FIGURE 7. Engraving of Roelandt Savery's dodo portrait, 1848. Based on overstuffed specimens or animals kept in captivity, early depictions of the dodo (like this one completed ca. 1625) often portrayed it is a plump, sluggish, and ungainly bird. Scientists now believe the dodo was much slimmer and more fleet of foot than these early images suggest. From Hugh E. Strickland and Alexander G. Melville, *The Dodo and Its Kindred* (1848).

inhabited coastal areas, where it nested on the ground and apparently lived on fruits, berries, and seeds.

In addition to the dodo of Mauritius (an island about 700 square miles in extent), the neighboring islands of Réunion (a little larger than and 100 miles southwest of Mauritius) and Rodrigues (a tiny island 360 miles east of Mauritius) each harbored their own distinct species of related birds. Even less is known about these species than the dodo of Mauritius. The Réunion solitaire (*Raphus solitarius*), also called the white dodo, was yellowish-white in color, with black-tipped wings, and about the same size as its distant cousin on Mauritius. The brownish Rodrigues solitaire (*Pezophaps solitaria*), on the other hand, was taller, more slender, and had a shorter bill than the dodo.

Although Arab merchants visited the Mascarene Islands sometime before the end of the first millennium, they failed to settle there, and we know nothing

about their long-term impact on the islands' flora or fauna.[12] The Portuguese began regularly stopping on Mauritius in the early sixteenth century, while plying the Indian Ocean to trade with Africa and the Indies. Only scanty accounts of their encounters with the region survive, but they did introduce the first monkeys and goats to the island, a common practice aimed at ensuring a ready food supply for future voyages. The Dutch became the first to stake a formal claim on Mauritius and the first to introduce the dodo to the Western world following Jacob Cornelius van Neck's expedition to the island in 1598. Seven years later, the French botanist Clusius offered the earliest scientific description of the species based on a foot preserved at the house of his friend, the anatomist Peter Pauw, together with accounts from ships' logs and sailors.[13]

The dodo soon gained a reputation for being gawky, dim-witted, and gastronomically suspect. The Dutch referred to it as the *walckvögel*, meaning "disgusting bird," apparently a reference to the toughness of its flesh.[14] Despite whatever qualms they might have had about how it tasted, the fearless bird offered an easy mark that proved irresistible to hungry sailors. The exact derivation of the term "dodo" remains uncertain. The *Oxford English Dictionary* relates it to the Portuguese word *duodo*, which means "simpleton" or "fool," while other scholars have associated it with the Dutch words *dod-aarsen*, which means "fat rump" or *doddor*, which means "sluggard." When Linnaeus provided the dodo with a scientific name—*Didus inpetus* or "clumsy dodo"—even he perpetuated the stereotypes that had developed around the species.[15] Buffon did the same, comparing the dodo to a "turtle that wrapped herself in the remains of a bird, and Nature, by giving it these useless frills, seems to have wanted to top them with the embarrassment of excessive weight, the ineptitude of movements, and the inertia of the mass, and to make its heavy thickness even more shocking because it belongs to a bird." At least most other flightless birds, like the ostrich, were capable of running fast; the dodo, on the other hand, "seems immobilized by its own weight, and to be able only of dragging itself; it seems to be composed of brute, inactive matter, where not enough living molecules were used."[16] As we shall see, the portrayal of the dodo as too slow, stout, and stupid to evade the new predators that arrived on the shores of Mauritius now seems a classic case of blaming the victim.[17]

Less than a century following its discovery the species had utterly vanished. The last definitive sighting of a dodo on Mauritius was in 1681, while the white dodo and the Rodrigues solitaire probably hung on for a few decades longer.[18] Overhunting and the proliferation of introduced animals—pigs, goats, rats, and monkeys—played havoc with the species that had evolved in an environment

with few predators and thus showed no fear of the humans or the introduced species that either pursued it, its young, and its eggs or that competed for its habitat and food. The dodo was, in the words of the science writer David Quammen, an "ecologically naive" species that through eons of time had flourished by successfully adapting itself to an unusually benign insular landscape.[19] That mode of living proved fatal, however, when Europeans and their biota suddenly arrived on the islands.

The destruction of the dodo and the record of its life proved so complete that by the end of the eighteenth century, naturalists began questioning whether it had ever truly existed.[20] Only the most fleeting of evidence—a handful of published and sometimes-contradictory accounts in voyages of discovery, a half-dozen illustrations (several of which seemed to be copies of each other), and a few scattered bone fragments in museums—was all that remained of the species. Was the dodo another mythological creature—like the mermaid, unicorn, phoenix, or griffin—the product of overactive imaginations and undisciplined minds? Or was it a hoax, as the British Museum curator J. E. Gray suggested after noting that the painting of the bird under his care appeared to have artificially joined the head of a vulture-like bird with the feet of a gallinaceous species?[21]

In the 1840s, the British naturalist Hugh Strickland sought to definitively establish the dodo's reality as a once living, breathing creature that humans had driven to extinction. Strickland, who developed an interest in collecting birds and fossils from a young age, began making systematic geological studies following matriculation from Oriel College, Oxford, in the late 1820s.[22] By 1842, his scientific standing was sufficiently advanced that he played a leading role in a British Association for the Advancement of Science committee charged with framing a set of standard rules for zoological nomenclature. Charles Darwin and Richard Owen were among the other prominent members of this committee, whose findings soon gained wide acceptance. Not long afterward, Strickland developed an interest in the plight of the dodo. In addition to authoring several articles and offering reports at scientific meetings on the species, he and the anatomist and physician A. G. Melville published *The Dodo and Its Kindred* (1848), the first scientific monograph on the bird. There Strickland declared that the dodo and its cousins provided the "first clearly attested instances of extinction of organic species through human agency," although he did note that humans also probably killed off the Irish elk and the aurochs—a form of wild ox—in ancient times and the northern dugong more recently. The process of human-induced extinction seemed to be accelerating, he noted, and numerous animals and plants were now "undergoing this inevitable process of destruction before the ever-advancing

tide of human population."[23] Strickland shared the widely held belief that species had definite life spans, not unlike individuals. But he also thought that they could be cut off prematurely by "violent or accidental causes," especially "the agency of Man."[24]

Although the specter of anthropogenic species loss clearly haunted Strickland, like his colleague Lyell, he faced the prospect with some degree of resignation:

> We cannot see without regret the extinction of the last individual of any race of organic beings, who progenitors colonized the pre-adamite Earth; but our consolation must be found in the reflection that Man is destined by his Creator to be "fruitful and multiply and replenish the Earth and subdue it." The progress of man in civilization, no less than his numerical increase, continually extends the geographical domain of Art by trenching on the territories of Nature, and hence the Zoologist or Botanist of future ages will have a much narrower field for his researches than that which we enjoy at present.

