Adaptive radiation of Darwin's finches: Recent data help explain how this famous group of Galapagos birds evolved, although gaps in our understanding remain.

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A powerful metaphor for evolutionary diversification is a tree. A typical spreading tree has a single trunk, two or more major branches, several minor branches and many twigs. Its foundations--its roots and the remnants of the original seed--remain hidden from sight. The metaphor applies to the full set of living things on Earth--"the tree of life"--as well as to small groups of species, whether they are marsupial mammals or Hawaiian Drosophila. We can think of the typical crown of a tree as resembling the shape of an umbrella, with twig-bearing branches radiating in all directions (Figure 2, top). The ends of the twigs represent organisms adapted to separate microenvironments; the tree overall represents an adaptive radiation.

Darwin's finches are a prime example of an adaptive radiation. Fourteen or perhaps 15 species, all derived from a common ancestor, occupy individual ecological niches to which they are adapted, principally because of the size and shape of their beaks in relation to the food they eat. Yet on close inspection, we now know that their evolutionary relationships depart radically from the orthodox view of an adaptive radiation with one trunk, a few branches and many terminal twigs. The most striking difference from the idealized model is that near the base of the tree, where the main trunk--representing the ancestral species--splits, only one of the resulting trunks leads to several branches and many twigs (Figure 2, bottom). The other trunk gives rise to little more than thin twigs, although they have persisted in growing to the crown. The next division is also asymmetrical. The third division is more orthodox, producing two branches that radiate approximately equally, one yielding the ground finches and the other yielding tree finches. Nevertheless, the tree as a whole is lopsided.

Even if a model fails to fit the data perfectly, it is useful to describe evolutionary branching with a metaphor in mind, because the confrontation between data and metaphor encourages the posing of sharp questions. Being forced to fit data to an idealized concept may lead to new insights and revised idealizations. For example, as we discuss in more detail later, thinking about the loss of lower branches in evolutionary trees forces us to consider past extinctions and the contribution of those losses to the current form of a tree.

The concept of adaptive radiation raises four main questions in our minds:

Origins: Where did the ancestors come from, when and how?

Speciation: How and why are new species formed?

Diversity: Why are there x number of species?

Disparity: Why are these species as different, or as similar, as they are?

Now is an opportune time to address these questions: Estimating the structure of the evolutionary tree has become possible in the past few years as a result of studies on DNA sequence variation among the birds (Figure 3). The results ultimately compel us to reconsider the metaphor of a tree.

The Beginning of Radiation

Darwin's finches arose in South America. The ancestors arrived on the Galapagos islands by flying over water for at least 1,000 kilometers. There has been little debate about these two points. The only credible alternative is that the finches arose on Cocos Island, which lies 600 kilometers to the northeast of the Galapagos, where a solitary species of Darwin's finch still resides. Three years ago, molecular genetic data eliminated that possibility; the data demonstrated a phylogenetic origin of the Cocos finch after an initial evolutionary split among Darwin's finches on the Galapagos (Petren et al. 1999, Sato et al. 1999). It is now clear that ancestral finches first: colonized the Galapagos, then the populations began to diverge, and only after that did the Cocos finch species arise. A warbler finch (Certhidea fusca, see Figure 2) may have colonized Cocos Island and evolved into the Cocos finch there. Alternatively, the warbler finch may have given rise to the Cocos finch (Pinaroloxias) on the Galapagos, with the species colonizing Cocos island later, eventually becoming extinct on the Galapagos. We favor the second of these possibilities because the black plumage and song of the Cocos finch so closely resemble the next branch in the finches' evolutionary tree.

