adaptive differences between them that were crafted by natural selection are readily found. Biologists can then study those differences genetically. For example, Douglas W. Schemske of Michigan State University and H. D. Bradshaw, Jr., of the University of Washington analyzed natural selection in two species of monkeyflower. Though closely related, *Mimulus lewisii* is pollinated primarily by bumblebees, whereas *M. cardinalis* is pollinated primarily by hummingbirds. Data from other species show that bird pollination in the genus *Mimulus* evolved from bee pollination.

Flower color alone—*M. lewisii* has pink flowers, and *M. cardinalis* has red [*see box at right*]—explains much of these differences in pollinator preference. When Schemske and Bradshaw crossed the two species, they showed that this color difference is controlled to a considerable extent by what appears to be a single gene called *Yellow Upper,* or *YUP.* On the basis of that finding, they created two kinds of hybrids. In the first kind, the *YUP* gene came from *M. cardinalis,* but the rest of the hybrid's genome derived from *M. lewisii.* The resulting flowers were orange. The second kind of hybrid was a "mirror image" of the first: the *YUP* gene came from *M. lewisii,* but the rest of the genome derived from *M. cardinalis.* The resulting flowers were pink.
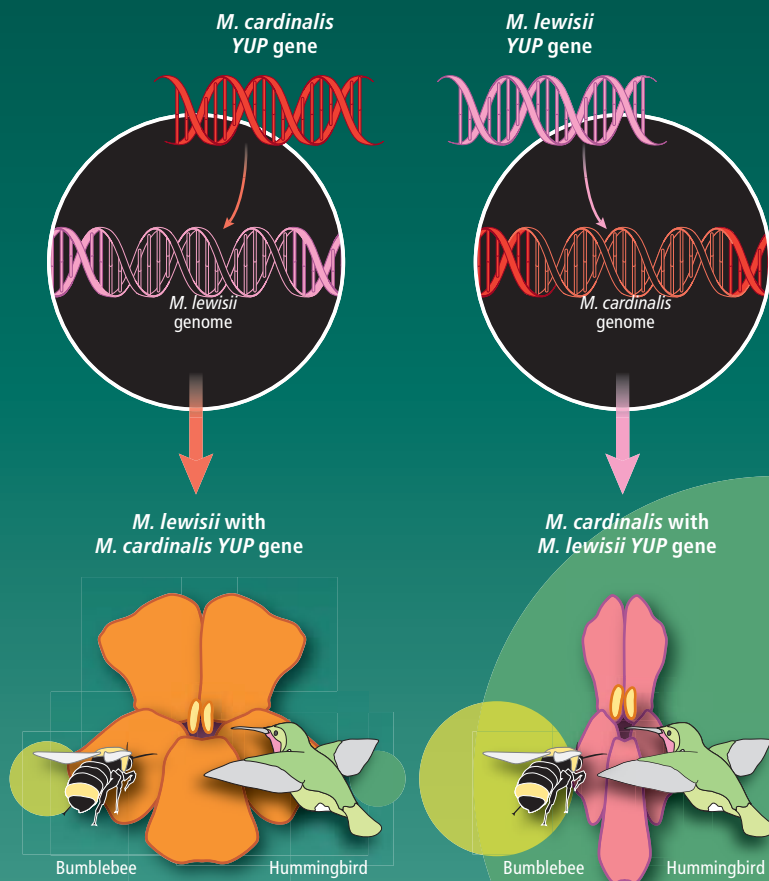
When the hybrids were transplanted into the wild, the investigators noted that *YUP* had an enormous effect on pollinator visitation: *M. lewisii* plants, for instance, that carried *YUP* from *M. cardinalis* were visited by hummingbirds about 68 times more often than were pure

○○○ Speciation and the Single Gene

Two species of monkeyflower that rarely interbreed in the wild owe much of their reproductive isolation to a difference in pollinators: bumblebees almost always pollinate *Mimulus lewisii;* birds almost never do (*below left*). Those patterns are reversed for *M. cardinalis* (*below right*). Flower color largely explains the differences, and a good deal of the color difference is almost certainly controlled by one gene: *Yellow Upper,* or *YUP.* The areas of the yellow and green circles in the diagrams reflect the frequencies of the pollinators' visits.