If human-caused extinction were an inevitable fact of modern life, as Strickland predicted, then naturalists had a duty to busy themselves with collecting, cataloging, and describing "these extinct and expiring organisms" before it was too late.[25] Strickland's response to the threat of extinction—his sense that his colleagues ought to actively gather vanishing organisms while it was still possible—would remain common within the scientific community for at least the next half century.

Strickland supported his claim about the reality of the dodo with historical, pictorial, and anatomical evidence. First, he reviewed fifteen "original and independent" accounts of the species, including a mid-seventeenth-century notice of a live specimen exhibited in London.[26] He then analyzed the five known oil paintings depicting the dodo, including three that were completed by the well-known Dutch artist Roelandt Savery and a fourth done by his nephew John Savery.[27] Finally, he turned to a discussion of the bird's meager surviving fragments: a foot in the British Museum, a cranium in the Gottorf Museum in Copenhagen, and a desiccated head and foot in the Ashmolean Museum in Oxford. The latter two fragments were all that remained of a once complete specimen that had decayed over the course of a century and barely escaped destruction during a bout of spring cleaning at the museum.[28] The episode prompted Lyell to remark: "The death of a *species* is so remarkable an event in natural history, that it deserves commemoration, and it is with no small interest that we learn, from the archives of the University of Oxford, the exact day and year when the remains of the last specimen of the dodo, which had rotted in the Ashmolean Museum, were cast away"—January 8, 1755.[29] Strickland noted that paleontologists often had much

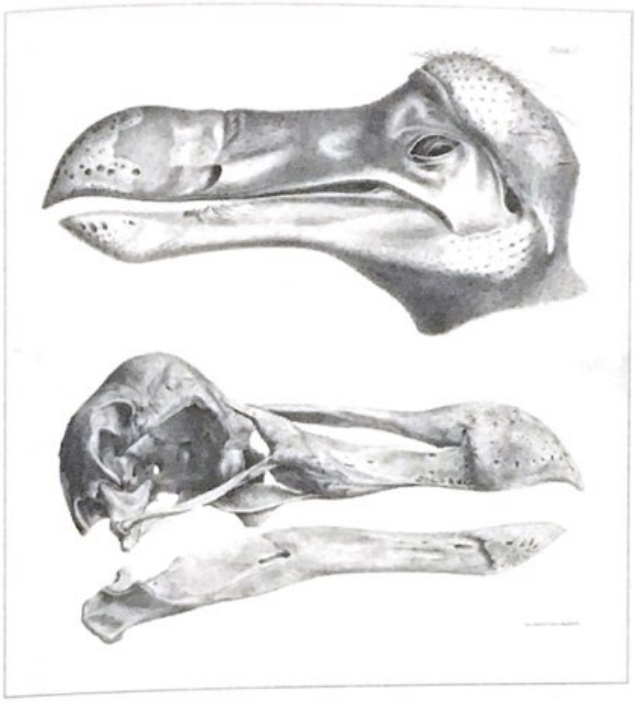

FIGURE 8. Engraving of dodo fragment in Oxford's Ashmolean Museum, 1848. This specimen represented one of the few surviving remains of the dodo at the time of its publication. The initial paucity of physical evidence for the bird led many to question whether the dodo had actually ever existed. From Hugh E. Strickland and Alexander G. Melville, *The Dodo and Its Kindred* (1848).

more data with which to characterize species that perished "myriads of years ago" than the surviving physical evidence for the dodo and its kin.[30] To rectify this shortcoming, he urged naturalists to search diligently in caves and alluvial deposits throughout Mauritius to locate additional remains for study.

Based on his limited range of sources, Strickland concluded that the dodo was a "massive, clumsy bird, ungraceful in form, with a slow waddling motion."[31] Still, despite his generally disparaging description, he remained tied to a providential view of natural history; he firmly believed that the Creator had assigned each class of animals a definite type or structure and that the overall form of each species was perfectly adapted to the circumstances in which it lived. The doddering dodo was no exception, and prior to the arrival of humans, it had apparently thrived on the island. As to its affinities with other known birds, Strickland rejected the arguments of his naturalist colleagues, who until then had speculated that it was a form of ostrich, vulture, albatross, or fowl. The dodo and its cousins were a kind of oversized pigeon, he asserted, an opinion that gained confirmation in the mid-1860s, when George Clark, a school teacher on Mauritius, located a large number of dodo bones in a marsh known as the *Mare aux Songes* (Pond of Dreams).[32] Clark unearthed enough bones to make several more-or-less complete skeletons, and after shipping some to England, he sold the remainder to museums throughout the world.[33]

These and other newly discovered bones then became the object of a long

series of scientific publications. Richard Owen, who had already published several articles on the flightless birds of New Zealand, for example, published his *Memoir on the Dodo* in 1866 from some of Clark's specimens. There he speculated that since the species had been "exempt from the attacks of any enemy" over the course of successive generations, it might have gradually lost its capacity for flight while gaining size and strength through the Lamarckian principle of use and disuse.[34] While the absence of predators had produced the species, their introduction proved fatal to it.[35] The Cambridge professor Alfred Newton and his brother Edward Newton, both founders of the British Ornithologists' Union, also showed a keen interest in the dodo.[36] Part of their curiosity about the lost bird was undoubtedly related to the fact that Edward served in the foreign service in Mauritius from 1859 to 1877, rising to the rank of colonial secretary. In addition to their researches on the Mauritius dodo, Edward visited Rodrigues island in 1864, where he unearthed bones of the Rodrigues solitaire in a cave.[37]

The fame of the dodo and its status as an archetype of extinction, however, ultimately rested not so much on the labors of Strickland, Owen, Newton, and other naturalists, or even the many bones placed on exhibit at leading museums around the world. Rather, public knowledge of the species probably owed much more to the labors of the eccentric mathematician and Oxford don Charles L. Dodgson (a.k.a. Lewis Carroll). In 1865, the same year that Clark reported on the cache of dodo bones he had discovered, Carroll incorporated the creature into the fantasy adventure *Alice in Wonderland*. Carroll's book, which became one of the most popular children's stories of all time, began as a series of tales he began recounting to the children of his colleagues and neighbors.[38] The illustrator of the first edition, the well-known *Punch* magazine cartoonist John Tenniel, based his depiction of the dodo on the ungainly image that Roelandt Savery had created two centuries earlier.[39]

Although the dodo remains the ultimate symbol of human-caused extinction, naturalists have recently begun to rehabilitate its reputation as a fat, clumsy bird. Following a series of calculations based on its bones, the Scottish naturalist Andrew Kitchener has concluded that the prevailing image of the dodo is false.[40] That stereotype, he argues, emerged from drawings and observations made of captive birds that had grown excessively large from overfeeding, improper diet, and lack of exercise. The species was swifter and leaner in the wild, Kitchener claims, a view that he confirmed after discovering several early drawings of the bird that had apparently been sketched in the field. While many questions remain about the dodo, one thing remains certain: history has not been kind to the species or its image.

