A Commemorative Issue All About Birds **$2.50**

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The Joy of Birds

From Ernst Mayr's introduction on the inside cover to Ray Sokolov's scrambled eggs on the last page, this entire issue is dedicated to the science, the art, and the pleasure of birds. It commemorates the centennial meeting of the American Ornithologists' Union this month at the American Museum of Natural History, where the AOU held its founding meeting. The articles that follow show that ornithology—one of the oldest sciences and one particularly open to amateurs as well as professionals—is as vital and fascinating as ever. This special issue was edited by senior editor Rebecca B. Finnell.

Cover: *Armed with asymmetrical ears, a face that functions as a sound collector, and a mental map, the nocturnal barn owl uses sound to locate its prey. Photograph by Rick McIntyre; Tom Stack. Story on page 56.*

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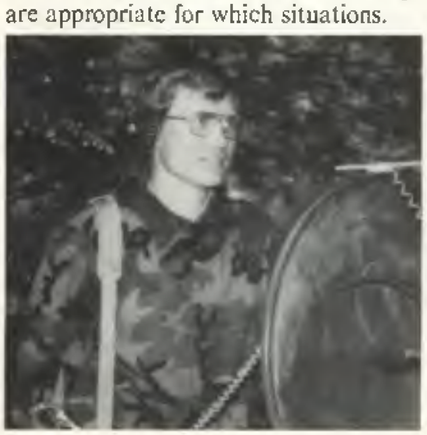
A bird watcher since childhood, **Kenneth P. Able** was impressed early on by the dramatic migration of birds in northern latitudes every spring and fall. As his studies of birds became more formal, he learned that just how birds find their way during these migrations is far from completely understood. Since that revelation, his research has centered on orientation and navigation mechanisms in animals, especially those of migratory birds. Able is associate professor of biology at the Albany campus of the State University of New York.

Both **Helen F. James** and **Storrs L. Olson** work in the Division of Birds of the Smithsonian Institution's National Museum of Natural History, James as a research assistant and Olson as curator. An interest in paleontology and the evolution of birds has taken them several times to the Hawaiian Islands, where a number of exciting bird fossil finds have been made in the last decade. Their research in the Pacific and elsewhere has clearly demonstrated that bird fossils, often thought to be too scarce or fragmentary to be of much scientific use, can contribute significantly to our understanding of avian evolution. In addition to her work on Hawaiian fossils, James plans to study 5-million-year-old bones of cormorants and parrots from South Africa. Olson's projects include bird fossils from Bermuda, the North Atlantic, and North America.

Convinced that much remains to be learned about bird song by looking at species with complex song systems, **Donald E. Kroodsma** examined different populations of one of North America's most voluble songsters—the marsh wren. Associate professor of zoology at the University of Massachusetts in Amherst, Kroodsma is currently focusing on species of warblers that use different songs in different contexts. He hopes to determine to what extent the birds learn, rather than know innately, which songs are appropriate for which situations.



When **Melinda Pruett-Jones** arrived in Papua New Guinea in 1980 with her husband and coauthor, **Stephen**, she found Macgregor's bowerbirds in the forest near the Wau Ecology Institute where they planned to work. "There was no doubt in my mind what I was going to study," she says. Ever since she was an undergraduate at the University of Washington, she has been aware of the unique behavior of bowerbirds, which build and decorate terrestrial display sites for courtship. Melinda had come to New Guinea to conduct research for her M.S. degree at Brigham Young University; Stephen to initiate his Ph.D. research in association with the University of California at Berkeley. His dissertation will focus on the evolution of social behavior in Lawes's six-wired bird of paradise. The couple work on independent projects, but the underlying questions in their studies are the same and they collaborate in much of their work. Their scholarly interests are evolutionary biology and promiscuous mating patterns in birds. When not in the field, they enjoy sailing, the ballet, good Italian restaurants, and gourmet ice cream—none of which can be found in Wau.

Flightless Birds

Recent fossil finds in Hawaii suggest that in prehistoric times, islands in the Pacific supported a rich assortment of flightless birds

by Helen F. James and Storrs L. Olson

Hundreds of years ago, a group of hard-pressed, sun-baked navigators sailed a double canoe through unfamiliar waters for day after weary day, until the sudden appearance of a string of majestic mountains, rising out of the middle of the Pacific Ocean, revived their withered spirits. With fearful anticipation, they paddled ashore and became the first human beings ever privileged to walk on a Hawaiian beach. This is a scene that we have played over and over again in our minds with unsuppressed envy in recent years. Our research on fossil bird bones of the Hawaiian Islands has given us a special insight into what these Polynesian discoverers must have found, and we now know that it was very different from what anyone had previously imagined.

