Natural Selection and Darwin's Finches

The finches of the Galápagos—the classic example of how natural selection works over millions of years—have now been observed to evolve in real time. A single drought can change a population

by Peter R. Grant

Every year vast numbers of eggs are produced by creatures as small as parasitic nematode worms and as large as salmon and cod. Orchids may disperse a thousand seeds. Other organisms, such as tortoises and coconuts, reproduce much more slowly than this. Yet one demographic feature is common to all: when a population remains at about the same size for a long time, each parent, on average, replaces itself with just one breeding offspring. That ecological simplicity belies a subtle evolutionary complexity. Although the population replaces itself, some parents leave more offspring than others, and this imbalance provides the condition for evolution to occur by natural selection.

Natural selection is differential success. A population of sexually reproducing organisms comprises many different individuals: some are larger, thicker, greener or hairier than others. When some organisms survive or reproduce better than others because they are larger or smaller, or because they are more or less hairy, natural selection occurs.

Charles Darwin devised the concept of natural selection while attempting to explain the evolution of organic diversity. His theory has been elaborated, extended and corrected; it has been founded in physical evidence of which he was unaware, such as DNA and the genes it encodes. The evolutionary mechanism is key to any general understanding of how the world came to be the way it is. Yet it is remarkable that 132 years after the publication of his masterpiece, *On the Origin of Species by Means of Natural Selection*, natural selection is still not widely understood.

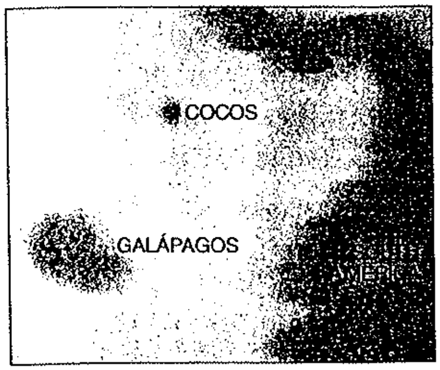
There are three reasons for this incomprehension. Natural selection has been discussed in misleading terms, such as "fitness," which are charged with unfortunate meanings. Also, popularizers have confused natural selection with related concepts, such as inheritance. Finally, Darwin himself mistakenly assumed that natural selection necessarily proceeds at a snail's pace and that it therefore cannot be observed but merely deduced. He said as much in a famous passage in *Origin of Species:*

> It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapses of ages, and then so imperfect is our view into long past geological ages, that we only see that the forms of life are now different from what they formerly were.

Darwin argued that new species are formed when persistent selection over many generations changes a population so much that its members will no longer breed with individuals from a related population. But if natural selection indeed occurs solely on a historical scale, the study of evolution would be seriously impeded. The subject would not be amenable to scientific observation and experimentation.

Fortunately, this is not the case. John A. Endler of the University of California at Santa Barbara has recently compiled a list of more than 100 studies that have demonstrated natural selection in action. Some of the most easily interpreted cases have been witnessed in environments altered by human activities. Certain grasses, for example, have become tolerant to the high concentrations of lead in mine tailings. The most common and dangerous cases occur

PETER R. GRANT is the Class of 1877 Professor of Zoology at Princeton University, where he is chairman of the department of ecology and evolutionary biology. He first visited the Galápagos Islands in 1973 and has returned almost every year since then to pursue long-term and detailed field studies of Darwin's Finches on two islands. He is author of *Ecology and Evolution of Darwin's Finches* and co-author with his wife, B. Rosemary Grant, of *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos.* Grant is a fellow of the Royal Society and was a Guggenheim Fellow in 1985-86. He received his Ph.D. from the University of British Columbia in 1964 and taught at McGill University and the University of Michigan before joining the faculty of Princeton in 1985.



ADAPTIVE RADIATION, in which a population differentiates after dispersing from one habitat to the next, is believed to have produced the 14 species of Darwin's Finches in the past one to five million years. Thirteen of the species live in the Galápagos Archipelago (*above*).