THE MYSTERIOUS MOA

A few years before Strickland began reconstructing the story of the lost dodo, the paleontologist and comparative anatomist Richard Owen was busy studying another enigmatic flightless bird and erstwhile island dweller: the moa. The Hunterian Professor of Comparative Anatomy at the Royal College of Surgeons, Owen had first earned a reputation as one of Britain's leading naturalists in part through his careful analysis of the mammalian fossils that Charles Darwin brought back from South America.[41] Later, following the publication of the *Origin of Species* (1859), he would become one of Darwin's staunchest critics. Standing at six feet tall, Owen was literally and figuratively a towering presence in British natural history circles, with a list of honorary distinctions that contained over a hundred items and a scientific output that numbered a staggering six hundred papers and twelve book-length studies. He also introduced countless creatures to the public, including the archaeopteryx and many dinosaurs. His family and close colleagues considered him to be warm, affable, and charming. Yet, he could also be a petty, autocratic, and jealous, the sort of fellow who was clearly not one to hide his light under a bushel.

In late 1839, one of Owen's colleagues at the Royal College of Surgeons, John Rule, approached him with an unusual bone fragment, a portion of a femur that he had received as a gift two years earlier.[42] The six-inch-long segment had come from Rule's nephew, a mercantile agent and native trader who had settled at Poverty Bay, on the east coast of North Island, New Zealand, and taken a Maori bride. When he gave the fragment to Rule, who was then practicing surgery in Australia, Harris indicated that local Maori tradition held that it belonged to a "bird of the Eagle kind, which has become extinct. They call it 'A Movie.' They are found buried on the banks of rivers."[43] After returning to London in 1839, Rule compared his femur to those of other birds found in several museum collections. To his delight, his specimen seemed larger, and at some point, it dawned on him that he might parlay the gift into a tidy profit. After failing to interest the British Museum in the fragment, he sent a letter to Owen offering it for ten guineas. There Rule speculated that the femur belonged to a large, extinct "bird of flight" from New Zealand.[44]

When Rule visited the Royal College of Surgeons with the bone in hand, Owen was busy preparing for a lecture and thus understandably distracted. Nonetheless, even from a quick glance, he immediately surmised that the bone before him appeared too massive to have come from a bird with the powers of flight. He initially dismissed Rule as a crank and his fragment as "a tavern deli-

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cacy" from an ox, a "marrow-bone like those brought to the table wrapped up in a napkin."[45] When Rule pointed out the unusually porous, cancellated structure of the bone's interior wall, and produced a greenstone *mere*, a distinctive type of Maori war club, to emphasize the bone's geographic origin, he finally gained Owen's attention. The famed comparative anatomist agreed to get back to Rule as soon as he had the chance to examine the specimen more carefully.

After comparing the bone in question to the skeleton of an ox and a number of other domesticated animals, Owen quickly realized that he had clearly erred in his initial hunch about its origin. Turning to the ostrich, he found Rule's bone was similar in size but different in shape from the femur of this well-known African bird. Following comparisons with several other large flightless birds—the cassowary, emu, and rhea—he became convinced that Rule's specimen belonged to some undescribed bird that was a more immense and sluggish species than its African relative. Later Owen and his supporters would tout the discovery as a demonstration of Owen's prodigious ability and a triumph of Cuvierian functionalism.[46] The British geologist and *Iguandon* discoverer Gideon Mantell, for example, praised Owen's deduction as "the most striking and sagacious application" of Cuvier's principles ever, "the felicitous prediction of genius enlightened by profound scientific knowledge."[47] Just as the famed Cuvier had long boasted that he could successfully predict the overall appearance of an animal from a single bone, so too had Owen—who once studied with Cuvier for several months—been able to predict the overall appearance of the moa from Rule's fragment. In actuality, the story of the discovery of the moa was much more complex than that, and Rule's initial information and his insistence that Owen take a closer look at the specimen deserve some credit.

At first his colleagues remained skeptical about Owen's characterization of the fragment.[48] The museum committee of the College of Royal Physicians, for example, refused to purchase Rule's specimen, while the publication committee of the Zoological Society inserted a disclaimer into Owen's brief account of the moa declaring that "the responsibility of the paper must rest with the author." Many naturalists questioned whether such a large bird could have inhabited such a modest-sized island.

In the meantime, several New Zealand residents with a keen interest in natural history had begun independently gathering information on the moa. The first mention of the bird in print actually came in 1838, four years after Joel Polack, the owner of a trading cutter damaged by storms off the east coast of New Zealand, had been forced ashore for repairs just north of Poverty Bay. The Maori there showed him several large "fossil ossifications" that they claimed belonged

FIGURE 9. Richard Owen with a large moa skeleton, 1879. Here Owen is holding the bone fragment from which he originally described the moa forty years earlier. He stands next to a reconstruction of *Dinornis giganteus*, the largest of nearly two dozen moa species he introduced to science. From Richard Owen, *Memoirs on the Extinct Wingless Birds of New Zealand* (1879), vol. 2, plate 97.

to "very large birds" that had once roamed the countryside before being exterminated through overhunting. Polack decided that the bones belonged to some kind of large "emu" or similar bird of the genus *Struthio*, but he published his findings in a relatively obscure travel account and failed to produce the bones of the creature or to give it a name.[49]

The term "moa" first surfaced in 1838, the same year that Polack published his account of the species, when the missionary William Williams and the mission printer William Colenso traveled to the east coast after seeing a Maori translation of the New Testament through to publication. As Colenso later pointed out, "moa" was the Malay term for the cassowary (another flightless bird that inhabits Australia and New Guinea) and Polynesian for the domestic fowl.[50] The Maori that Williams and Colenso encountered told stories of a huge domestic rooster with the face of a man that inhabited a cave in the Whakapunake Mountain. While no one still living in the area claimed to have seen the bird firsthand, its bones were frequently found. A year later, Williams returned to the site with the Rev. Richard Taylor, and he began offering a reward for any remains of the

moa that might be delivered to him. Each of these men—Williams, Colenso, and Taylor—subsequently published accounts of the species, leading to a bitter priority dispute that simmered for many years.[51]