The original ancestors of Darwin's finches have been identified as a group of South American birds known as seed-eaters. A recent survey of mitochondrial DNA sequence variation among 30 candidate species and their relatives has pinpointed the most likely closest living

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relatives of Darwin's finches--members of what are known as the grassquit genus Tiaris (Sato et al. 2001). As for when the ancestors arrived on the Galapagos, the difference in mitochondrial DNA between Darwin's finches and the Tiaris species suggests an approximate answer. The answer depends on the standard assumption that nucleotide changes accumulate in mitochondrial DNA at a rate of 2 percent per million years. This assumption may not be exactly true; studies of birds on Hawaii have detected a slightly slower rate of divergence of 1.6 percent per million years (Fleischer and McIntosh 2001). But even at this slower rate, the origin of Darwin's finches would be no earlier than three million years ago.

Youth and rapid diversification distinguish Darwin's finches compared with other avian radiations on other islands. Robert Fleischer and Carl McIntosh (2001) have estimated that the famously diverse Hawaiian honeycreepers started diverging 6.4 million years ago. In the same archipelago five or more thrushes evolved in 4.2 million years. three goose-like ducks called Moa-Nalos evolved in 4.3 million years, and four species of crows evolved in 5.2 million years. In all these cases the rate of species accumulation--that is, speciation minus extinction--was slower than among Darwin's finches as judged by the average time to double the existing number of species. Darwin's finches have a doubling time of three-quarters of a million years. Even the spectacular radiation of Hawaiian honeycreepers, which resulted in more than 50 species before the actions of humans decimated the group, had a species doubling time that exceeded 1.0 million years. We know of no group of birds that has diversified faster than Darwin's fi nches.

Formation of New Species

The central problem of adaptive radiation--indeed, of the origin of biological diversity in general--is the question of how and why one species gives rise to two. For the radiation of Darwin's finches, we gave one answer in this magazine 21 years ago (Grant 1981). That answer was the allopatric model of speciation, a model first sketched by Leopold von Buch in 1825, independently developed by Darwin and Alfred Russel Wallace, elaborated by Theodosius Dobzhansky and Ernst Mayr, and adopted by almost all biologists up to and beyond the first monograph on the evolution of Darwin's finches by David Lack in 1947.

In the allopatric model of speciation, geographical separation (that is, allopatry) promotes evolutionary divergence. In the first step of this model as applied to Darwin's finches, an ancestral species colonizes an island (Figure 4), say San Crist6bal, the island closest to the continent. The newly established population evolves by natural selection, becoming better adapted to the prevailing conditions, as well as by genetic drift. In the second step, a few dispersers colonize a second island and adapt to the new conditions. The geographically separated populations diverge, and the process of island-hopping divergence may be repeated several times before two populations encounter each other again in sympatry, the third step.

The meeting of the two populations can result in three possible outcomes: interbreeding of members of the two populations without a loss in fitness, despite the genetic differences acquired during their separation; interbreeding with fitness loss, because of the reduced viability of the offspring or because of partial sterility; or finally, no interbreeding. In the first case, there has been no speciation, whereas in the third case, two species have formed from one. The second case is the most interesting because it represents a stage in the process of speciation on the way to the reproductive isolation of one species from the other.

The second case is unstable and can lead, in its turn, to three alternative outcomes: increasing mixing of the two populations despite reduced fitness of the hybrids until they have fused into one; divergence driven by natural selection, sexual selection or both, when the most different individuals of the two populations are favored over the most similar ones, since the former are less likely to mate with members of the other population and suffer a loss of fitness and because they are less likely to compete for the same resources; or the competitive elimination of one population by the other, most likely, elimination of the new population by the incumbent, unless the island is large and diverse enough to allow their coexistence in separate habitats. All these may take a long time. The complexity of the outcomes is fascinating to biologists who study the process of speciation, but it presents a formidable challenge to those who seek a definition of species that has sharp boundaries, especially if the criteria for distinguishing the species are to be solely genetic.

Thus, as David Lack first pointed out in 1947, speciation of Darwin's finches involves the evolution of significant ecological and reproductive differences. Explaining the full radiation in terms of the allopatric model is accomplished by invoking a repetition of the same speciation process several times, but with the species produced differing according to the particular ecological circumstances that

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guided each pathway.