We had long known that the islands were once clothed in virgin forests composed mostly of plants found nowhere else in the world, but only in the last twelve years have we begun to realize the extent to which the forests were home to a remarkable variety of endemic species of birds, most of them doomed to rapid extinction at the hands of humans. More than half of Hawaii's endemic species of land birds would never be seen by westerners. Forty-five or more species—including ibises, geese, rails, owls, a hawk, an eagle, ravens, and a plethora of songbirds—vanished in the prehistoric Polynesian period. Curiously, a large number of these birds, no fewer than seventeen, were incapable of flight. The existence of these unusual birds was Hawaii's best kept secret up to the last decade.

Partly because of two unsubstantiated but prevalent bits of wisdom—that volcanic islands are unlikely spots for fossil collecting and that fossils of birds are rare in any case—no paleontologist or biologist seriously considered looking for fossil birds in the Hawaiian Islands until 1971. In that year, Joan Aidem, an ardent naturalist from Molokai Island, managed to ignite some interest with her discovery of the complete skeleton of an extraordinary flightless goose weathering out of a windblown sand dune on Molokai. Since then, fossil sites have been discovered on five of Hawaii's eight main islands, in settings as diverse as limestone sinkholes, a sea cliff, collapsed lava tubes (tunnellike caves formed after rivers of molten lava drain away), and a flooded cavern where skeletons were found under fifteen feet of fresh water.

Archeological sites containing the remains of prehistoric meals have proved to be another good source of bones of extinct birds. These are doubly interesting because, in combination with stratigraphic and radiometric dating studies, they confirm that many extinct species still survived when the Polynesians first arrived, about 1,500 years ago.

The fossils from all these sources, now gathered at the Smithsonian's National Museum of Natural History, number in the tens of thousands. The tasks of identifying and cataloging the bones, isolating new species, writing scientific descriptions of them, and tracing the evolutionary relationships among them are complex and time consuming. The work is sometimes tedious, but it is amply rewarded by occasional breakthroughs, each augmenting our knowledge of evolution on islands.

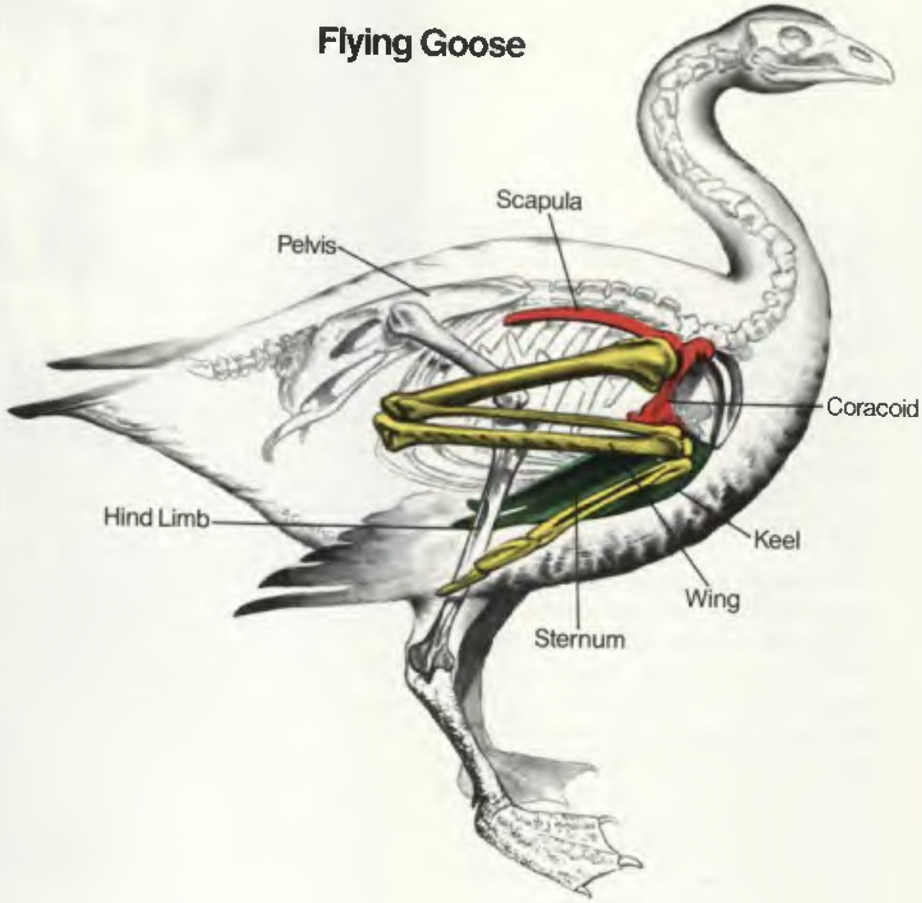
The flightless species of the Hawaiian Islands were not representatives of some obscure, long-extinct lineage but were descendants of such familiar kinds of birds as ducks, geese, rails, and ibises. Their ancestors had to have been excellent fliers; otherwise they never could have crossed the more than two thousand miles of ocean between the Hawaiian Islands and the nearest significant land mass. Once arrived in the Islands, many species of birds responded to the changed conditions of life by losing the ability to fly. Evolutionarily speaking, the process may have happened fairly rapidly: the oldest of the main islands, Kauai, is a mere six million years old, and the youngest, the island of Hawaii, may be less than a million years old. Less time than this was available for the evolution of flightlessness because the ancestors of the flightless birds could not colonize a particular island until after enough soil had formed and plants arrived to create an environment suitable for terrestrial birds.