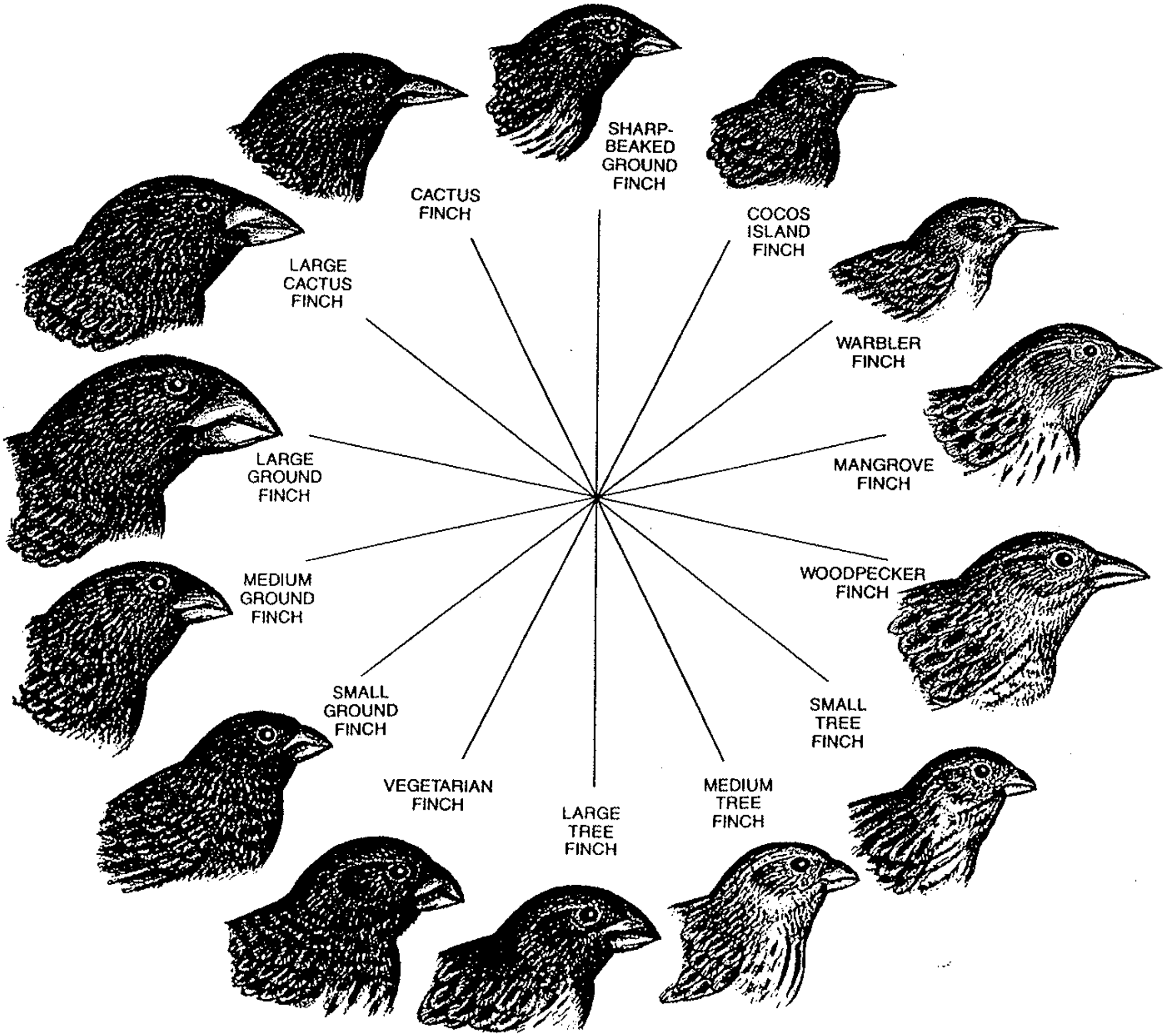
when an antibiotic fails to kill all the bacteria infesting a patient because a few of them are naturally resistant to it. In evolutionary terms, the treatment has selected for resistance to the drug. If the surviving microorganisms can pass their resistance on to their daughter cells, a new strain evolves.

Studies of natural selection in natural environments have broader implications, for they help us understand more directly the evolution of organic diversity over the long history of the earth, the problem Darwin tried to solve. The finches named after him provide an unusually clear illustration.