In 1842, Williams and Colenso sent two large consignments of moa bones to the geologist and paleontologist William Buckland, one of Owen's colleagues in London. After Buckland granted Owen access to the specimens in the first package, he felt confident that he finally had enough material to formally name the new species. Owen proclaimed that the bones represented the remains of a new genus, which he dubbed *Dinornis*, from the Greek *deinos*, meaning "prodigious," "surprising," or "terrible."[52] He chose the name to make a splash, and he would recycle the prefix later that decade when he described the first dinosaurs.[53] The first species in this genus he dubbed *Dinornis nova zealandiae*, after the nation where it had been unearthed. Over four decades, he named and described more than twenty different kinds of moa in more than thirty papers, many of which were gathered into a two-volume anthology entitled *Memoirs on the Extinct Wingless Birds of New Zealand* (1879).[54]

Most of the bones that Owen studied had not yet fossilized. That fact, along with occasional reports of sightings, led to much speculation about whether the giant bird, which grew to as tall as twelve feet, might still roam the vast unexplored regions of that remote colony.[55] In his first notices on the moa, Owen hedged his bets by describing the species as one that had clearly once lived and might still exist somewhere in New Zealand. With increasing exploration and settlement, however, the likelihood that a bird that massive would continue to elude naturalists seemed increasingly slim. The failure to find any living examples of the mysterious bird coupled with the discovery of large caches of moa bones associated with human remains and artifacts—including apparent cooking and butchering sites—led to speculation that the Maori might be responsible for the extinction of many moa species.[56] Although the case for human culpability was not as clear-cut as it had been for the dodo, the suspicion that Maori had done the species in remained strong. As early as 1844, Owen himself began blaming humans for the presumed extinction of the moa: "It is not altogether improbable that the species of Dinornis were in existence when the Polynesian colony first set foot on the island; and, if so, such bulky and probably stupid birds, at first without the instinct and always without adequate means of escape and defence, would soon fall prey to the progenitors of the present Maoris."[57]

The German geologist Johann F. J. Haast, who came to New Zealand in 1858 as a British shipping company agent, was also fascinated with moas.[58] An indefatigable worker, he became instrumental in establishing the Canterbury Museum, at Christchurch, which began on a relatively modest scale in 1861 and opened the

doors to its newly constructed building in 1870. In addition to figuring prominently in the exhibits at the museum, moa bones proved crucial to the growth of the collections; Haast engaged in a brisk trade in moa bones, which proved in great demand because, as one contemporary observer described it, "what Niagara is to ordinary waterfalls, the Moa was to all the bird-tribe."[59] Through sale and barter of this unique resource, Haast acquired biological organisms from around the world, and by 1873, the Canterbury Museum boasted an impressive fifty-six thousand specimens. Haast also published widely in the fields of natural history and archeology, including twenty-three papers on extinct birds.

Even if Maori were ultimately responsible for the extinction of the moa, over a century and a half after Owen published the first scientific account of the species, countless mysteries remain. What role did Maori fires, which transformed the habitat of much of the eastern South Island, play in the decline of the species? Did the introduction of poultry diseases, dogs, and rats that had accompanied the Maori contribute to the decline? Before the arrival of the Maori, New Zealand was a relatively small, faunistically impoverished island that contained only a handful of amphibian and reptile species, two mammals (both bats), and numerous birds. How did so many species of the moa come to inhabit an island that small and with so few other vertebrate species? Even more basic questions—like, Exactly how many species of moa were there? And when had each gone extinct?—continue to elicit comment and provoke controversy, despite the development of sophisticated new methods of analysis, like carbon dating. Writing in 1931, the longtime New Zealand resident T. Lindsay Buick noted that of all the ratites, past and present, "the Moa is indisputably the bird shrouded in the greatest mystery and steeped in the richest glamour."[60] In fact, more recent research has shown it to be only one of more than two dozen other endemic birds driven to extinction shortly after the arrival of the first humans to the islands.

IN SEARCH OF THE GREAT AUK

The same year that Owen first blamed the demise of the moa on the Maori, the last definite encounter with another flightless bird took place on Eldey, a small volcanic island surrounded by steep cliffs located ten miles off the coast of Iceland.[61] Prompted by a Reykjavik natural history dealer who had previously brokered the sale of nearly two-dozen auk skins and eggs, a local fisherman named Vilhjalmur Hakonarrson organized a party of fourteen men to row out to the island. Their aim was to capture specimens of this increasingly valuable bird, which had become a prized commodity as word of its rarity had spread through the natural history community. The three fishermen who landed on

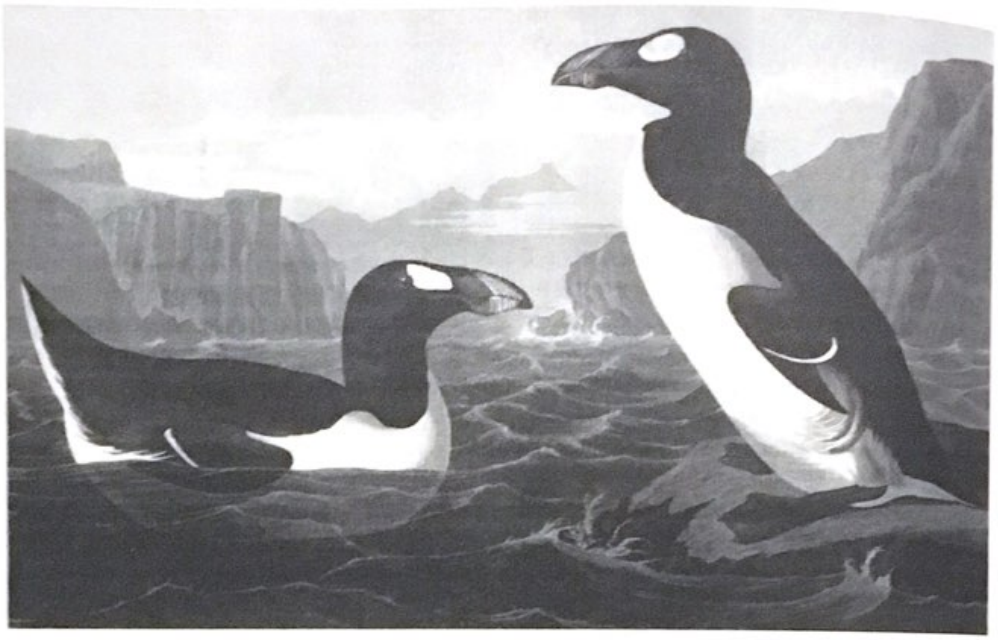

FIGURE 10. Audubon engraving of the great auk, 1827–38. Audubon ventured to Labrador in 1833 with the hope of locating a specimen of this rare species to sketch. Although he found several other desirable species, he failed to discover a single great auk and was forced to use museum specimens as models. From John James Audubon, *Birds of America* (1827–38). Courtesy of the Darlington Memorial Library, University of Pittsburgh.

