Perspective

The Routes Not Taken

If the *Beagle* had sailed a different course, what would Darwin have seen and how might that have shaped his thinking?

BY JONATHAN B. LOSOS

During Charles Darwin's journey on the *Beagle*, two aspects of what he saw were particularly influential. First was the phenomenon of geographic variation. The then-vice-governor of the Galápagos, Mr. Lawson (born Nicolai Olaus Lossius in Norway), told Darwin that he could tell what island a tortoise was from by looking at its shell. This surprised Darwin—why should tortoises vary from one island to another? Then he noticed the same thing when he started looking at mockingbirds, which also differed among the islands. These observations led Darwin to question the idea that species were immutable, produced in their present form by a creator. Maybe they could change, evolve.

The second key feature of the Galápagos concerned its common land birds. Darwin collected a number of these mostly seed- and fruit-eating species, and thought that the big-beaked bird was a grosbeak, the small one with a slender beak was a warbler, and the others were common finches. Consequently, he paid the birds little attention, considering them the local representatives of families that are found in Europe and elsewhere.

When the *Beagle* arrived back in England, Darwin turned his collections over to specialists. The birds went to John Gould, the most noted ornithologist of the time. After studying the specimens for several weeks, Gould reported back to Darwin that he was wrong: the birds were not members of different families that occurred in Europe. Rather, they were all members of a single family—a family of birds hitherto unknown to science that apparently only occurred in the Galápagos. He gave them the taxonomic name Geospizinae, and we now call them "Darwin's finches."

Darwin quickly realized the significance of this discovery. As he wrote in the second edition of his travelogue, *Voyage of the Beagle,* in 1845, "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

Hawaiian honeycreepers, exhibiting a wide array of specialized beaks, all evolved from a common finch ancestor.

The wording may have been coy, but the meaning was clear: species evolve, diverging into multiple descendants and adapting to different circumstances. It took him another twenty years to fully develop his ideas about the mechanism of this evolution, natural selection, but it's clear that his observations on the Galápagos and the evidence he uncovered there were instrumental in shaping his ideas.

But what if Darwin never visited the Galápagos? Suppose the British Admiralty's orders to the *Beagle's* captain, Robert FitzRoy, were not "to proceed with all convenient expedition, successively to Madeira or Teneriffe; the Cape de Verd Islands; Fernando Noronha," but rather to go somewhere else—say, the Caribbean Sea? What would Darwin have seen there, and how would it have affected his thinking?

In the Caribbean he would have seen lizards, and lots of them, particularly those in the genus *Anolis.* Darwin was a great naturalist, a keen observer. He

*Cuvier's anole (*Anolis Cuvieri*) is a crown giant that occupies the canopy of trees on Puerto Rico.*

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Although trunk crown anoles are known on Cuba (left), Jamaica (middle), Puerto Rico (right), and Hispaniola (bottom), they are distant relatives genetically. They have evolved independently to occupy the same ecological niche on each island.

would have noted these lizards, and studied their differences. Although Darwin saw some fantastic lizards in the Galápagos, their unattractive appearance forced his attention elsewhere. Referring to the marine iguana, the only sea-going modern-day lizard, now famous for eating seaweed underwater and blowing the excess salt out of special glands in its nostrils, he wrote in the *Voyage*, "It is a hideous-looking creature of a dirty black color, stupid and sluggish in its movements." And of its golden-yellow cousin, the five-foot-long, cactus-munching land iguana, Darwin noted, "They are ugly animals. From their low facial angle, they have a singularly stupid appearance."

He might have taken more favorably to the beautiful, sleek, and energetic anoles of the Caribbean. Certainly, he could not have failed to see them, given their extraordinary abundance. He would have discovered that many species occur on each of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). The species live in different habitats and have different anatomical features that are adaptations to the part of the habitat they occupy. Strikingly, if you go from one island to the next, you see the same set of habitat specialists on each island.