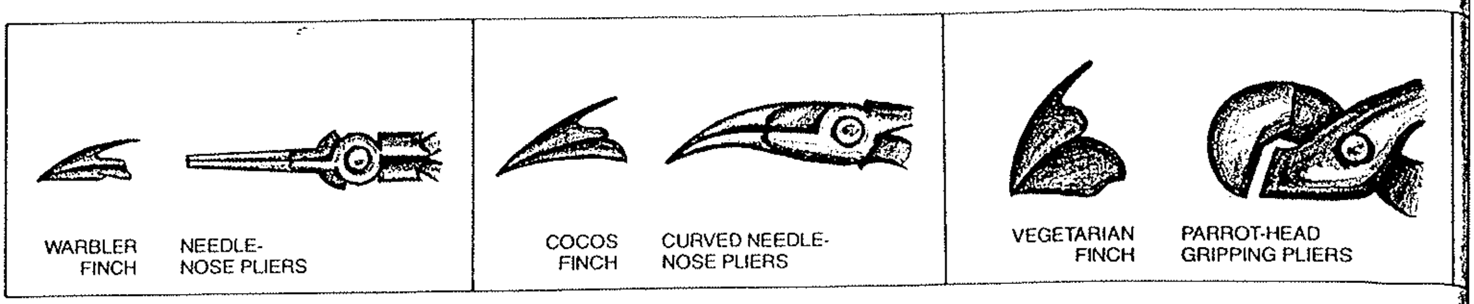
Thirteen species of Darwin's Finches live on the Galápagos Islands, having evolved from a common ancestor, it is believed, in the past one to five million years. The birds are darkly colored and of similar bodily proportions, but they vary in length from about three to six inches (seven to 12 centimeters)—the range between a warbler and a rather fat sparrow—and in the shape of their bills, which reflects their different diets. The common names label their niches and affinities: tree finches, ground finches, cactus finches, a warbler finch, a vegetarian finch, a woodpecker finch and a mangrove finch.

The finches provide a prime example of adaptive radiation, as described in these pages nearly 40 years ago [see "Darwin's Finches," by David Lack; SCIENTIFIC AMERICAN, April 1953]. Lack noted that the only other group of birds that display a similar pattern, the sicklebills (honeycreeper finches) of Hawaii, also live in an archipelago, and he suggested that many or even most species differentiated in some kind of physical isolation. "What is unique about the Galápagos and Hawaii," he wrote, "is that the birds' evolution there occurred so recently that we can still see the evidence of the differentiations." The evidence is in fact more than recent, it is ongoing: I have seen the finches evolve in response to climatic changes during the past dozen years. These changes can be dramatic. In some years the islands are drenched by rains precipitated by El Niño events; in other years they are parched by drought.

In 1973 I began studying the finches living on Daphne Major, an islet that covers only about 100 acres. This area was small enough to limit the two resident populations—the medium ground finch, *Geospiza fortis*, and the cactus finch, *G. scandens*—to a number that could be studied exhaustively. I have



Beaks as Tools



been aided in this endeavor by my wife, Rosemary, and, each year, by two graduate students or other assistants.

We captured the birds in mist nets, so called because their fine filaments are scarcely visible against a dark background. We measured the birds and banded their legs with a numbered metal band and three plastic bands, which allowed us to identify each bird from a distance. Each triplet of colors was coded to correspond to the number on the metal band. By 1977 we had banded more than half of the island's birds, a proportion that passed 90 percent in 1980 and has remained near 100 percent ever since. Thus, from an early stage we were in a position to detect natural selection, if it occurred.

In 1977 it did. In that year Daphne Major had a drought: less than an inch (25 millimeters) of rain fell in the normal wet season. Deciduous plants produced few leaves, and caterpillars were scarce. Some pairs of cactus finches bred, but within three months all their offspring had vanished. Medium ground finches did not even breed. There was a long, dry and unproductive period from the middle of 1976 to early January 1978, when the rains resumed.

During the 18 months, many birds disappeared. Medium ground finches were the hardest hit—only 15 percent remained. Moreover, the winnowing process selected for large size in both species. Although birds of all sizes were reduced in number, the smaller ones were reduced the most. In addition, a conspicuous feature of the survivors was their large beak size.