The genetic mechanism for the evolution of a flightless bird from a flying one is actually quite simple. All birds are flightless when they are small chicks, and the young of flying birds have the same features that characterize the adults of flightless birds—proportionately large legs, reduced wings, and a small or no keel on the sternum, or breastbone. (In flying birds, the bony keel is where the large flight muscles are attached.) Merely by retaining the skeletomuscular structure of infancy into adulthood—probably by the alteration of a few regulatory genes—almost any bird species could become flightless. This process of retention of juvenile characters, known as neoteny, is a fairly common evolutionary phenomenon.

But why become flightless? To most people, birds symbolize flight, and most of the evolutionary history of the class Aves has indeed revolved around the opportunities created by flight, on the one hand, and the physical constraints of flight, on the other. Yet the Hawaiian Islands are not unique; flightless birds occur on islands throughout the world's oceans. What great selective pressure spurs the development of flightlessness on islands?

Beginning with Darwin, some scientists suggested that flying organisms on islands might be blown away by winds and perish, thus leading to the evolution of flightlessness. Many flightless birds, however, are found on New Zealand and other large is-

Flying birds, like this modern goose, have well-developed scapulae and coracoids, which meet at a fairly sharp angle and help to brace the wing bones. They also have a sizable keel, for the attachment of flight muscles.
Douglas Cramer



lands, where there is ample protection from winds. Moreover, tiny islands—Laysan and Nihoa in Hawaii, for example—are home to small birds that retain the ability to fly. The wind theory therefore is not a satisfactory one.

The real evolutionary advantage of flightlessness on islands may revolve around more efficient use of energy. Mainly because of the difficulty terrestrial mammals have crossing large bodies of water, predators—other than birds of prey—are relatively scarce on oceanic islands. When neither escape from predators nor seasonal migration is necessary, individual birds with a reduced ability to fly could have an important advantage. With no large wings or massive flight muscles to support, they would need less food to survive and reproduce. Loss of the ability to fly would not be an advantage for all types of birds, however. Species that must fly to obtain food, such as birds of prey and small arboreal species that forage in treetops, do not become flightless, while those that feed on or near the ground frequently do.

Among the most conspicuous species that must have greeted the first Hawaiians were large, ungainly gooselike creatures. Flightlessness in these birds had proceeded to the extreme stage in which the sternum no longer bore any trace of a keel. The rest of the skeleton had taken on a somewhat comical aspect, with tiny, distorted, and useless wings contrasting with a massive pelvic girdle and large, stout leg bones. These were not fleet-footed birds. The early Hawaiians doubtless had little trouble catching them for dinner.

The evolutionary process had so profoundly altered the skeleton of these Hawaiian geese that for years we despaired of ever being able to pinpoint their closest relatives. Then in 1982, an important clue turned up in the form of a fossil tracheal bulla that we received in a collection of goose bones found by naturalist Michael Severns in a lava tube on Maui. The tracheal bulla is a hollow, bony expansion of the windpipe that occurs in males of most groups of ducks but not in true geese (genera *Anser* and *Branta*) or swans, which can therefore be eliminated as possible ancestors of the odd Hawaiian birds. Further osteological comparisons have narrowed the field to sheldrakes and the typical ducks, such as mallards.