Eldey in June 1844 found only two great auks and managed to capture both; in the process they also smashed an auk egg they found. While numerous observers claimed to have spotted the species after 1844, these were not only the final two specimens to be collected but also the last incontrovertible evidence of the great auk's existence in the wild.

The great auk (or garefowl), known to scientists as *Pinguinus impennis*, originally ranged across the boreal and low-arctic waters of the north Atlantic.[62] It was a large bird, coming in at about thirty inches tall and weighing about eleven pounds, with a massive laterally flattened bill, black upperparts, white underparts, white patches in front of its eyes, and small wings that it used to help propel itself while diving for fish. The bird was the first to be called a penguin, which is probably derived from the Latin word *pinguis* (meaning fat); Europeans familiar with the north Atlantic species later applied the same name to an unrelated family of flightless birds in the Southern Hemisphere.

During the summer breeding season, great auks concentrated on a small number of offshore islands in the Gulf of St. Lawrence, east Newfoundland, Iceland, northern Scotland, and a handful of others sites. There they incubated a single egg on bare rocks. The most famous of these nesting sites was on Funk Island,

off northeastern Newfoundland, which probably earned its name from the overwhelming aroma of bird excrement greeting those who dared to land there. At the time of first European contact, as many as one hundred thousand pairs of the great auk crowded onto the site, which was about a half a mile long and a quarter of a mile wide.[63] Isolated from the mainland and surrounded by steep cliffs, predators rarely ventured to this or other major auk nesting grounds. As had been the case of the dodo and the moa, the relative lack of predators meant that the great auk showed little fear of the humans.

Hungry sailors who began plying the north Atlantic waters in the sixteenth century feasted on the fat, fearless birds with abandon. In 1620, Captain Richard Whitbourne sang the virtues of the species, pointing out that they were "as bigge as Geese, and flye not, for they have but little short wings, and they multiply so infinitely, upon a certain flat Iland, that men drive them from thence upon a boord, into their boates by hundreds at a time, as if God had made the innocency of so poore a creature, to become such an admirable instrument for the sustenation of man."[64] In addition to being hunted down for its meat, the great auk was also aggressively pursued for its eggs, feathers, and oil.

By the end of the eighteenth century, the first calls of alarm about the plight of the species began to be sounded. In 1785, Captain George Cartwright predicted that if the practice of slaughtering the birds on Funk Island did not soon end, "the whole breed will be diminished to almost nothing."[65] A year later, the governor of Newfoundland issued a proclamation protecting the island's great auk and its eggs, though it exempted birds captured for fish bait and seems to have been rarely enforced. Even as their numbers became thinned, persecution continued from individuals attracted to the islands by the other sea birds that congregated there in large numbers.[66]

In 1833, when John James Audubon traveled to Labrador to collect specimens, make observations, and complete drawings for his *Birds of America*, he landed on several immense seabird colonies in the Gulf of St. Lawrence.[67] There Audubon and his party witnessed several small, motley bands of men engaged in wholesale bird and egg destruction for profit. He was so disgusted that he included a graphic account decrying the "eggers'" predations in the text that accompanied his plates. According to Audubon, on their first visit to a given site, the men engaged in this barbarous trade often destroyed every single egg they found. After repeating this process on as many islands as they could reach over the course of about a week, the party returned to each island to gather the freshly laid eggs. The men also massacred vast numbers of some species for their feathers. To add insult to injury, the eggers Audubon met up with failed to fulfill his request for specimens of rare great auk or eggs for his work. "So constant and persever-

FIGURE 11. John James Audubon in the field, ca. 1845–50. Featured here with his horse, dog, gun, and knapsack, the tools he used to obtain the specimens he drew for his monumental *Birds of America*. Audubon's widely reproduced images helped cultivate sympathy for the plight of vanishing birds. Courtesy of the Library, American Museum of Natural History, New York.

ing are their depredations," he lamented, that species that "were exceedingly abundant twenty years ago, have abandoned their ancient breeding places, and removed much farther north in search of peaceful security." "This war of extermination cannot last many more years," Audubon grimly predicted.[68] While he had no qualms about collecting specimens—sometimes dozens of examples of a single species—to produce his drawings, the large-scale commercial slaughter he witnessed in Labrador appalled him.

After three months of traveling in the region, Audubon managed to bring back seventy-three bird skins and to complete twenty-three large drawings for his magnum opus, despite the often cold, damp, and stormy conditions he and his party of five men encountered in the field.[69] One of the trip's greatest disappointments, however, was the failure to locate a single great auk. Local residents had spoken of "penguins" that they thought continued to reside on some of the islands in the region, but Audubon was unable to find any of them himself, and it now seems likely that by the time he arrived the birds had been lost from the area for many years. In the end, he was forced to base his great auk drawing on a skin

purchased from a natural history dealer, a specimen that probably came from the island of Eldey, where the last pair of auks was collected in 1844.[70]

By the time of Audubon's visit, a run on great auk specimens had commenced, fueled by egg and skin collectors who vied keenly with one another to possess examples of the creature before it was altogether lost. Then, quite suddenly, in the mid-1840s, the supply of new specimens dried up, fueling an escalation in prices for the remaining birds and eggs. The price of stuffed specimen reached the considerable sum of £50 by the 1860s; twenty years later, auk eggs sold for as much as £110 and auk skins for up to £225.[71] Having been commodified in life, the great auk became even more valuable following its extermination. In all, about seventy-eight skins and about seventy-five eggs were gathered up before the species passed into oblivion.[72]

Among the many keen auk aficionados during the middle and later decades of the nineteenth century were two British naturalists, John Wolley and Alfred Newton.[73] With an passion that bordered on obsession, both men sought to amass specimens of the lost bird and its eggs, learn more about its life history, and reconstruct the story of its demise. Their curiosity ran so deep that in the early 1850s Wolley and Newton traveled to Iceland with the hope of learning what had transpired on Eldey in 1844. Somehow they managed to locate and interview several of the men involved in the slaughter of what seemed to be the last pair of great auks collected from the wild, though they never could track down the two specimens gathered that fateful day.[74] Wolley filled several notebooks with his auk research and ultimately hoped to publish a monograph on the species, but he died prematurely in 1859. Newton, who continued the research, remained among those who initially refused to accept the idea that the auks were gone. In a letter written in 1858, he still clung to a ray of hope:

