II

OLD VERSUS young is just one crucial dichotomy that affects the biological richness of an island. Small versus large is another. Continental versus oceanic, in the sense that biogeographers use the terms, is a third. These three dichotomies give pattern to a world of spectacular confusion.

Madagascar is a large island, fourth largest on the planet, behind only Greenland, New Guinea, and Borneo. It measures 230,000 square miles, roughly the size of Montana and Wyoming together. Like Montana and Wyoming, Madagascar is psychologically distant from the rest of the world and burdened with a culture that venerates cows. Bali is a small island. It measures 2,100 square miles, just a hundredth the size of Madagascar or Montana-Wyoming. Bali is roughly the size of Yellowstone National Park, though in Bali you see fewer Winnebagos.

Large islands harbor more species than small islands, as a general rule. To be specific, Madagascar harbors more species than Bali—many more birds, many more plants, many more reptiles, many more insects, and (though Madagascar itself isn't rich in this category) significantly more mammals. Among primates, for instance, Madagascar has about thirty living species of lemur and a dozen others recently extinct. Bali has a leaf monkey and a long-tailed macaque.

Most of the Madagascan species are endemic; they evolved there and occur nowhere else. Eighty percent of the plant species are unique to the island. Among trees alone, more than ninety percent. More than ninety percent of Madagascar's reptiles, nearly all of the amphibians, all of the tenrecs, and (if several small offshore islands are counted as part of the Madagascan region) all of the lemurs are endemic. Even among birds, with their greater powers of dispersal, half are special to Madagascar.

Most of the Balinese species, on the other hand, aren't endemic to Bali. Many of those species occur also on Java, and some on Sumatra and mainland Asia. Bali does have *Leucopsar rothschildi*, informally known as the Bali starling, a gorgeous and nearly extinct bird with gleaming white plumage and a mask of turquoise. But aside from the starling and the extinct subspecies of tiger, there are few other creatures that Bali can claim exclusively.

This difference in endemism derives from several causes. The size

of the two islands has played a role. So has the difference in elapsed time since each became insular. One other factor is the difference in distance of isolation. Madagascar is much more remote, sitting 250 miles off the African coast. Bali is just a long downwind spit from Java. The remoteness of Madagascar, along with its size and its ancientness, has made it more conducive to speciation and the maintenance of endemism.

But these two very different islands, Bali and Madagascar, do share one essential trait: They are both *continental* islands, as distinct from *oceanic* islands. That is, each was formerly connected to its neighboring continent.

Continental islands tend to be close to the mainland, whereas oceanic islands are more remote. A continental island generally lies on a continental shelf, surrounded by shallow water and therefore subject to reconnection with the mainland by a land bridge during episodes of lowered sea level. Continental islands, for that reason, are known also as land-bridge islands.

An oceanic island is one that never has been and never will be connected to a mainland. It comes into existence as a rising welt off the deep ocean floor, elevated into daylight by some geological process—most commonly, volcanic eruption. After a relatively short lifetime it gets eroded by waves and disappears again below the surface of the sea. The Galápagos are volcanic islands in midocean. The Hawaiian Islands are volcanic. Mauritius and Réunion are volcanic. Among the planet's newest volcanic islands is one called Surtsey, which came steaming up near the southeastern coast of Iceland in 1963. The land-building action of coral is sometimes also involved in erecting oceanic islands. Coralline limestone is laid down just beneath the water's surface and then elevated by volcanic or tectonic pressures. Guam, part limestone and part lava, is a case in point.

Whether built from elevated coral or from extruded lava, every oceanic island comes up from below, like a gasping whale. It starts its terrestrial existence, therefore, completely devoid of terrestrial forms of life. This is the most fundamental distinction between the oceanic and the continental categories. Every terrestrial animal on an oceanic island, and every plant, is descended from an animal or plant that arrived there by cross-water dispersal after the island was formed. A continental island like either Bali or Madagascar, in contrast, already contains a full community of terrestrial species at the moment of its isolation.

A continental island begins with everything, and everything to lose. An oceanic island begins with nothing, and everything to gain. Island biogeography, over the past century and a half, has been the scientific record of those gains and losses.

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"FROGS ARE NOT found in volcanic islands," Charles Lyell told his notebook in April of 1856. What did it mean, what did it mean?

He added that "Darwin finds frogs' spawn to be very easily killed by salt water." Darwin for years had been conducting quiet little experiments on the question of whether various animals and plants could disperse across a wide stretch of sea. Would the seeds of a given terrestrial plant survive weeks of immersion in salt water? In some cases the answer was yes. Would the eggs of a frog survive that treatment? No. Would an adult frog survive? No. Was it a coincidence that the creator, whoever He was, however He worked, had neglected to put frogs on remote islands? Maybe not. Lyell's faith was weakening.

The subject of islands had begun to occupy Lyell's attention several years earlier, when he and Lady Lyell took a cruise to the Canaries and the Mādeiras. These two island groups, standing not far apart in the eastern Atlantic, were regular stops on the oceanic trade route of those years, salubrious and civilized getaways where a Victorian gentleman and his wife could check into a decent hotel. Lyell's main purpose there was to study the volcanic geology. But he couldn't help noticing some remarkable species and some remarkable patterns among the fauna and flora. Many of the Madeiran beetles were endemic; a good number of those endemic species occurred on one Madeiran island but were absent from the other. The land snails of the Canaries caught his eye too. And at least one island of the Canary group, Grand Canary, was strangely empty of wild mammals. Also with reference to Grand Canary, he noted: "I never was in a country where the vegetation was so exclusively . . . unEuropean & so peculiar."

When he got back to England, Lyell sorted through his biological collections and notes, trying to make sense. Late in the autumn of 1855 he confided to his sister in a letter: "It seems to me that many species have been created, as it were expressly for each island since

they were disconnected & isolated in the sea. But I can show that the origin of the islands, which are of volcanic formation, dates back to a time when"—and then, instead of dilating on the evidence, he cut himself short. Although in a letter to Darwin, say, he might follow that line out relentlessly, in a letter to his sister he wouldn't. "But I must not run on as it would take me too long to point out how all these bear on one & the same theory—of the mode of the first coming in of species."

A week later he picked up *The Annals and Magazine of Natural History* and read Alfred Wallace's paper, the one written in Sarawak, about "closely allied species." Immediately he started his new species notebook. He began filling it with data from the Canaries, from the Madeiras, from his readings and correspondence about island biogeography; packing it with insular snails, insular beetles, insular plants, and other closely allied species coincident in space and time. Lyell was just realizing what Wallace had lately grasped and what Darwin had known for two decades: that the answer to the riddle of evolution was best sought by a study of islands.

Winner of the John Burroughs Medal for Natural History Writing and the Helen Bernstein/NY Public Library Award for Excellence in Journalism

The Song of the Dodo

Island Biogeography in an Age of Extinction

David Quammen

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