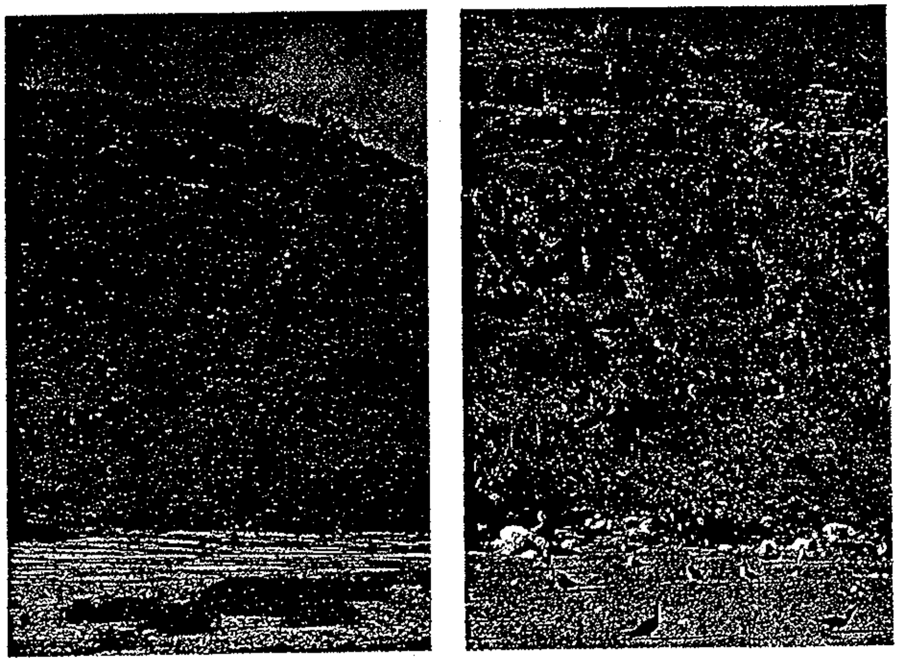
The missing birds had either died or emigrated. Although the emigration of a few individuals cannot be ruled out, there are two reasons to believe that death was the major cause of the disappearance. First, none of the birds that disappeared in 1976 and 1977 reappeared in 1978. Second, a sample of 38 birds found dead on the island had measurements much closer to the failures than to the successes.

The pattern was repeated in 1982, when there was little rain, scarcely any breeding and heavy mortality, particularly among the small birds. The recurrence of size-selective mortality under similar conditions suggests a common environmental cause. The major environmental consequence of drought (besides the lack of water) is the decline in the food supply. For the ground finch, this means seeds.

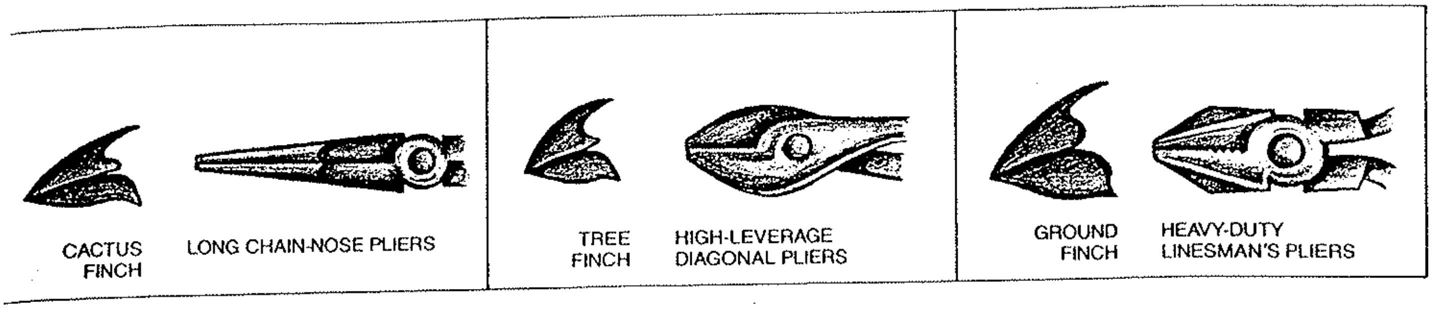
During normal wet seasons, many grasses and herbs produce an abundance of small seeds, and a few other plant species produce a much smaller number of large seeds. As the finches deplete the supply of small seeds, they turn increasingly to the large seeds. That is when larger birds have the advantage: their bigger, deeper beaks equip them better to crack open the large seeds and get to the kernels. This advantage would tell in the drought years, when the birds' dependence on the crop of large seeds was more pronounced and prolonged than in other years.