M. lewisii

Bumblebee   Hummingbird

M. cardinalis

Bumblebee   Hummingbird
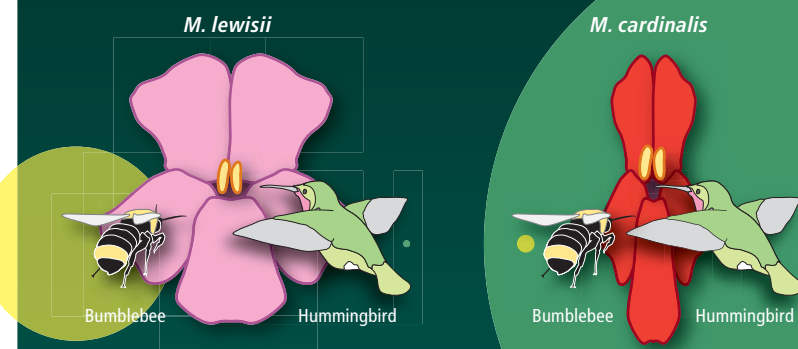
Research on monkeyflowers shows that mutations in what appears to be just one gene can contribute to the divergence of new species. Investigators created two kinds of hybrids by moving a small chromosome region known to contain the *YUP* gene, as shown below, and found that hummingbirds visited *M. lewisii* hybrids 68 times more often than they did pure *M. lewisii* plants. Similarly, bumblebees visited *M. cardinalis* hybrids 74 times more often than they did pure *M. cardinalis* plants.

M. cardinalis YUP gene

M. lewisii genome

M. lewisii YUP gene

M. cardinalis genome

M. lewisii with M. cardinalis YUP gene

Bumblebee   Hummingbird

M. cardinalis with M. lewisii YUP gene

Bumblebee   Hummingbird

M. lewisii plants; in the reciprocal experiment (*M. cardinalis* plants with *YUP* from *M. lewisii*), the effect was a 74-fold increase in bumblebee visits. There can be no doubt, then, that *YUP* played a major role in the evolution of bird pollination in *M. cardinalis*. Schemske and Bradshaw's work shows that natural selection sometimes builds adaptations from what appear to be fairly simple genetic changes.

The Origin of Species

One of Darwin's boldest claims for natural selection was that it explains how new species arise. (After all, the title of his masterpiece is *On the Origin of Species*.) But does it? What role does natural selection play in speciation, the splitting of a single lineage into two? To this day, these questions represent an important topic of research in evolutionary biology.

To understand the answers to those questions, one must be clear about what evolutionists mean by "species." Unlike Darwin, modern biologists generally adhere to the so-called biological species concept. The key idea is that species are reproductively isolated from one another—that is, they have genetically based traits preventing them from exchanging genes. Different species, in other words, have separate gene pools.

It is thought that two populations must be geographically isolated before reproductive isolation can evolve. The finches that inhabit various islands in the Galápagos Archipelago, which Darwin famously describes in *Origin of Species,* obviously diverged into the distinct species observed today after they became geographically isolated.

Once reproductive isolation does evolve, it can take several forms. For example, during courtship females of one species might refuse to mate with males of another (if the two species ever do come into geographic contact). Females of the butterfly species *Pieris occidentalis,* for instance, will not mate with males of the related species *P. protodice,* probably because the males of the two species have different wing patterns. And even if two species do court and mate, the inviability or sterility of any resulting hybrids can represent another form of reproductive isolation: genes cannot move from one species to another if all hybrids between them are dead or sterile. To contemporary biologists, then, the question of whether natural selection drives the origin of species reduces to the question of whether natural selection drives the origin of reproductive isolation.

For much of the 20th century, many evolutionists thought the answer was no. Instead they believed that genetic drift was the critical factor in speciation. One of the most intriguing findings from recent research on the origin of species is that the genetic drift hypothesis about the origin of species is probably wrong. Rather natural selection plays a major role in speciation.

A good example is the evolutionary history of the two monkeyflower species mentioned earlier. Because their pollinators seldom visit the "wrong" species of monkeyflower, the two species are almost completely isolated reproductively. Even though both species sometimes occur in the same locations in North America, a bumblebee that visits *M. lewisii* almost never visits *M. cardinalis,* and a hummingbird that visits *M. cardinalis* almost never visits *M. lewisii*. Thus, pollen is rarely transferred between the two species. In fact, Schemske and his colleagues showed that pollinator differences alone account for 98 percent of the total blockage in gene flow between the two species. In this case, then, there can be no doubt that natural selection shaped the plants' adaptations to distinct pollinators and gave rise to strong reproductive isolation.

Other evidence for the role of natural selection in speciation has come from an unexpected quarter. In the past decade or so several evolutionary geneticists (including me) have identified half a dozen genes that cause hybrid sterility or inviability. The genes in question—studied mostly in species of *Drosophila* fruit flies—play various normal roles within the species: some encode enzymes, others encode structural proteins, and yet others encode proteins that bind to DNA.

These genes exhibit two striking patterns. First, among the genes that cause problems in hybrid offspring, it turns out that many have diverged extremely rapidly. Second, population genetics tests show that their rapid evolution was driven by natural selection.