The allopatric model is an abstraction designed to capture the essence of speciation from a mass of particulars. Much data support the model in the case of Darwin's finches. These data include quantitative ecological data on the differences in food supply among islands, differences among species in feeding behavior and diets in relation to beak sizes and shapes, as well as indirect evidence of competition for food among species. Twenty-one years after we wrote about the allopatric model in this magazine, how does the model fare when confronted with new details of the radiation of Darwin's finches?

Ecology, Time and Change

Because of the proximity of the Galapagos islands, the finches can easily travel among the islands. If two populations of one kind of finch diverge to a large degree, they should eventually be able to coexist, and we therefore expect to find them together on the same island. In two respects we now know that the allopatric model we proposed in 1981 (Figure 4) is wrong. Neither error is fatal to the abstraction, although each requires that the model be modified. The first error is to suppose that the initial speciation process gave rise to two species that came to live on the same island after a period of geographical separation. That is, speciation does not require step 3 shown in the illustration. As indicated in our discussion of the trunk and branches of the Darwin's finch tree, after the two groups of warbler finches were formed from one, they apparently remained on different islands. Similarly, the sharp-beaked ground finch populations have remained geographically separated even though they have diverged morphologically to a large degree (Grant et al. 2000). In contrast, the more recently evolved ground finches and tree finches have established sympatric populations in various combinations. These observations are surprising in that given enough time, populations are expected to diverge sufficiently to permit coexistence, and coexistence will be achieved as a result of dispersal among islands. Evidently there are constraints on both divergence and dispersal, constraints that are probably ecological in origin, and we suspect that they increase with the passage of time.

The second mistake was to assume that all the islands existed at the outset. This is not a serious mistake because the islands we arbitrarily chose for illustrating the model--San Cristobal, Espariola, Floreana and Santa Cruz--are all fairly old and were probably involved in the first speciation cycle. Exposure of the mistake nevertheless has far-reaching consequences for interpreting the radiation.

Geological reconstructions of the archipelago over the three-million-year time period during which the finch radiation unfolded has established that an increasing number of islands formed volcanically in the region of a western hotspot and in the region of a northern spreading center. As the number of islands increased, so did the number of finch species (Figure 5); we estimate the number of finch species by ignoring the unknown extinctions and simply back-calculating from the estimated ages of contemporary species.

This new view of an adaptive radiation taking place in a changing environment is profoundly different from the previous conception. It requires understanding how a changing environment--differing numbers of islands, climate and vegetation--acts as a force driving the radiation. The Galapagos were probably not a diverse environment full of ecological opportunity for all 14 species of Darwin's finches when the ancestral species arrived. Rather, the archipelago was much simpler; over three million years it grew in complexity and changed in character.

The change in the character of the archipelago resulted, in part, from global cooling that started well before the onset of the recent ice age about 2.8 million years ago and has continued to the present. The amplitude of temperature oscillations--and probably of precipitation--has increased in the past million years. These two climatic features probably affected the Galapagos vegetation, although there is no direct evidence for this. The ancestral finches arrived on the Galapagos at a time close to the onset of the Ice Age, possibly aided by new wind patterns set up by changes in ocean circulation resulting from the closure, reopening and closure of the Panamanian isthmus. The original Galapagos finches encountered an environment that was possibly like Cocos today--more equably warm and wet and less seasonal than the present climate. Food resources also differed. The ancestral species changed in response, acquiring a long and narrow beak better suited to exploiting nectar and insects and spiders, which we pr esume were common on Galapagos at that time. Subsequently, speciation cycles were influenced by the changing number of islands, increasing seasonal aridity and the resulting changes in the composition and distribution of vegetation, arthropods and food sources generally.

