Darwin, Lizards, and Evolution

The Latin American Connection

BY JONATHAN LOSOS

Much has been said about the life of Charles Darwin on the occasion of the 200th anniversary of his birth and 150th anniversary of publication of his magnum opus, *On the Origin of Species by Means of Natural Selection*. A point that has not received much attention, however, is the significance of Darwin's years in Latin America, which helped shape his views about the diversity of the natural world and how it came to be.

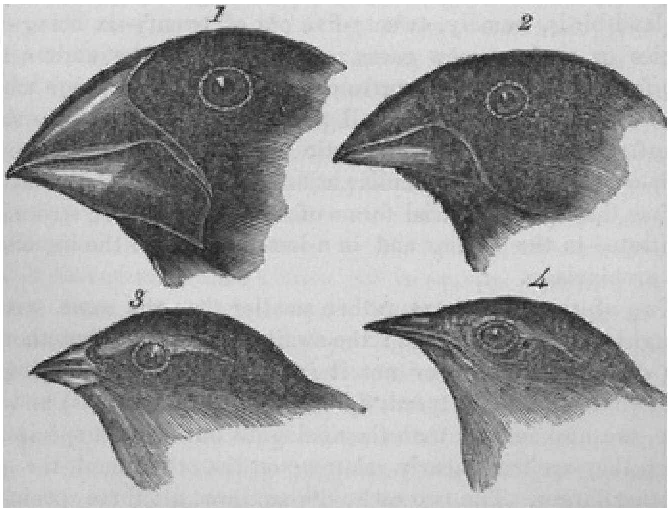
Without question, the most significant event in shaping Darwin's thinking was his five-year voyage on the British royal naval ship, the H.M.S. *Beagle*. A primary purpose of the expedition was to survey the coast of South America. As a result, the ship spent a large portion of its time in and near that continent, allowing Darwin to disembark and spend considerable periods of time exploring (and avoiding the seasickness that plagued him throughout the trip). The biological and geological observations that he made during this time were crucial in sculpting his idea that living forms had not remained static through time, but rather had changed, evolved. For example, he discovered a new species of rhea, a flightless bird similar to, but slightly smaller than, an ostrich, and marveled that there should be two species of rhea occurring in different parts of the continent, similar, but noticeably different.

In addition, his paleontological explorations uncovered fossils of species different from those currently found on the continent, yet clearly related to them. These observations made a strong impression on Darwin, as he recounted in the *Origin*: "When on board H.M.S. 'Beagle,' as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species—that mystery of mysteries."

And, as is well known, Darwin's five weeks in the Galápagos Islands, a volcanic archipelago 600 miles due west of Ecuador, offered rich material for his discoveries. As the *Beagle* progressed through the islands, Darwin noted that populations of species differed slightly from one island to the next. The mockingbirds differed in plumage pattern and bill size, the tortoises in shell shape. Again, why should this be? All of Darwin's observations suggested the same possibility: populations and species across time and space are connected by descent; species are not immutable, but, rather, change through time, with the result that related species in different

A trunk-crown anole from Jamaica

PHOTOGRAPH BY JONATHAN LOSOS



Darwin's Finches: (1) Geospiza Magnirostris, (2) Geospiza Fortis, (3) Geospiza Parvula, (4) Certhidea Olivacea

places or times will be similar, but not identical.

Probably the most famous subject of Darwin's interest are the eponymous finches of the Galápagos, a group of 15 species that have diversified into many ecological niches, including seed-eaters, insect catchers, fruit and flower bud specialists, and even a tool-user that employs twigs to probe crevices for tasty grubs. Paradoxically, Darwin failed to see the significance of these birds at first, misidentifying them as members of different bird families. It was only when the *Beagle* returned to England in 1836 and Darwin sent his specimens to the famed ornithologist John Gould that he learned that all of the birds were members of a single, extraordinarily diverse family. At this point, Darwin recognized their significance, noting in his best-selling travelogue : "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" (*Voyage of the Beagle*, p. 380). These observations set the stage for Darwin to develop his radical theory. Through careful observation, analysis, and painstaking data accumulation, he slowly (slowly!) honed his ideas, finally publishing them in his masterpiece over two decades later.

The situation illustrated by Darwin's finches is now termed "adaptive radiation," the phenomenon in which a single ancestral species diversifies, producing descendants adapted to a wide variety of ecological niches. Many biologists consider adaptive radiations to be responsible for a large part of the diversity in life we see around us. What causes one type of plant or animal to radiate and not another continues to be a question of intense scientific investigation. One factor that appears important is ecological opportunity – when a species finds itself in a setting with ample resources and few other species, adaptive radiation often results.

Such ecological opportunity can arise for many reasons, but perhaps the most common is colonization of a distant island. Many islands are formed by volcanic eruptions that create a new landmass where none previously existed. This is true for the Galápagos, as well as the Hawaiian Islands and many others. The result is that the early arrivals to these islands have an open playing field, often free of competitors and predators. As ecosystems develop, resources become available, and the early colonists can diversify in ways not possible on species-packed mainlands. This is exactly what happened with Darwin's finches, and it turns out that similar phenomena have occurred in other archipelagos around the world.