The hypothesis for size-selective mortality could be tested in a controlled experiment by altering the composition and abundance of the food supply for one group of birds but not for another. Such experiments are not feasible in the Galápagos National Park but can be done with other bird species elsewhere. This untested hypothesis is plausible, but it is not the only explanation. Large birds may have survived well because their body size allowed them to dominate other finches in social interactions at restricted sources of food or moisture.

Since body size correlates with beak depth, it is not immediately apparent whether one or the other, or both, played a role in survival. A statistical analysis is needed to isolate the association that each factor, considered separately, has with survival. We used partial regression and found that body



FAT AND LEAN YEARS are evident in these photographs of a craterlet on Daphne Major, a small island in the Galápagos, taken in April 1987 (*left*) and in March 1989 (*right*). The changing weather alters the mix of foods, affecting different populations in different ways. The blue-footed boobies (*right*), for example, live in the craterlet only during times of drought.



size and beak depth each correlated positively—and about equally—with survival. Beak length, on the other hand, did not. Thus, a combination of morphological, behavioral and possibly physiological factors helped to determine which birds survived and which ones succumbed to environmental stress.

Interestingly, Darwin may have witnessed a similar instance of natural selection without noticing it. He estimated that as many as four fifths of the birds in southern England perished during the severe winter of 1854-55. Selection may have been at work, for mortality was similar to what we observed among the medium ground finches in 1977.

I have thus far referred to survival rather than fitness in order to avoid a misunderstanding created more than a century ago by Herbert Spencer. Spencer erroneously equated natural selection with "the survival of the fittest," a catch phrase he coined to popularize Darwin's work. The problem is one of circular reasoning: when the fittest are manifested as such only by surviving, the phrase reduces to the survival of the survivors. Nevertheless, survival of the fittest—or better, the higher frequency of survival among the fittest—does convey part of the essence of natural selection, provided two points are understood. First, some individuals are more fit than others by virtue of their particular traits; second, fitness is ultimately judged by the number of offspring an individual contributes to the next generation.

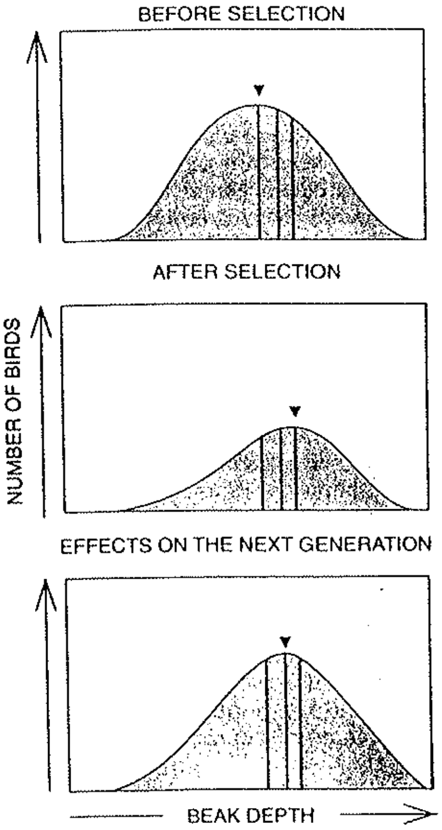
It is equally essential to avoid confusing selection with genetic variation, that is, with the genes that control variation in the traits on which selection operates. As the British geneticist J.B.S. Haldane emphasized, selection has no effects on the next generation unless it influences traits that are to some degree under genetic control and thus heritable. If the traits are heritable, however, then selection causes a small evolutionary change in the population. Therefore, an important question to ask is whether beak depth and body size in the medium ground finch population are heritable.

The heritability of a trait is a measure of the degree to which the trait varies in a population as a result of the additive effect of genes. Thus, large birds may be large in part because of the particular set of genes they inherit from their parents and in part because of the favorable conditions they experience in early life while growing to their final adult size. Similarly, small birds may be small for a combination of genetic and environmental reasons. The degree to which genes influence body size or beak size can be measured by the average similarity between offspring and their parents. This is accomplished by regressing the average of the offspring measurements on the average of the mother's and father's measurements for as many families as possible, a standard procedure in quantitative genetics. The heritability of the trait is estimated by the slope of the function, which can vary between zero and one.