Observed Selection and Adaptation

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In our 30 years of field work in the Galapagos, we have observed small-scale environmental changes that mirror large-scale environmental changes over the past three million years, leading to adaptive changes in beak size and shape. Our studies have concentrated on the small island of Daphne Major, where the residents are seed-eating ground ground finches. In 1977 a drought prevented the regrowth of most of the seed-producing plants. The population of medium ground finches (Geospiza fortis) declined in number in inverse proportion to their size: Small-beaked birds disappeared from the population at a faster rate than large-beaked birds. The reason for the size selectivity was that after they had depleted the supply of small seeds, the finches increasingly depended on the remaining medium and large seeds. Birds with large beaks could crack them open easily, whereas those with small beaks could crack them only with time-consuming difficulty if at all. This was a clear example of natural selection that led to evo lution in the next generation because the variation in beak size that we measure largely reflects an underlying variation in genetic factors. Offspring of the survivors had larger beaks, on average, than did the population before natural selection.

A repeat performance of selection and evolution took place nearly 10 years later when the island suffered a drought again, but the outcome was different. This time plants with larger seeds suffered, and small seeds overwhelmingly dominated the food supply, creating a selective advantage for small birds with small beaks. Another resident on the island, the cactus finch (G. scandens) suffered less size-selective mortality both times because it depends less on seeds in its diet.

Observing selection and evolution when environmental conditions fluctuate in the short term affects our views of evolution in the long term. In the short term of a few decades, the oscillations cancel out leaving the population with a beak size that's, more or less, in dynamic equilibrium. Over the long term of many decades, centuries or even millennia as food resources change, a vector of directional change runs through the oscillations toward a larger or smaller overall beak size, or more pointed or blunt beak shape.

Reproductive Isolation

As David Lack stated long ago, divergence of reproductive traits leads to the severing of a breeding connection between populations and, hence, to speciation. If populations remain separated geographically, like the warbler finches, we have no means of knowing whether they could interbreed, and with what consequences, under natural circumstances. We are left to construct the probable outcomes of natural encounters with artificial methods, such as, hypothetically, breeding them in captivity. On the other hand, there is no ambiguity about the reproductive connectedness of populations on the same island; therefore, we concentrate on them.

Our long-term field studies of banded birds on Daphne Major (Grant 1999) and Genovesa (Grant and Grant 1989) reveal that sympatric species (those on the same island) belonging to the same genus do hybridize, albeit rarely. Reduced fitness in hybrids is thought to result from genetic incompatibilities acquired while the populations are separated. Surprisingly, this expectation is not always realized on Daphne Major. Sometimes hybrid individuals with beak sizes intermediate between those of the parental species suffer a disadvantage because the particular seeds they are best suited to eat are rare. At other times the hybrids appear to be at no disadvantage compared with the parents that produced them. The fitness of the hybrids is a function of the environment; there is no evidence of a genetic barrier to hybridization. But perhaps that is because not enough time has passed for such barriers to evolve. Our long-term study of medium ground finches and cactus finches has documented the passage of alleles between the two species.

These observations are valuable in showing where it is not profitable to look for barriers to gene exchange: after mating has taken place. Instead the usual barriers arise before mating. Since different finch species have almost identical courtship behaviors, the barriers must lie not in how courting individuals act but in how they appear--whether visually or acoustically. Related species are often distinguished by their beak sizes and shapes rather than their plumage; they also sing different songs. Experiments with motionless stuffed specimens and other experiments with tape-recorded songs have demonstrated that both visual and acoustic cues elicit species-specific recognition from medium ground finches.

Both male and female hybrids respond to the song type of their fathers when they choose a mate. Only males sing, and they sing only one type of advertising song throughout their lives. If pairs form between species, say between a female ground finch and a male cactus finch, the offspring eventually mate with members of their father's species--in this case, other cactus finches. The sons will sing cactus finch songs, and the daughters will mate with males singing cactus finch songs.

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Morphology also plays a role in mate choice. On Daphne Major, an exceptional hybrid male that sang a cactus finch song but whose beak was closer in shape to that of a medium ground finch first mated with a cactus finch female and later with a medium ground finch female. Thus, visual and auditory cues appear to act in association.