Many different species of these geese have been found in fossil deposits on various Hawaiian islands. They probably evolved in response to the absence of native herbivorous mammals in the islands. Several species belong in the peculiar genus *Thambetochen*, meaning "astonishing goose," and are characterized by bony, toothlike projections on the jaws. These birds may have fed by browsing or grazing on coarse vegetation. Another genus had a very broad, flat lower jaw, almost like that of a turtle, and an extremely heavy upper jaw higher than it was long, giving it a most unusual appearance. This bill form may also have been an adaptation for browsing or grazing.

Intriguing as these gooselike birds are, they had diverged so much from the ancestral species that they are of little use in our efforts to track down the very beginnings of flightlessness. Hawaii does boast one true goose, however, which may prove helpful in this respect. The living nene, or Hawaiian goose (*Branta sandvicensis*), is the only endemic Hawaiian goose to survive into historical times, probably because it is perfectly able to fly, whereas the other species of geese were not. Threatened with extinction during this century, the species was rescued by a captive breeding program and survives in the upland regions of Hawaii and Maui.

Unlike the big, flightless forms of *Thambetochen*, the nene still closely resembles its nearest continental relative, the Canada goose (*B. canadensis*). In addition, fossil finds have turned up some interesting relatives of the nene. Remains have been found on many Hawaiian islands, including ones where no nene has ever been recorded alive. Some of the fossil skeletons resemble those of typical modern nenes; others belonged to bigger-bodied birds with shorter wings, birds that were barely capable of flight, if at all. We hope that comparisons of the various fossils will elucidate patterns of speciation during the early stages in the evolution of flightlessness.

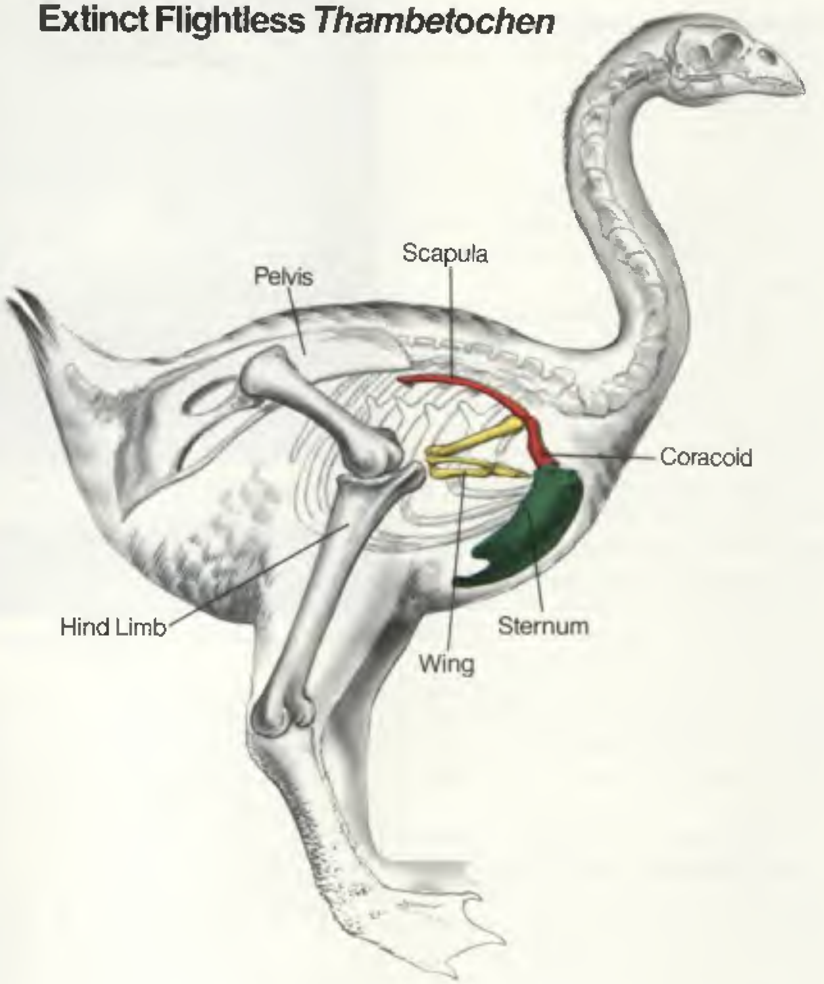
Among the other flightless birds found on the islands of Hawaii are rails and ibises, the latter being familiar to most people as long-legged water birds with long, curved, curlewlike bills and excellent powers of flight. Before the discovery on Molokai and Maui of the remains of two or three species of ibises that were absolutely unable to fly, no one had given the first thought to the possibility that a flightless ibis might have existed. Yet within a year after the first Hawaiian ibises had been described, bones of another, even stranger, flightless ibis from Jamaica were found in the American Museum of Natural History's Department of Mammalogy, scattered among drawers of fossil mammal scraps.