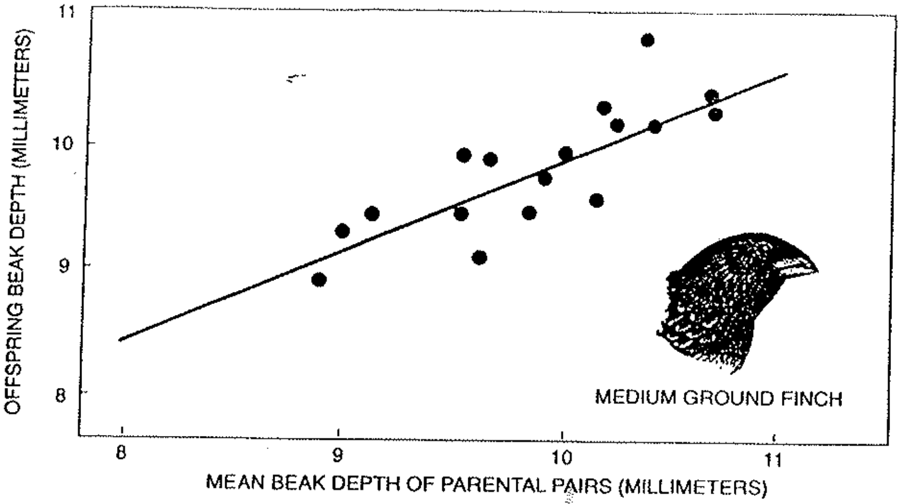
This technique enabled us to estimate the heritability of beak depth in the medium ground finch population at 0.74 [*see top illustration on next page*]. In other words, 74 percent of the variation in beak depth can be attributed to the additive effects of all the relevant genes. The remaining 26 percent is largely attributable to environmental causes. Body size has a somewhat higher heritability, 91 percent. Other morphological traits, including beak length and wing length, have similarly high heritabilities.

Such estimates are subject to the effects of hidden biases, above all the possibility that organisms resemble their parents in part because they grow up in similar environments. Birds might, for example, grow to relatively large adult size in the better territories. If, when seeking their own territories, they outcompete smaller birds for the better territories, they would be able to rear offspring that also reach large adult size. The same self-perpetuating process might work on small birds, leading to an inflated estimate of the genetic contribution to the resemblance between relatives.

One can identify such a bias by randomly exchanging eggs or nestlings among nests in the same population and determining whether final adult size varies between birds raised by true and by foster parents. We have not done this but have preserved the population in an entirely natural state. Where it has been done, with other species of birds, no evidence has been found that the rearing environment distorts the



MICROEVOLUTION occurs in three stages: a population with a given distribution of a trait, such as beak depth (*top*), undergoes selection for that trait (*middle*) and then bequeaths some fraction of the selection's effect to the next generation (*bottom*). The difference between the second and third stages depends on the heritability of the trait.



HERITABILITY OF BEAK DEPTH is estimated by finding the slope of the line that graphs the measurements of each pair of parents against those of their offspring.

estimation of heritability. Our check was different: we compared birds in food-rich and food-poor territories and looked for a tendency for offspring to breed in the kind of territory in which they were raised. We found no such tendency.

Other small errors may also be present, but there is little doubt that body size and beak depth are highly heritable in this population. Therefore, effects of selection on these two traits are passed on genetically to the next generation, causing evolutionary change in the population.

The change is quantified by selection and heritability factors, the product of which should account for the difference between the mean measurement of a trait before selection occurs and the mean in the next generation. The difference, which is normally expressed in standard deviations, is called the evolutionary response to selection.

If selection occurs but the trait has a heritability of zero, then the offspring should not differ from the parental generation before it underwent selection. In Haldane's words, selection will have been ineffective. On the other hand, if all variation in the trait is genetic and the heritability is one, then there is no discounting: the offspring will have a mean identical to that of their parents. These are the extremes; most cases fall in between.

Evolutionary response to selection becomes more complicated when more than one trait is influenced by selection at the same time, for then the genetic variation of each trait interacts with that of the others. Such genetic covariance affects the response. We can minimize these complications by replacing the several traits with an index, which functions as a single synthetic trait. The index accounts for most of the variation among individuals in all dimensions—body size, beak depth and so forth.