On Cuba, one species lives on tree trunks near the ground and has long legs for running quickly and jumping far to capture prey and confront territory intruders on the ground. A verdant green species occurs up in the canopy. Its large, sticky toepads help it move on slick leaves. Another green species lives high in the canopy, but is much larger; the giant of the anole world, its massive head enables it to gulp down other anoles and even baby birds. A fourth species patrols narrow twigs on the trees' periphery, with very short legs that are well-suited for moving on narrow and irregular surfaces. Yet another species lives amidst the grass, its slender body able to maneuver between grass blades, with a tail as much as four times the length of its body.

If Darwin visited the other Greater Antillean islands, he would have seen the same set of habitat specialists as on Cuba (except no grass-dweller in Jamaica). All three islands have trunk-ground, leaf-canopy, canopy giant, and twig specialists very similar to the Cuban species.

Darwin wouldn't have known it (nor, probably, the specialists back in England), but this suite of specialists evolved independently on each island. Modern-day examination of DNA indicates that, for example, the twig anoles on the different islands are not closely related to each other—they've evolved their twiggy adaptations independently, an example of convergent evolution. What is unusual about the anoles is that the entire community is convergent: the same set of habitat specialists has evolved on each island.

Caribbean anoles have an important parallel with Darwin's finches. Both are examples of what is called "adaptive radiation," the phenomenon in which an ancestral species gives rise to a variety of descendants, each adapted to occupy a different ecological niche, using a different part of the environment or eating different foods.

And just as Darwin was influenced by the adaptive radiation of Galápagos finches, he would have been impressed by Caribbean anoles; indeed, he wouldn't even have needed James Gould to realize that the "gradation and diversity of structure" in anole habitat specialists were all variations on the same theme, the result of divergence from a common ancestor. Moreover, just as with the Galápagos mockingbirds and tortoises, he would have noticed the

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differences among the twig anole species from one island to another (and among members of each of the other habitat specialist types). In sum, had Darwin been sent to the Caribbean instead of the southern continents, he would have observed very much the same phenomena and most likely been led to the same conclusions. Had Darwin been sent to the Caribbean, *The Voyage of the Beagle* account of what he saw may have been quite different, but *On the Origin of Species* would have been very much the same.

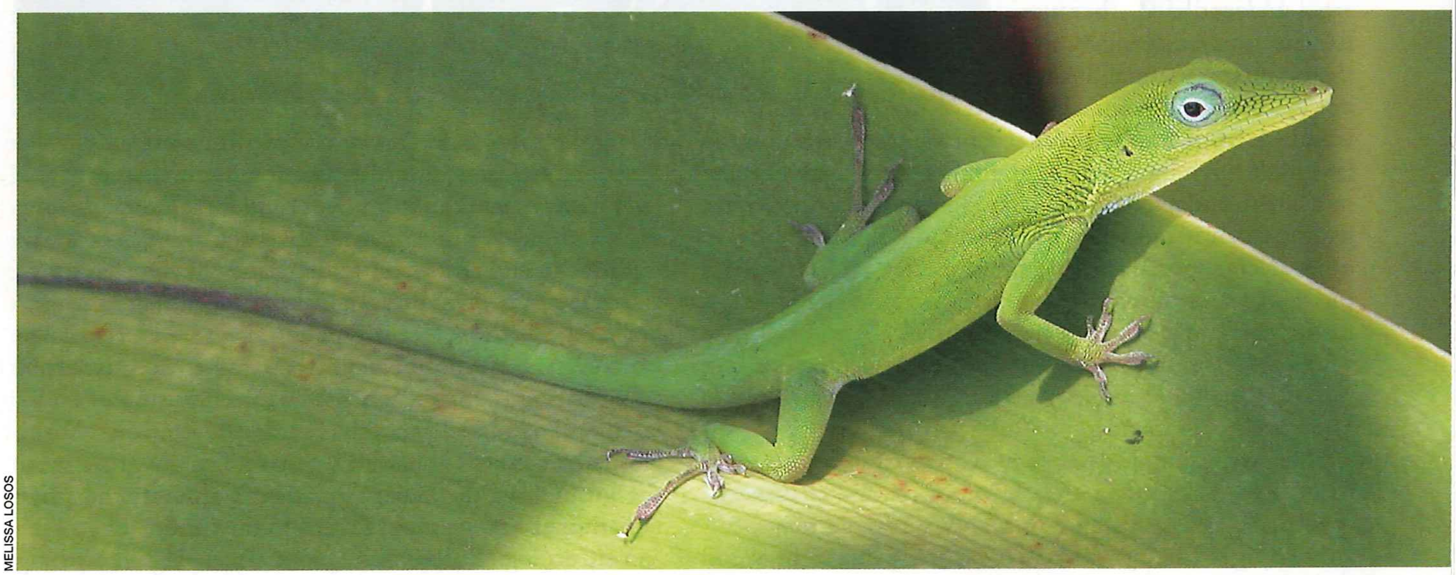
How robust is this counterfactual conclusion? Suppose instead of going to the Galápagos or the Caribbean, the *Beagle* had sailed to Hawaii. There, Darwin would have seen the amazingly diverse honeycreepers—all the descendants of a single species of finch—with their extraordinarily variable beaks adapted to using different food sources: very long curved beaks for sipping nectar, big beaks for crushing seeds or eating fruits, and little beaks for picking out insects. The significance of these beak differences among honeycreepers would not have escaped Darwin. He would have noted other adaptive radiations as well, such as the silversword and lobelia plants.