The leg bones of our Hawaiian ibises are much shorter and stouter than those of typical ibises, so much so that we were not confident they belonged to an ibis until most of an associated skeleton was found in a lava tube on Maui. With such short legs, these ibises were certainly no longer water birds but had shifted to foraging on land. They must have made their living fossicking about in litter much like the New Zealand kiwis.

If there is one group of birds that paleontologists can almost always expect to find represented by flightless species on unexplored islands, it is the rails (family Rallidae). Rails are well known for their ability to colonize distant islands, and on many of these islands, flightless species have evolved. Most flightless rails are extinct, but at one time they were a common feature on oceanic islands. At least two species survived into modern times in the Hawaiian Islands: one on the island of Hawaii and one on the tiny northwest atoll of Laysan. Both are now extinct. The fossil record shows that there was an additional

Compared with a flying goose, the extinct flightless Thambetochen, *below, had stout hind limbs and a massive pelvis, small and unsculptured wing bones, and a small sternum with no keel. The angle between the coracoid and scapula is wide, a trait common among flightless birds but never found in adult flying birds. Some of the skeletal features of adult flightless birds result from the retention of juvenile characters, or neoteny. This hatchling of a flying goose, bottom, is too young to fly. Notice the open angle between coracoid and scapula, reduced wings, and absence of a keel.*

Douglas Cramer



species on Hawaii, and at least one flightless rail on Kauai, two on Oahu, three on Maui, and one on Molokai, a species that was smaller than any other rail ever found.

Why so many species? Archipelagoes have certain characteristics that promote speciation. A colonizing species that invades an archipelago usually spreads to most or all of the islands present. Each population may become sedentary, minimizing gene flow between islands and allowing the various island populations to drift apart genetically, which may lead to speciation.

The South American rhea belongs to an assortment of flightless birds, known as ratites, that are distinguished by peculiarities of the palate and often considered to be an ancient group descended from a common ancestor. The new fossil evidence from Hawaii, however, suggests that many of the ratites may have evolved independently of one another.

C. Haagner; Bruce Coleman

In time, flying birds in an archipelago can recolonize neighboring islands, so that a single island could eventually be host to numerous species, all evolved from the original colonizers. In contrast, populations that become flightless are effectively held captive on their home island. The only easy way for them to spread to nearby islands is via land bridges, which rarely form between oceanic islands. In the Hawaiian Islands, such bridges did occur between the islands of Maui, Molokai, and Lanai during the last ice age. At that time, so much water from the world's oceans was frozen in glaciers and the polar icecaps that sea levels worldwide were about three hundred feet lower than they are today. The shallow channels that now separate Maui from Lanai and Lanai from Molokai were then exposed as dry land, forming a single large island called Maui Nui (Big Maui) and permitting overland dispersal among three formerly separate islands. While there can be little doubt that such dispersal occurred, establishing precisely how the joining and subsequent fractionation of Maui Nui has influenced the distribution of a particular species or group of species remains frustratingly out of our reach.

Since land bridges are rare, most flightless species never had the opportunity to colonize a neighboring island. This means, significantly, that flightlessness has arisen independently again and again in the Hawaiian Islands and an untold number of times on oceanic islands the world over. It is a common evolutionary response to the conditions of life on oceanic islands of all sorts, from tiny atolls to huge, mountainous land masses. This repeated evolution of flightlessness is a testimony to the tremendous potential of organisms to independently evolve convergent or parallel adaptations in response to similar selective pressures.