Peter T. Boag, now at Queen's University in Kingston, Ontario, adopted this approach while working as my graduate assistant in the late 1970s. He used the first component from what is called a principal components analysis of morphological variation. This synthetic trait, which has the high heritability of 0.75, is best interpreted as a body-size index. It accounts for 64 percent of the variation in the size of the beak, wing, leg and other body parts of the medium ground finches.

Selection on this synthetic trait produced an evolutionary response of 0.36 standard deviation (SD). This accorded well with the predicted value of 0.40 SD, obtained from the measured selection differential and heritability. Thus, a microevolutionary change took place in this population as a result of natural selection. It amounted to an increase in the average beak depth and body size of about 4 percent.

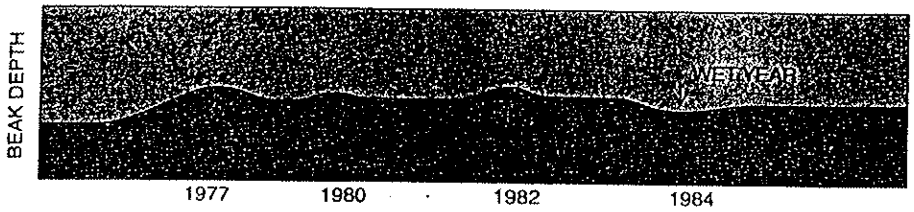
Studies of natural selection as an observable process help us to understand retrospectively processes of evolution that took millennia to unfold. This is particularly true of the pattern of change involved in speciation. In the case of Darwin's Finches, for example, we can extrapolate the observed microevolutionary change to infer the magnitude, causes and circumstances of changes in the formation of one species from another.

Trevor D. Price, now at the University of California at San Diego, and I attempted to do this by taking into account the genetic variation governing morphological traits and the magnitude of the directional selection that occurred in 1977. The two quantities allowed us to estimate the number of such selection events required to transform the medium ground finch, *G. fortis*, into its close relative, the large ground finch, *G. magnirostris*, which is about 50 percent larger.

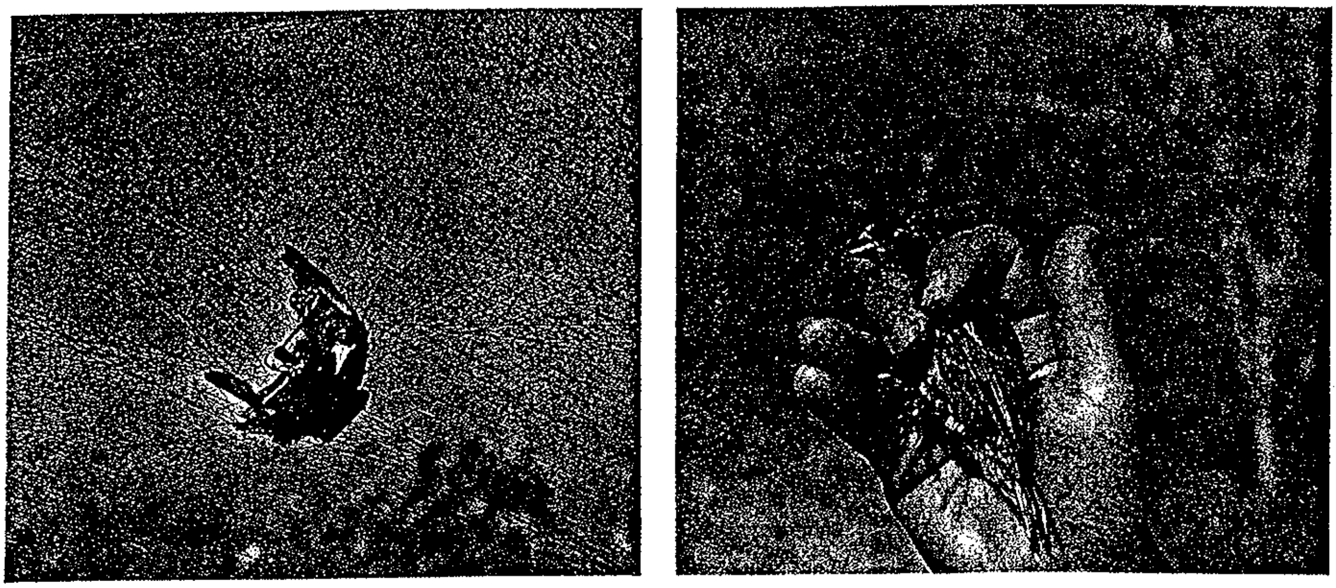
The number is surprisingly small: about 20 selection events would have sufficed. If droughts occur once a decade, on average, repeated directional selection at this rate with no selection in between droughts would transform one species into another within 200 years. Even if the estimate is off by a factor of 10, the 2,000 years required for speciation is still very little time in relation to the hundreds of thousands of years the finches have been in the archipelago.