My own research, and that of many students and colleagues, has been focused elsewhere in Latin America, in Central America and the islands of the Caribbean. Anyone who has visited the Caribbean and managed to travel inland from the beach has probably noticed a small lizard with an odd appendage — its throat sports a brightly colored flap of skin, which it flashes as a form of lizard communication. These lizards are members of the genus *Anolis*, commonly called "anoles," and they belong to one of the most diverse groups of vertebrates (back-boned animals), with nearly 400 recognized species.

Anoles have adaptively radiated across the islands of the Greater Antilles. What is most remarkable about these lizards is that they have not radiated once, but four times independently, on Cuba, Hispaniola, Puerto Rico, and Jamaica. On each of these islands, diversification has occurred, producing a suite of species, each adapted to its own part of the environment. What is particularly amazing is that the same set of habitat specialists has evolved independently on each island. Thus, each island has a species that specialized to use narrow surfaces such as twigs. These lizards have very short legs, an elongated body, and they creep slowly along narrow branches, counting on their gray-color camouflage to avoid detection by both predator and prey. Similarly, each island has a robust, long-legged species that lives low on tree trunks and dashes quickly to the ground to capture prey and find its mates; and a slender green lizard with large toepads that give it the sticking ability to climb over slick leafy surfaces high in the canopy. Laboratory studies have confirmed that each type of habitat specialist is modified to function best in the environment it occupies: twig anoles have the best agility to navigate their narrow and irregular surfaces without falling off, long-legged trunk species have the greatest sprinting and jumping abilities, and the canopy species have the best clinging capabilities. In other words, each type is well adapted to the environment it uses.

And, it must be emphasized, these types have evolved repeatedly (and independently) on each island. DNA sequencing confirms that twig specialists on different islands are not each other's closest relatives; rather, each twig specialist is more closely related to other types of specialists on its own island, and the same is true for the other specialist types. Adaptive radiation has occurred independently on each island, producing, for the most part, the same set of habitat specialists.

Convergence—the evolution of similar body features in species adapting to the same environment—has long been taken as evidence of adaptation driven by natural selection. However, convergence of entire communities is a much less common phenomenon, one that is probably best documented in Greater Antillean anoles. Why anole evolution has produced the same outcome on each island is not clear. Most likely, the environments on the different islands are very similar, so that the same best ways for anoles to make a living recur from one island to the next.

But the story does not end there. Although most scientific research on these lizards has been conducted on Caribbean islands, there are even more species of anoles in mainland Central and

ILLUSTRATION BY JOHN GOULD

Clockwise, from top left: a twig anole from Cuba, trunk ground anoles from Jamaica and Hispaniola, the former displaying its dewlap; a trunk-crown anole from Hispaniola.

northern South America than on the Caribbean islands (approximately 220 vs. 150, with more being discovered every year, primarily on the mainland). The discrepancy in research efforts has to do with abundance; whereas anoles are abundant on the islands, they can be quite hard to find on the continent (one of the curses of studying island anoles is that working anywhere else, on any other type of organism, just seems like too much trouble).

One might well ask: does the same set of habitat specialists that occurs in the Greater Antilles also occur on the mainland? A few mainland species do, indeed, conform to the island specialist types. Most mainland anoles, however, clearly are not at all like the island species: they differ in body proportions, habitat use, or behavior (and sometimes all three). For example, the two most common species found at the Organization for Tropical Studies' (a consortium to which Harvard belongs) La Selva field station in Costa Rica are anoles that use the leaf litter and narrow saplings near the ground. In both ecology and behavior, these species are not like any of the Greater Antillean habitat specialists.

Why has evolution on the mainland taken a different route? At this point the answer is unclear, but the most likely explanation involves differences in levels of predation. On the mainland, a huge variety of predators occurs—not only many types of birds and snakes, but also monkeys, pig-like peccaries, cats and other carnivorous mammals, larger lizards and many more. By contrast, the predator fauna on the islands is much more limited. Thus, while island lizards are probably most concerned with competing with members of their own species for food and mates, the main priority for mainland species may well be avoiding being eaten. In other words, even if they used exactly the same habitat (e.g., the tree canopy), two species—one in the islands, the other on the mainland—might have to adapt differently because of the contrasting demands posed by their environmental settings. The greater abundance and longer lifespan of island species would seem to support this idea, but more work is needed.

A second question is whether replicated adaptive radiations occur on the mainland, as they do in the islands. As yet we don't have enough information on the biology of the mainland species that occur in different places. In addition, our DNA sequence data are not yet sufficient to resolve the evolutionary relationships of these species. Anole work in Central and South America is just getting started in my laboratory, as well as in other labs, so we hope to be able to answer these questions before too long.

I have often wondered what would have happened if the *Beagle*'s charge had been to survey the Caribbean islands, rather than South America. Darwin was an astute observer and naturalist; he surely would have noted the anoles, and probably would have picked up on their similarity from one island to the next. Perhaps, in fact, the lessons they teach might have been so clear that Darwin wouldn't have needed another 20-plus years to write his grand synthesis! And the lizards would have had a catchier, more marketable name—Darwin's lizards, surely. Alas, the *Beagle* didn't chart that course, but anoles are still allowing us to learn much about the evolutionary process and to test the ideas Darwin laid out 150 years ago.

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