Flightless birds are extremely vulnerable to introduced predators and other human disturbances, and an untold number of them must have vanished as humans discovered and settled islands everywhere. Why, with all the islands in the tropical Pacific, some of them larger and older than the Hawaiian Islands, have truly bizarre flightless birds been found only in Hawaii, New Zealand, and New Caledonia (home of the kagu)? In our minds, the lack of examples reflects, not reality, but our ignorance. Without doubt, flightless birds did exist on most major islands in the Pacific. The early Hawaiians, through habitat destruction, predation, and the introduction of foreign plants and animals, drove at least seventeen species of flightless birds, and no fewer than twenty-eight flying species, to extinction. There is no reason to believe that prehistoric human settlement did not also bring about great changes in the avifauna of other Pacific islands. The coming years may prove to be a golden age for paleontologists exploring the Pacific for bird bones.

From our studies, we can envision the Hawaiian Islands at a time in the past, when eagles soared over unbroken forests that swarmed with an undreamed-of variety of small birds, when troops of ungainly, waddling flightless geese grazed on plants no botanist has ever seen, and when flightless ibises probed among litter for insect species that never felt the thrust of an entomologist's pin. The material evidence for this former glory now consists mainly of tray upon tray of bare bones. But we are the lucky ones. The botanists and entomologists will unfortunately never know what they are missing. □

Lessons from a Flightless Ibis

The flightless birds of Hawaii, particularly the geese and ibises, raise some perplexing questions about the evolution of another assortment of flightless birds, the so-called ratites. These include running birds, such as ostriches, rheas, and emus; the giant, lumbering extinct moas of New Zealand; and the little, long-billed kiwis of shoe polish fame. Many scientists consider ratites to be an ancient group, descended from a single common ancestor, that is separable from all other birds by the paleognathous palate, a peculiar configuration of the bones in the roof of the mouth. The Hawaiian fossils, however, seem to suggest that at least some of the ratites may have originated more recently from more typical flying birds.

The term *ratite*, from the Latin *ratis* for raft, was originally applied to these birds because their sternum lacks a keel. But the keel may also be greatly reduced or even absent in flightless birds that are clearly not ratites. In some of the Hawaiian geese, the sternum has no trace of a keel and has lost all resemblance to the sternum in typical ducks and geese; instead, it is rounded and bowllike, more like the sternum of an ostrich or an emu.

In some of the ratites—moas, for example—the bones in the leg are relatively shorter and much stouter than in running ratites. Again, we see very similar adaptations in the flightless birds of Hawaii. Some of the geese had ponderous legs that contrasted greatly with their little wings. The flightless Hawaiian ibises had leg bones so much stockier than those of their long-legged wading ancestors that they are remarkably similar in proportion to those in the New Zealand kiwis.

We find that almost all the features in the body plan of ratites have evolved repeatedly in a variety of nonratites through the retention of juvenile traits (neoteny). Might the paleognathous palate likewise be a result of neoteny, and consequently something that could theoretically develop in many kinds of birds? This is the subject of current investigation, for if all of the characteristics of the paleognathous palate are present in the embryonic condition, as some of them are known to be, the various kinds of ratites might have evolved independently of one another by retaining such a palate into adulthood.

With this possibility in mind, the striking parallels between the flightless birds of the Hawaiian Islands and those of New Zealand become of even greater interest. Hawaii had an extensive radiation of gooselike birds, derived from at least two different ancestors, that were flightless and had widely divergent bill shapes, evidently for feeding on different kinds of vegetation. Similarly, in New Zealand, the moas were large, flightless, herbivorous birds with a variety of bill shapes. Taxonomists have at times divided the moas into two different families that might actually represent separate colonizations of New Zealand by flying ancestors. The resemblance between living kiwis and the extinct Hawaiian ibises are not restricted to leg bones; both also have long, probing bills quite unlike those of geese or moas.

Great spotted kiwi of New Zealand
Brian Enting, Photo Researchers

The flightless birds in the main Hawaiian Islands lost the ability to fly in considerably less than 6 million years. The flightless ibises, for example, which were restricted to the islands of Maui Nui, could not have colonized those islands more than 1.8 million years ago, the age of the oldest rocks found on Molokai, the oldest of the Maui Nui group. But New Zealand has been available for colonization by vagrant birds for tens of millions of years. If an ibis could become almost unrecognizable in less than 1.8 million years, what would it look like if it had continued to evolve for another 10 or 20 million years? Are the moas and kiwis of New Zealand merely the descendants of geese, ducks, and ibises that had much more time to diverge? Such intriguing questions would probably never have been raised had the Hawaiian fossils gone undiscovered. Perhaps more work with fossil birds from other Pacific islands will help us find the answers.

Storrs L. Olson