What would Darwin have seen if, instead of sailing just south of Madagascar, the *Beagle* had stopped there for a visit? In a word: lemurs. Ring-tailed, brown, ruffed, fat-tailed, and mouse lemurs, as well as the incomparable aye-aye. Those are only the smaller members of the lemur radiation, the ones that survived the onslaught that unfolded when humans arrived on the island. Darwin made important paleontological discoveries in Argentina, and might have done the same in Madagascar, finding remains of *Palaeopropithecus*, a 75-pound lemur that hung upside down like a tree sloth, using long curved arms and digits to suspend itself. Or *Megaladapis*, an animal whose proportions were very similar to a koala, but probably weighing in at about one hundred pounds. Or *Archaeoindris*, a terrestrial lemur the size of a gorilla.

Even aside from the lemurs, Madagascar could be called the island of adaptive radiations: vangas (a group of birds as diverse in beak form as the Hawaiian honeycreepers), tenrecs, chameleons, geckos, and many other animals and plants all exhibit the same phenomenon of diversification.

So the *Beagle's* itinerary almost didn't matter. Any large, isolated island probably would have revealed examples of adaptive radiation. Darwin would have noted the diversity and likely would have been moved in the same intellectual direction.

Adaptive radiation is a phenomenon most clearly seen on islands. Oceanic islands—those that were never connected to a mainland, but emerged out of the sea by volcanic action—are populated by species that can make their way across the intervening ocean. Not all species are capable of such expeditions; frogs and trees are particularly



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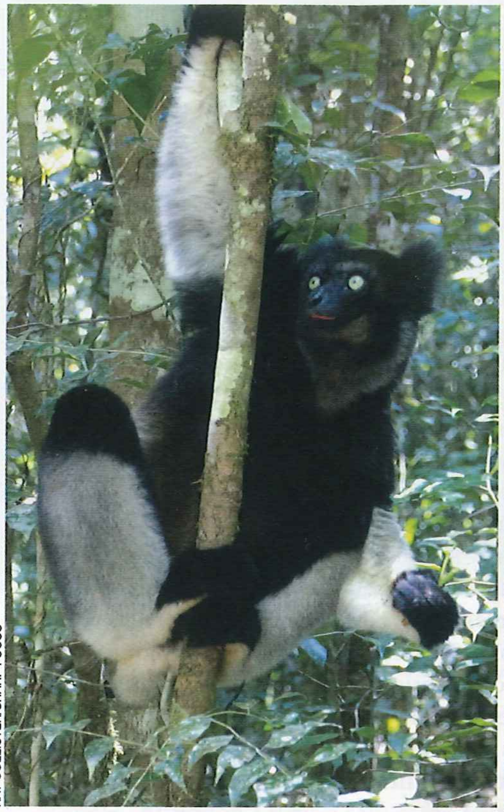