> As to the extinction of the Great Auk, if it is extinct I think it has been mainly accomplished by human means. . . . Under the influence of the "Almighty Dollar" . . . those poor birds were persecuted, their eggs plundered and their necks broken to supply the demand which museums were then creating. And so the number dwindled, until in 1844, the only two then to be seen were taken, their egg broken (the shell left on the rock) and their skins shipped to Europe. I do not think there is any good evidence of the bird being seen since that time; but I confess I do not give it quite up, nor shall I for the next five or six years, though the places suitable for its breeding station must be very few in number.[75]

Newton shared Wolley's dream of producing a monograph on the garefowl, and after his collaborator died, he published the first in a series of articles on the

species. He continued to amass information on the auk for more than thirty years, but never managed to complete the masterwork of which he dreamed.

As had been the case for the dodo, popular accounts of the great auk probably exerted more impact on the public's perception of the species than scientific ones. Charles Kingsley, a professor of history at Cambridge, naturalist, and friend of Newton, included the great auk in his well-known children's book, *The Water-Babies,* first published in 1863.[76] Kingsley depicted the last of the species standing all alone, crying tears of pure oil. Accounts of the sales of the auk and its egg also garnered media attention for the species, especially as the average selling price of specimens mounted. Eventually the great auk would be featured on prints, cigarette trading cards, and tobacco tins.[77]

It is often impossible to state with certainty exactly when a given species goes extinct. Lingering doubts about the status of the great auk probably blunted the potential impact of its loss, but the publicity surrounding both the decline of the great auk and its increasingly valuable skins and eggs contributed to raising awareness about human-induced population crashes in wildlife. The same was true of the dodo, where both the fact of extinction and human culpability seemed more straightforward. The case of the Maori and the moa proved more complex, but taken together, the loss of these three flightless island birds made a distinct impression not only within natural history circles but also in the broader culture. In the second half of the nineteenth century, all three species would be repeatedly deployed as reference points to document the threat of impending extinction of other wildlife.

DARWIN AND THE IMPORTANCE OF BEING INSULAR

While others were reconstructing the stories of the dodo, moa, and the auk, Charles Darwin and Alfred Russel Wallace struggled to understand the larger patterns of geographical distribution among island species. These cofounders of the theory of evolution by natural selection succeeded by combining broad reading in the scientific literature of their day with extensive firsthand experience with insular flora and fauna during their lengthy travels abroad. Both kinds of evidence proved crucial to the development of their ideas about how new species originated and distributed themselves across the globe. Prior to the publication of Darwin's *Origin of Species* in 1859, the most commonly held view was that an omnipotent, omniscient God had specially created plants and animals, which were therefore perfectly adapted for the environments in which they resided. Yet, this theistic explanation for the origin and distribution of life raised numerous questions when it came time to reconcile it with what had been learned

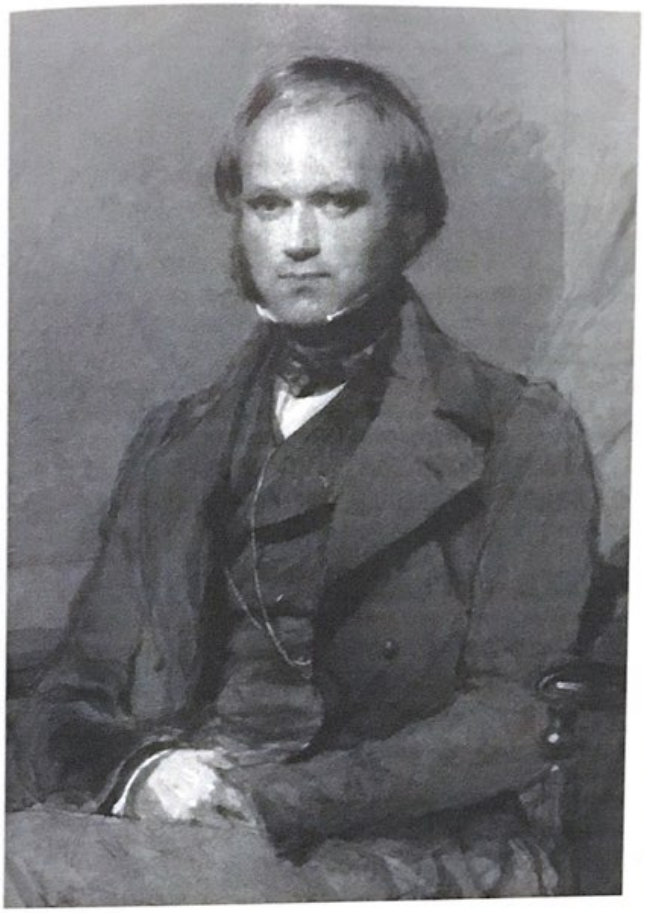

FIGURE 12. Watercolor of Charles Darwin, 1840. Drawn by George Richmond only a few years after Darwin returned from the voyage of the *Beagle*, a five-year expedition that proved central in his intellectual odyssey toward the theory of evolution by natural selection. Courtesy of the Darwin Heirlooms Trust.

about insular species. Why did islands contain so many unique species, like the dodo and the moa? Why did insular species seem so vulnerable to predation by humans and domesticated animals? And why did the number of species on islands seem to vary with their distance to neighboring mainlands? Darwin and Wallace's theory to explain how species came into being also offered compelling answers to these and other questions that increasingly puzzled naturalists. In the end, their evolutionary ideas ushered in a profound change in how not only the scientific community but also the public at large viewed the natural world. Far from being seen as an anomaly to be explained away, extinction became reconceptualized as central to the teeming diversity of life on earth.

Charles Darwin was the fifth child of a father who was a physician in Shrewsbury and a mother who came from the prominent, wealthy Wedgwood family.[78] As a child, he seemed more interested in collecting beetles than serious study of any sort. At the age of sixteen, he went off to Edinburgh University to train as a physician, but the sight of surgery performed without anesthesia so disturbed him that he left after two years; he spent the next three years at Cambridge Uni-

versity, where he hoped to train for the clergy. There he met the botanist John S. Henslow, who fired young Darwin's interest in natural history. Impressed with the potential of his otherwise unexceptional student, Henslow arranged for Darwin to become an unpaid naturalist on the *H.M.S. Beagle*, an Admiralty vessel charged with surveying the coast of South America and several Pacific islands. In the words of Gavin de Beer, the five years he spent on the voyage proved "the most important event in Darwin's intellectual life and in the history of biological science."[79] He left England late in 1831 with minimal formal training in science and the belief that creation was essentially static; he returned in 1837 as a seasoned naturalist convinced that the diversity of the natural world had resulted from gradual evolutionary change.