Isolation by Song

Perhaps the critical question for how species form is this: How do cues that guide mating decisions diverge in incipient species and lead to reproductive isolation? If beak morphology alone were involved, the answer would be easy: Adaptation to local food resources in geographically separate regions raises reproductive barriers between populations even if they come together again. If this were the whole story, reproductive isolation would evolve as a passive consequence or byproduct of ecological divergence caused by natural selection. This idea has a long history (Dobzhansky 1937), but song is also involved, and song is a fundamentally different trait because it is learned. In finches it is not under tight genetic control--as it is in insects such as Drosophila, crickets and lacewing flies--although genetic factors may determine the limits of the sounds that the birds can learn and reproduce. Experiments with finches in captivity (Bowman 1983) and pedigree analyses (Grant and Grant 1989, 1996) have establish ed that Darwin's finches learn songs early in life from the father and probably in conjunction with morphological features. Early imprinting accounts for the mating pattern of hybrids according to paternal song type.

The critical question should be rephrased: How do songs and responses to them diverge in incipient species? There is not one answer to this question but five. First, the few individuals that establish a population on a new island carry an incomplete range of songs or renderings of them. Second, sons may produce random errors when copying fathers' songs, a cultural analogue to genetic mutation. Third and fourth, the frequency of newly arisen rare variants may increase either by chance or selectively; a selective advantage may arise if the songs transmit better in the new environment (Bowman 1983), and as a result more effectively repel intruding males or attract females. The fifth reason is close to the original Dobzhansky idea: The mean frequency, its range and the trill rate of songs may change as a passive consequence of changes in either body size and hence the syrinx (sound box) volume (Bowman 1983), or changes in beak size (Podos 2001). But even related populations with similar morphology and ecology, oc cupying acoustically similar environments--as with the sharp-beaked ground finches on Wolf and Darwin

islands--can differ profoundly in song (Grant et al. 2000). It is difficult to escape the conclusion that chance, in addition to selection, contributes to changes in song characteristics after a new island is colonized.

Experiments that play tape-recorded songs of related but geographically separated finch populations simulate what would happen if birds from the separated populations came together. They test the finches to see if they would respond to a song as if it were sung by a member of their own population, or not. Although the conditions are artificial, the experiments show that the birds discriminate the alien song from that of their own species only when the songs differ substantially. Ongoing experimental research with warbler finches has so far found little evidence of discrimination, leading us to question whether the two forms (C. olivacea and C. fusca) have reached the status of separate species. But perhaps inn natural circumstances, given enough time, birds may learn to make finer discriminations. Nevertheless, the logical implication is that in the past, there may have been many such natural experiments where the result was complete intermixing, because the morphological and song differences between the popu lations had not become sufficiently large to allow a new and independent population to become established on the island. Such may have been the case with the two groups of warbler finches.

Numbers and Differences of Species

Another easily constructed metaphor can explain patterns of diversity and disparity in terms of environmental resources, principally food. However, few relevant data are available to test it. The concept is an adaptive topography or landscape (Figure 7). Sewall Wright first developed the idea in terms of genotype frequencies; G. G. Simpson then extended it to phenotypes--or the physical manifestations of inherited traits (Schluter 2000). The idea is to represent variation in two morphological characteristics that affect resource use along two axes of a landscape. The third, vertical axis represents fitness. Fitness peaks occur in the landscape because of the distribution of food resources and because of favorable combinations of morphological characteristics that permit different populations to use the available resources effectively. Natural selection causes populations to ascend to fitness peaks in the adaptive landscape.

The adaptive landscape has been made operational by using seed resources to construct maximum density profiles in relation to beak sizes of the seed-eating species of Darwin's finches. Mean beak sizes of these species on

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16 islands were then predicted from peaks in the expected density profiles (Schluter and Grant 1984, Schluter et al. 1985), with two main results. First, no more than one species was associated with a peak. Second, with few exceptions the association between predicted and observed beak sizes was tight. One factor affecting the closeness of fit was the presence or absence of a similar competitor species. We are encouraged to think that with complete knowledge of the food resources on the Galapagos islands, we might find at least 14 peaks, and by their spacing better understand why the species are as different from one another as they are. We have not attempted to obtain anything dose to a complete quantitative knowledge of food resources on the islands because of the difficulty of combining, i n one analysis, the full range of resources exploited by Darwin's finch species. The birds consume seeds, fruits, nectar, pollen, blood from seabirds and from sea-lion placentae, caterpillars, spiders, insect larvae hidden beneath the bark of trees or in the tissues of leaves, and several other things (Grant 1999)!