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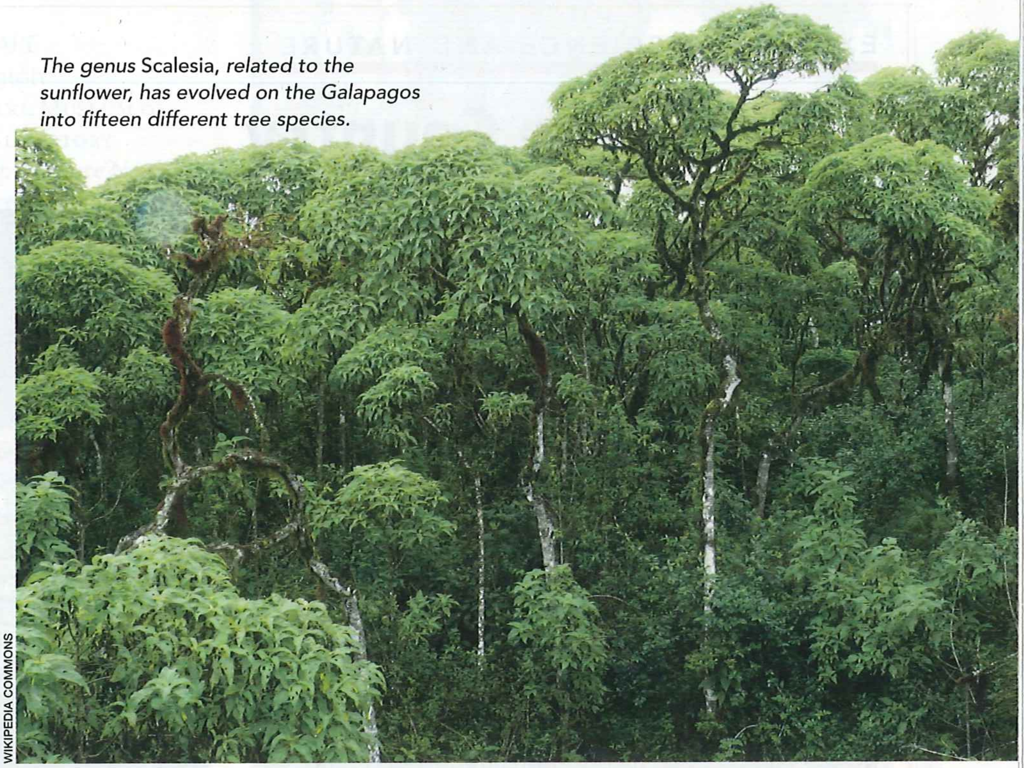
Examples of the diverse lemurs found on Madagascar: clockwise from above, the indri, Coquerel's sifaka, Milne-Edwards' sportive, fat-tailed dwarf, and brown lemur


ill-equipped, whereas flying animals generally fare much better. And chance plays a role: a tortoise might reach one island and not another.

On islands, many resources are underutilized because the species that normally use them on the mainland have not successfully colonized the island. A finch on the mainland may not be able to sustain itself sipping nectar because other species are already much better adapted for the task. However, if a finch finds its way to an island where there are no hummingbirds or other nectar specialists, that finch species can start using the nectar and over time develop adaptations to specialize on it. This "ecological opportunity," the result of the varying colonization success of different species, is what sets the stage for adaptive radiation and explains why it so often occurs on islands.

