Chapter 17
The Real Great Dinosaur Extinction

When we applied to graduate school two decades ago, every applicant was required to take the Graduate Record Exam - the GRE. Our GRE scores would, it seemed, be the most important numbers in our life. Images of our own academic extinction loomed in our imaginations as we studied. Even now the memory remains vivid and searing. But our spirits were buoyed when we encountered a couple of simple questions about vertebrate evolution. One asked, "Which is the oldest bird? (a) *Australopithecus afarensis*, (b) *Archaeopteryx lithographica*, (c) *Escherichia coli*, (d) *Drosophila melanogaster*, or (e) *Penicillium notatum*?" Paraphrasing the second, "If a human generation averaged 20 years long, how many generations back would you have to go for humans to overlap in time with dinosaurs?"

Both questions can be traced back more than a century, to Richard Owen's description of the oldest bird and his naming of the first-known extinct dinosaurs. Even with a modern evolutionary perspective, the answer to the first question hasn't changed, although the meaning has been altered a bit.

But the answer to the second question has changed. When we took the GRE, the correct answer was about 3,250,000 human generations. The answer was qualitatively the same to university aspirants in Richard Owen's day. Even though the age of the Earth was not then known, it was clear that the Cretaceous ended long ago, and that thousands or millions of generations separated humans and dinosaurs. Today, however, our map of vertebrate phylogeny indicates that the correct answer is 0. Possibly the most meaningful lesson gleaned from mapping dinosaur phylogeny is that our own history has overlapped with dinosaurs for about 20,000 generations, depending on what you choose to call a human.

In previous chapters we traced the rise of dinosaurian diversity, but we now reach a profound reversal of that trend, as we investigate one of the greatest episodes of mass extinction in tetrapod history. This change in fortune for birds and many other species occurred at basically the same time that the world became inhabited by people. Unlike the great K-T extinction, humans witnessed this one.

Human Evolution

Humans are members of the primate lineage, whose fossil record now traces back to the very beginning of the Cenozoic. Lev Nessov's discovery of fossil zhelestid mammals in Cretaceous rocks provided a benchmark for calibrating the age of many of the living mammal lineages (see fig. 15.04), and David Archibald mapped the primate ghost lineage back into the Cretaceous[1]. Although we have yet to find a Cretaceous fossil that is unequivocally a primate, our phylogenetic map indicates that the ancestral primate species probably lived during the mid- or Late Cretaceous, and that one or more of its descendants survived the K-T boundary. Without a better fossil record, we can't say much about early primate diversification, or how they were affected at the K-T boundary, excepted that the lineage survived. Like dinosaurs, primates underwent a long history of post-Cretaceous diversification, and today there are about 200 living primate species. But over the whole of the Cenozoic, the pace of bird diversification exceeded that of primates 50-fold, to produce today's approximately 9672 species.