Instead, we have developed a two-dimensional diagram (Figure 9) that attempts to show how the full range of Darwin's finch beak morphologies evolved, without regard to the unknown resource distributions that determine fitnesses. An initially slow exploration of one part of the total morphological space was followed by rapid exploration of the remainder with repeated reversals in direction. The contrast between early and late may be more apparent than real if large birds with blunt beaks evolved early but were then competitively replaced by more efficient, newly evolved species.

It is highly unlikely that fitness peaks existed on the Galapagos islands for each of the 14 current species when the single ancestral species arrived. Peaks increased in number when new plants and arthropods arrived. As resources increased, decreased or changed in proportions, peaks increased or decreased in height, shifted in position, were deformed by accretion of new resources to existing peaks, became established in new locations or disappeared altogether, taking their finch occupants with them or precipitating their extinction.

This dynamic view of Galapagos adaptive landscapes raises questions that cannot be answered with present data, among them: To what extent were adaptation, speciation and extinction impelled by environmental changes in the past? Have unrecorded extinctions deprived us of evidence showing how species became isolated on peaks? Once a species became adaptively specialized on an isolated peak--for example, warbler finches--how did a portion of its population break out of its specialization straightjacket and give rise to a new species? Are there peaks that remain unoccupied because they are too far from existing peaks or because there has been insufficient time to occupy them, with previous occupants perhaps becoming extinct recently? Are parts of the landscape composed of ridges rather than peaks (Schluter 2000), occupied by more than one species spaced apart along the ridge by competitive or other interactions?

The River of Life

Two decades ago, we applied the allopatric model of speciation to Darwin's finches, and tested and illustrated it with data from studies on ground finches-representing some of the twigs and minor branches of the finches' evolutionary tree. Now, with an estimate of the shape of the tree available from DNA studies, we have examined the causes of the adaptive radiations at the level of the trunk and major branches. For this, we have adopted a principle of evolutionary uniformitarianism, analogous to the principle of geological uniformitarianism of James Hutton and Charles Lyell. In essence the principle we started with is that the branches of today were the twigs of yesterday and that the processes of adaptation and speciation occurred uniformly throughout the tree. However, extending the patterns of recently formed twigs backward does not fully account for the patterns of the branches. Some twigs persist for a very long time as twigs without ever becoming branches. Part of the reason for this is that the enviro nment early in the history of old twigs differed from the environment that twigs have experienced recently. This fact and the likelihood of extinction mean that the parts of the tree that formed early on cannot be entirely known in terms of what we can discover about recent speciation in current environments. Understanding the base of the tree requires knowing the particulars of how the environment has changed through time.

Adopting metaphors like the evolutionary tree is a useful way to organize information and to suggest new insights, but it can have a strong potential to mislead when interpreted too literally. G. G. Simpson's famous metaphor of evolutionary diversification being a process of filling the "ecological barrel" nicely captures the importance of ecological opportunity in speciation, but misleads us into thinking the environment has a fixed and unchanging capacity for accommodating species. Meanwhile, the metaphor of an evolutionary tree, although obviously valuable, deflects us from seeing that species hybridize--branches anastamose--and that the ancestors

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of modern species may have become extinct without their derived species doing so-the "supporting" branches have fallen. A metaphor that avoids these two unrealistic features is a river that divides several times as it runs across a landscape. This is closer to the metaphor of an adaptive landscape than a tree is, and has the interesting implication that speciatio n--the evolution of isolated gene pools (another metaphor)--requires special, rare and perhaps capricious circumstances, like floods.

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