No better example of ecological opportunity exists than island trees. Most trees are very poor overwater dispersers—their large seeds have difficulty surviving long oceanic voyages (though the coconut, the palm tree's seed, is an exception), and they're too big to be carried on the feet or in the guts of birds. As a result, almost no mainland trees, other than palms, get to islands. Consequently, there's an ecological opportunity for any weed or small bush lucky enough to get to an island. In the absence of large trees, any plant that is a little bit taller than its neighbors and able to soak up all the sun's rays will have an advantage. Many types of plants that are herbaceous shrubs or bushes on the mainland have evolved into trees on islands. On Saint Helena in the South Atlantic, the cabbage tree comes from a plant family that normally grows near the ground. In the Galápagos, there's an entire adaptive radiation of *Scalesia* trees, related to the sunflower.

Yet, ecological opportunity doesn't explain everything about island evolution. About three hundred and fifty miles off the Costa Rican coast in the Pacific Ocean, Cocos Island is biologically rich, blanketed in rainforest. Of particular interest is the Cocos Island finch, a small, nondescript, warbler-like bird. What makes this species a celebrity to evolutionary biologists is its heritage. It is a member of the Darwin's finch family, the only one not found in the Galápagos, which lie five hundred miles to the south. If these finches diversified so wildly in the Galápagos, why not also in the tropical cornucopia that is Cocos? A number of possibilities come to mind.


The genus Scalesia*, related to the sunflower, has evolved on the Galapagos into fifteen different tree species.*

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Perhaps they haven't been there long enough—but DNA analyses suggest that the birds arrived from the Galápagos long ago, sufficient time for diversification to occur.

Perhaps ecological opportunity doesn't exist or other birds got there first and usurped the resources. This hypothesis is also unlikely, given the richness of the island and the lack of radiation of other bird groups. Moreover, the Cocos Island finch is extraordinarily varied in diet, much more so than other birds, suggesting that ecological opportunity does exist, and that the finches have taken advantage of it through behavioral variability.

Perhaps the species doesn't have the genetic capability to adapt to the resources available—but given that the species is a member of the Darwin's finch clan, this explanation does not seem viable.

Or perhaps, for some reason, the species has been unable to split into multiple species. Adaptive radiation requires not only adaptation to different niches, but also the sundering of one species into many. If speciation doesn't occur, then adaptive radiation will be forestalled. Traditionally, evolutionary biologists have thought that populations need to be geographically separated before they can evolve into different species. To the extent that this is true—and this point is currently hotly disputed—then an isolated island setting that prevents population fragmentation may preclude speciation and, consequently, adaptive radiation. By contrast, the Galápagos finches occurred in an archipelago consisting of several islands, where populations could become isolated, speciate, and then re-colonize. To me, a roadblock to speciation seems the most likely explanation for lack of adaptive radiation in the Cocos finch.

The Cocos finch is not alone in failing to diversify in the face of ecological opportunity. Indeed, speciation is almost unheard-of in birds on isolated islands smaller than Madagascar. A similar phenomenon occurs in *Anolis* lizards, where speciation is restricted to the large islands of the Greater Antilles and hasn't occurred on the smaller, yet resource-rich, islands of the Lesser Antilles. Studying the interplay between speciation dynamics and ecological opportunity is an important current direction in island evolution research.

Counterfactually, then, not all potential sailing routes would necessarily have led Darwin to his evolutionary insights. Had the *Beagle* been sent only to remote, small islands, it's possible that he would not have made the key observations that played such an important role in his thinking (although snails and beetles can radiate on much smaller islands than vertebrates can). What would have happened in that case? Would the other main lines of evidence that Darwin accumulated have been enough to lead him to the same conclusions? Quite possibly, given Darwin's analytical thinking. We do know, however, that what he discovered on the route that was taken has made a huge difference.

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