Fossils played a key role in the evolution of Darwin's ideas about species mutability. One of the books he took with him on the *Beagle* voyage was the first volume of Charles Lyell's *Principles of Geology,* and he received the second volume late in 1832, while in Montevideo. Darwin was immediately taken with Lyell's uniformitarianism, the belief that the earth has been shaped by the same terrestrial forces that were currently in operation and that those forces had always acted with similar levels of intensity.[80] This idea was in contradiction to the more widely held views of catastrophism, which stressed sudden, drastic, and more intense transformations in the earth's crust. In addition to applying Lyell's uniformitarian theory to numerous geological formations he visited during his five years on the *Beagle,* Darwin also absorbed many of his colleague's notions about the meaning of fossils, including his belief that extinction had been a regular part of the history of life on earth. Unlike many of his catastrophist colleagues, Lyell had blamed extinction on gradual environmental transformations.[81] As climatic conditions changed over time, species would be forced either to migrate or gradually perish as they became increasingly ill equipped to survive in the new environment.

The reality of extinction was brought home dramatically to Darwin when he found and excavated large quantities of fossil mammals in the vicinity of Bahía Blanca, on the eastern coast of South America. "I have been wonderfully lucky with fossil bones," he boasted after nearly a week of work at the first site in September 1832. "Some of the animals must have been of great dimensions: I am almost sure that many of them are quite new."[82] He was convinced that one of the massive jaws unearthed at the site belonged either to the megalonyx or a megatherium; a year later he found remains of the mastodon at another site. How and why had these large mammals become extinct? Darwin rejected the catastrophist explanations that Cuvier had proposed, variations of which remained common

in his day. Rather, following Lyell's lead, he embraced the notion that extinction involved the gradual loss of individual species.

But there were problems with Lyell's idea that imperceptible changes in environment caused the destruction of these and other organisms. For example, the mastodon bones he located in 1833 were buried in a gully, in loam that had been deposited over shelly gravel. So the remains he exhumed had apparently come from mastodons that lived after the mollusks found at the site. Since many of the fossil shellfish he found appeared similar to species that were still alive, Darwin surmised that the climate could not have dramatically changed in the intervening years. If not killed off by climate change, could species be analogous to individuals, with a definite life span? he wondered.[83] In his published account of his *Beagle* voyage, issued in 1839, he once again resorted to this common analogy: "All that can be said with certainty, is that, as with the individual, so with the species, the hour of life has run its course, and is spent."[84]

By the time he published these words, Darwin was already toying with evolutionary explanations not only for fossils but also for the many perplexing facts of geographical distribution he observed during the voyage of the *Beagle*. Different regions of the globe often had different though similarly structured species, he noted, like the two forms of rhea he collected on the South American pampas, which resembled but were also clearly not the same as the African ostrich. At the same time, the flora and fauna of oceanic islands tended to resemble but also be distinct from species found on neighboring continents. Finally, adjacent islands that were nearly identical in climate and similar in physical features often held different assemblages of organisms. For Darwin, traditional creationist explanations of the origin of species failed to offer satisfying explanations for these observations.

The five weeks Darwin spent exploring the Galápagos Archipelago, six hundred miles west of mainland Ecuador, proved especially crucial in the development of his ideas about evolution.[85] Darwin prepared for his keenly anticipated visit by reading several previously published accounts of the islands. He became quickly enchanted with the biota he encountered there, including the islands' famous tortoises, iguanas, and boobies that exhibited no fear of humans. He quickly sensed that the flora and fauna bore a general resemblance to that of South America, but with important differences. In the process of collecting prodigious numbers of plants and animals on the four largest islands in the archipelago, he noted something unusual about the mockingbirds he encountered: "The specimens for Chatham [San Cristóbal] and Albemarle [Isabela] Isd. appear to be the same, but the other two are different. In each Isd. each kind is *exclusively*

found; habits of all are indistinguishable." Darwin then remembered a comment from a British-born Ecuadorian official on the islands who claimed that local residents could tell from which of the individuals islands a tortoise had come by observing the form of its body, the shape of its scales, and its general size. During the long voyage home Darwin recognized that if these observations proved correct, they might "undermine the stability of species."[86]

With a new appreciation of the potential significance of his Galápagos material, Darwin lamented the fact that he had not been careful to note on which particular islands he had collected a long series of ground finches. Shortly after his return home, the British ornithologist John Gould named and described fourteen new species of finches based on the *Beagle* collections. Darwin then consulted the finch specimens that Captain Fitzroy and other *Beagle* crewmembers had collected and labeled in the hope of discovering the pattern of their geographical distribution, but he was never entirely successful at doing so. While the finches remained a muddle, Gould did confirm Darwin's hunch that the three different types of mockingbirds he collected were three separate species. Darwin knew that these three species were isolated on different islands; now he came to believe that they had descended from a common ancestor.[87]

Within a few months of his return to England, Darwin began a journal, his *Notebook on the Transmutation of Species*, in which he systematically gathered information relevant to the idea of species change. In a diary entry made at the time, he noted that identifying "species on the Galapagos Archipelago" provided the principal source of "all my views."[88] Although now convinced of the reality of evolution by common descent, he struggled for more than a year to come up with an explanation for how evolution occurred.

The eureka moment, when all the pieces finally fell into place, came in September 1838, after reading the grim speculations of the British political economist Thomas Robert Malthus.[89] Malthus had argued that the tendency for human populations to increase geometrically was inevitably checked by various forms of severe restraint: war, famine, disease, pestilence, and the like. While thinking through the implications of Malthus's insight for the natural world, Darwin came up with a mechanism that could drive the process of evolution: natural selection.