The studies of the monkeyflower and of hybrid sterility in fruit flies only begin to scratch the surface of a large and growing literature that reveals the hand of natural selection in speciation. Indeed, most biologists now agree that natural selection is the key evolutionary force that drives not only evolutionary change within species but also the origin of new species. Although some laypeople continue to question the cogency or adequacy of natural selection, its status among evolutionary biologists in the past few decades has, perhaps ironically, only grown more secure. ■

MORE TO EXPLORE

Pollinator Preference and the Evolution of Floral Traits in Monkeyflowers (*Mimulus*). Douglas W. Schemske and H. D. Bradshaw, Jr., in *Proceedings of the National Academy of Sciences USA,* Vol. 96, No. 21, pages 11910–11915; October 12, 1999.

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What's Good for the Group

Does natural selection drive evolution at levels higher than selfish genes and fertile individuals? **BY STEVE MIRSKY**

Want to start a brawl at an evolution conference? Just bring up the concept of group selection: the idea that one mixed bag of individuals can be "selected" as a group over other heterogeneous groups from the same species. Biologists who would not hesitate to form a group themselves to combat creationism or intelligent design might suddenly start a pie fight to defend the principle that "it's every man for himself."

Yet Charles Darwin himself argued for group selection. He postulated that moral men might not do any better than immoral men but that tribes of moral men would certainly "have an immense advantage" over fractious bands of pirates. By the 1960s, however, selection at the group level was on the outs. Influential theorist George Williams acknowledged that although group selection might be possible, in real life "group-related adaptations do not, in fact, exist."

Richard Dawkins of the University of Cambridge, whose writings have reached millions, maintains that selection might not even reach such a high level of biological organization as the individual organism. Instead, he claims, selection operates on genes—the individual is the embodiment of the selection of thousands of selfish genes, each trying to perpetuate itself.

In the past few decades, however, group selection has made a quiet comeback among evolutionary theorists. E. O. Wilson of Harvard University and David Sloan Wilson (no relation) of Binghamton University are trying to give group selection full-fledged respectability. They are rebranding it as multilevel selection theory: selection constantly takes place on multiple levels simultaneously. And how do you figure the sum of those selections in any real-world circumstance? "We simply have to examine situations on a case-by-case basis," Sloan Wilson says.

But the Wilsons did offer some guidelines in the December 2007 issue of *Quarterly Review of Biology.* "Adaptation at any level," they write, "requires a process of natural selection at the same level, and tends to be undermined by natural selection at lower levels."

Experiments with actual groups illustrate the point. *Pseudomonas fluorescens* bacteria quickly suck all the dissolved oxygen out of a liquid

habitat, leaving a thin habitable layer near the surface. But some bacteria spontaneously develop a beneficial mutation. These group-saving individuals secrete a polymer that enables bunches of individuals to form floating mats. As a mat, all the bacteria survive, even though most of them expend no metabolic energy producing the polymer. But if the freeloaders get greedy and reproduce too many of their kind, the mat sinks and everybody dies, altruists and freeloaders alike. Among these bacteria, then, groups that maintain enough altruists to float outcompete groups with fewer altruists than that minimum number. The former groups survive, grow and split up into daughter groups. Thus, altruistic individuals can prosper, despite the disadvantage of expending precious resources to produce the polymer.

Perhaps the biggest change that group selection brings to evolutionary theory is its implication for so-called kin selection. What looks like group selection, some theorists argue, can actually be understood as genetic relatedness. Evolutionist J.B.S. Haldane pithily explained kin selection: "I would lay down my life for two brothers or eight cousins." In this view, altruistic bacteria in the *Pseudomonas* mats are saving close relatives, thereby ensuring the survival of most of the genes they themselves also carry.

Turning that argument on its head, the Wilsons assert that kin selection is a special case of group selection. "The importance of kinship," they note, "is that it increases genetic variation among groups." The individuals within any one group are much more like one another and much less like the individuals in any other group. And that diversity between groups presents clearer choices for group selection. Kinship thus accentuates the importance of selection at the group level as compared with individual selection within the group.

The Wilsons think evolutionists must embrace multilevel selection to do fruitful research in sociobiology—"the study of social behavior from a biological perspective." When doing so, other investigators can keep in mind the Wilsons' handy rule of thumb: "Selfishness beats altruism within groups. Altruistic groups beat selfish groups."

Steve Mirsky is a member of the board of editors at *Scientific American.*

INDIVIDUAL SELECTION

"Altruist" *Pseudomonas fluorescens* bacteria (*below left*) carry a gene for secreting a polymer that enables mats of bacteria to float and thus access oxygen easily; "freeloaders" (*below right*) lack the gene. Producing the polymer costs extra energy, so freeloaders reproduce faster than altruists. Natural selection acting on individuals alone would drive the altruists to extinction.

GROUP SELECTION

But group selection appears to operate, too—at least in the laboratory— favoring mats of *P. fluorescens* bacteria in which some altruists persist. Only mats that include enough polymer-secreting altruists will float and thus survive to reproduce themselves, altruists included (*below left*). Mats in which individual selection leads to too many freeloaders will sink, drowning the entire bacterial colony (*below right*). Such mats leave no progeny.

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