Far more time is needed to form a species differing from its progenitor in shape rather than size, for then selection must work in opposite directions on different traits, in the face of positive correlations between them. The transformation of the medium ground finch into the cactus finch, for example, would require a relative increase in beak length but a relative decrease in beak depth and in body mass—a process we estimate would take six times longer than the transformation into the large ground finch.

An alternative to this scheme of speciation occurring on a single island is one involving the colonization of several islands in the archipelago. One species becomes transformed into another through the cumulative effects of se-



OSCILLATING TRAIT, in this case beak depth, reflects the fluctuating selective effects of the weather. Droughts (*arrows*) favor birds having the deeper beaks, which are more effective in cracking large seeds, a critical food when rainfall is scant.



BIRD IN THE BUSH is snagged in a mist net (*left*) and then banded by hand (*right*) as part of the author's long-term project to follow the life histories of all the finches living on two small islands of the Galápagos.

lection, predominantly or solely in one direction, on not one but a series of islands. That suggestion is plausible because, as our field studies have shown, each island has a distinctive constellation of types of food for the finches, so in dispersing from one island to another they encounter a different food supply.

In each case, selection will drive the traits of newly established populations fairly rapidly toward the optimal attainable form. Stabilizing selection will then hold the population near that optimum until the environment changes, causing an alteration in diets, perhaps as a result of a rise or decline in the number of competing organisms.

Most species observed in nature appear to have attained stable forms and behaviors. One might conclude, then, that Darwin's Finches on Daphne Major constitute an exception, in that the population is currently heading in the direction of becoming a larger species. This hunch may be right, but I doubt it: other factors are also at play.

Effects of the droughts of 1977 and 1982 were approximately offset by selection in the opposite direction—toward smaller body size—in 1984-85 [*see bottom illustration on opposite page*]. A relative scarcity of large seeds, together with an ample supply of small ones, favored small finches. Because the food supply on this island changes in composition and size from year to year, the optimal beak form for a finch is shifting in position, and the population, subjected to natural selection, is oscillating back and forth with every shift. Whether or not there is a net directional trend toward larger size, like an arrow through the oscillations, is unclear and could be determined only by a much longer study. Such a trend may come to pass, if human-induced global warming increases the incidence of drought in the Pacific.

We have observed fluctuations of a somewhat different kind in the population of the large cactus finch, *G. conirostris*, on Genovesa, 55 miles to the northeast of Daphne Major. In this case, the foods provided by cactus bushes changed as a result of extremely wet conditions produced by El Niño in 1983. In the next year long-billed birds were at a disadvantage because the food they are best equipped to exploit, cactus flowers and fruits, declined drastically. In 1985, a drought year, the birds had little to eat except the arthropods living under the bark of trees and in the tough pads of cactus bushes. Under these changed circumstances, the finches with strong, deep beaks were best equipped to extract the arthropods. As a result of this advantage, they had the highest rate of survival.

Oscillating direction selection may furnish a general model for what happens elsewhere—and not just to populations of birds. Annual variation in environmental conditions is pronounced, as we know from the summers in the U.S. during the past decade. We also know that many populations of animals, from insects to mammals, fluctuate greatly in numbers under the influence of a varying climate. Most of these populations live in the temperate zone, but even the inhabitants of tropical rain forests are not as stable in numbers as was once assumed.

When a population fluctuates, gene frequencies are likely to change as a result of random processes, especially when the population declines to low numbers. The unanswered question is whether, in addition to this process, demographic fluctuations in a wide variety of organisms are accompanied by microevolutionary changes in phenotypic traits as a result of natural selection. My guess is that they often are, but proof will require detailed studies of individually recognizable members of a population. If oscillating selection is indeed widespread and not just a peculiarity experienced by Darwin's Finches and a few other organisms, then the model will constitute a powerful tool to help us achieve Darwin's goal: the explanation of the causes of organic diversity.

FURTHER READING

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