The basic idea seems relatively simple in hindsight. The reproductive capacity of organisms is incredibly high, yet most individuals fail to survive long enough to reproduce. Species also exhibit a great deal of variation, which results in some individuals being better adapted than others to the conditions of life in which they find themselves. These are the same individuals most likely to pass on their favorable traits to their progeny. Over the course of countless generations, these small heritable variations build on one another to produce major transformations

in the physiology and structure of species. Under the constant pressure of natural selection, given enough time, not only new species, but also new genera, families, and orders will result. Using another metaphor, that of the wedge, Darwin attempted to capture a sense of the results of the fierce competition between species and the inevitability of extinction: "Take Europe, on an average every species must have the same number killed year with year by hawks, by cold &c—even one species of hawk decreasing must affect instantaneously all the rest—The final cause of all this wedging, must be to sort out proper structure, & adapt it to changes . . . One may say there is a force like a hundred thousand wedges trying [to] force every kind of adapted structure into the gaps in the oeconomy of nature, or rather forming gaps by thrusting out the weaker ones."[90]

After struggling to flesh out his ideas for several years, Darwin drew up a sketch of his theory in 1842 and a more developed version in 1844, but he refused to publish either essay for fear of the controversy his ideas would provoke. In the latter document, he argued that history demonstrated that "the disappearance of species from any one country has been slow—the species becoming rarer and rarer, locally extinct, and finally lost." While more recent species loss might ultimately be due to "man's direct agency" or his "indirect agency in altering the state of the country," the fossil record demonstrated a similar state of affairs: "decrease in numbers or rarity seems to be the high-road to extinction."[91] Moreover, naturalists thought nothing of the fact that one species of an existing genus was rare and another abundant, even if the exact cause of this phenomenon remained uncertain. Whether trying to explain the mysteries of species abundance, historical extinction, or prehistoric extinction, for Darwin natural selection provided the key: "We should always bear in mind that there is a recurrent struggle for life in every organism, and that in every country a destroying agency is always counteracting the geometrical tendency to increase for each species."[92]

Darwin was finally provoked to publish his evolutionary ideas after receiving a letter from Alfred Russel Wallace, who had independently arrived at the idea of evolution by natural selection. After receiving a draft of Wallace's paper in 1858, Darwin quickly wrote up his own results in *On the Origin of Species*, published a year later. Accounting for extinction loomed large in this, one of the most influential books of the nineteenth century. According to Darwin, "the extinction of old forms and the production of new forms are intimately linked together."[93] Because of the high reproductive potential of organisms, he argued, each area of the globe remained perpetually full. Yet, under the constant pressure of natural selection some forms would slowly but continually be modified, and as this occurred, they would out compete existing forms: "As new species in the course of time are formed by natural selection, others will become rarer and rarer, and

finally extinct."[94] He had once been astonished at the fossil bones he unearthed in La Plata as he struggled to comprehend the force that had caused those species to perish. Now Darwin argued, "We need not marvel at extinction" for species loss was part of the regular order of nature, even if we could not pinpoint the precise events that allowed some species and even entire groups to survive across long stretches of time and forced others to fade away.[95]

WALLACE AND ISLAND BIOGEOGRAPHY

Darwin devoted an entire section of the *Origin of Species* to an explanation of species distribution on oceanic islands.[96] Here he argued that a combination of initial migration and subsequent descent with modification provided a convincing explanation for the patterns of island biogeography that had long puzzled naturalists, while the more prevalent idea of multiple independent creations failed to do so. Oceanic islands, he noted, possessed fewer total species, more endemic species, few or no representatives of some animals (e.g., reptiles, amphibians, and mammals), and trees or bushes belonging to orders that elsewhere include only herbaceous species. The "most important and striking" fact regarding island inhabitants, however, was "their affinity to those of the nearest mainland, without being actually the same species."[97] The example he used was the Galápagos Islands, where "almost every product of the land and the water bears the unmistakable stamp of the American continent." Twenty-five of the twenty-six species of land birds on the archipelago were endemic, yet in terms of their structure and behavior, they closely resembled those found on the South American coast. "Why should this be so?" Darwin asked, if these birds were created in the Galápagos and nowhere else, especially when the conditions there were so different from those in South America?[98] At the same time, the archipelago was populated by closely related but often distinct species, as, for example, the three mockingbirds of the Galápagos, each of which is confined to its own island. Again, Darwin argued that migration followed by gradual evolutionary change over time provided the best explanation for these and other distributional phenomena.

Darwin's cofounder of the theory of evolution by natural selection, Alfred Russel Wallace, also developed a deep interest in the problem of geographical distribution, especially on islands. Born the eighth of nine children to a family of modest means, Wallace became an apprentice in the surveying business of his oldest brother at the young age of fourteen, and for most of the next decade, he mapped and surveyed in Bedfordshire and Wales.[99] He relished the time he spent outdoors, which allowed him to indulge his growing passion for natural history, a passion he also nurtured by reading widely in the field. In 1848, he set out for

Brazil with his friend, the naturalist Henry Walter Bates, to collect specimens for the booming natural history market. The two young men honed their field skills, began speculating about the source of the bewildering array of life they found in the Brazilian rain forests, and gathered a variety of exotic specimens to send back to a London dealer who acted as their broker. Unfortunately, save for one shipment, all of Wallace's collections were lost when the ship on which he was sailing home caught fire. The four years he spent in South America was not a total financial loss, however, since he managed to publish two books based on his experiences, including a well-received narrative of his travels that established his reputation as naturalist on the make.[100]

In 1854, only two years after his return from the Amazon, Wallace set out again, this time for the Malay Archipelago. Over the next eight years, he hopped from island to island, collected more than one hundred thousand plant and animal specimens, and authored numerous scientific and popular articles on myriad subjects. One of the primary items on Wallace's desiderata list was the bird of paradise, an exquisitely beautiful, secretive, and rare bird that proved in strong demand among European collectors at the time. He was ecstatic, then, when he managed to capture a young king bird of paradise while on the island of Aru in 1857. His aesthetic interest in the species—which had long been an important dimension of natural history collecting—led him to openly speculate about the destructiveness of so-called civilized societies:

> I knew how few Europeans had ever beheld the perfect little organism I now gazed upon, and how imperfectly it was still known in Europe . . . I thought of the long ages of the past, during which the successive generations of this little creature had run their course—year by year—being born, living and dying amid these dark and gloomy woods, with no intelligent eye to gaze upon their loveliness—to all appearances such a wanton waste of beauty. Such ideas excite a feeling of melancholy. It seems sad that on the one hand such exquisite creatures should live out their lives and exhibit their charms only in these wild inhospitable regions, doomed for ages yet to come to hopeless barbarism; while on the other hand, should civilized man ever reach these distant lands, and bring moral, intellectual, and physical light into the recesses of these virgin forests, we may be sure that he will so disturb the nicely balanced relations of organic and inorganic nature as to cause the disappearance, and finally the extinction, of these very beings whose wonderful structure and beauty he alone is fitted to appreciate and enjoy. This consideration must surely tell us that all living things were *not* made for man.[101]

While important as an early example of lamenting the destructive changes that had accompanied European expansion, Wallace's revelation did not deter him