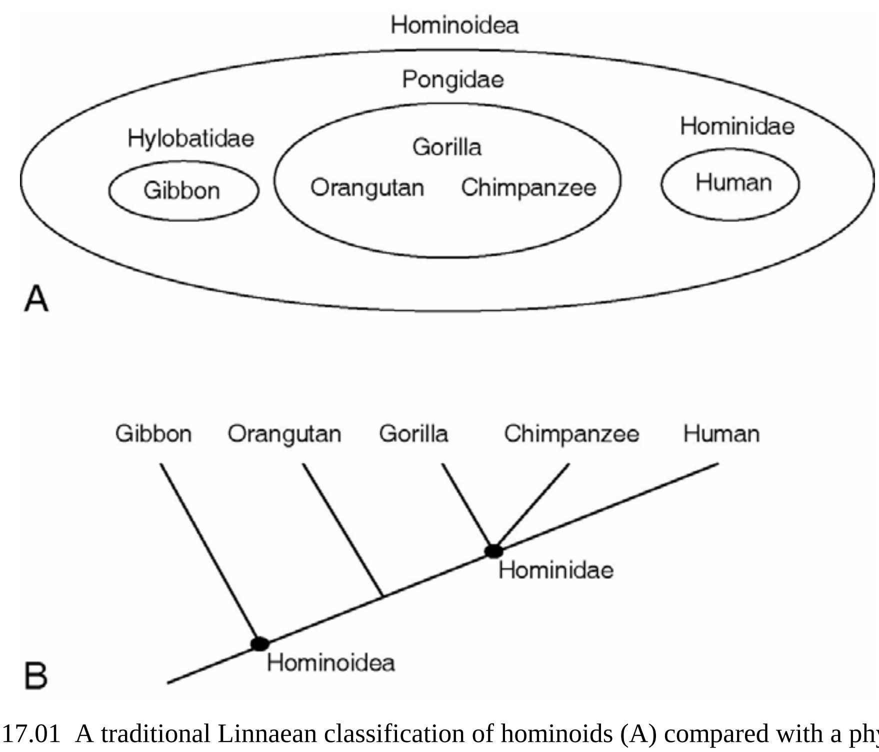


Figure 17.01 A traditional Linnaean classification of hominoids (A) compared with a phylogeny for hominoids (B). Note that the term 'Hominidae' denotes different assemblages of species in the two diagrams. Also note that the traditional classification reflects very little of the knowledge about relationships that is recorded in the phylogeny. Whether the Chimpanzee is closer to Gorilla or to Homo is controversial.

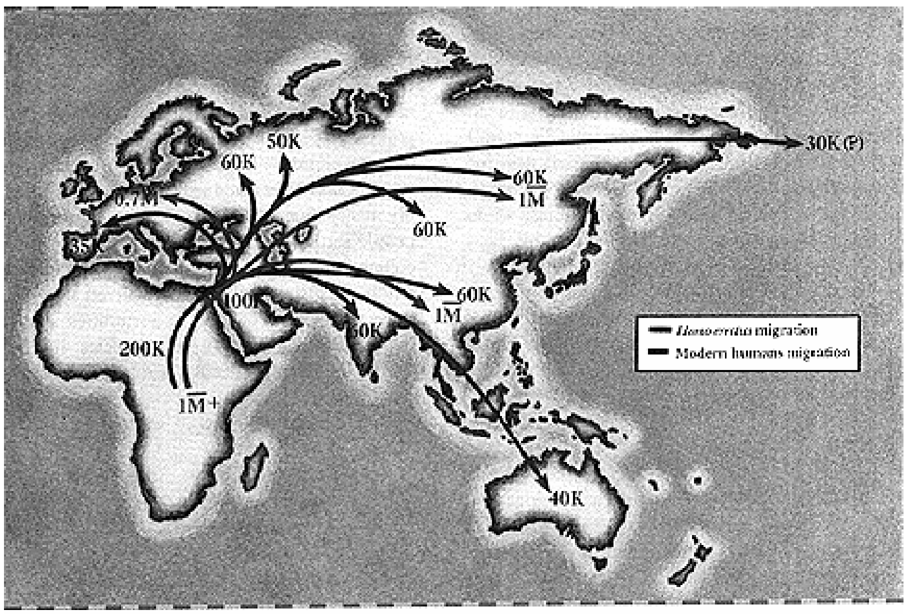
Modern primates include tarsiers, lorises, lemurs, galagos, monkeys , and our own group—Hominoidea (fig. 17.01). The hominoids today include our own species, *Homo sapiens*, plus several other lineages of apes. The evolutionary path closest to our own includes the two species of chimps, and it may include the Gorilla as well. Alternatively, the Gorilla might be first cousin to chimp-human sister lineages. Still further from humans is the Orang Utang, and further still the gibbons. Hominoidea arose in Africa between 20 million and 30 million years ago. Although sparse, the fossil record of hominoids preserves a diversity of extinct species[2]. *Sivapithecus*, one of the oldest fossil hominoids, lived between thirteen million and seven million years ago in Turkey, northern India, Pakistan and China. Most anthropologists think that *Sivapithecus* was related to the modern Orang-Utan. More recent fossils mark the split between modern chimps and the lineage named Hominidae, which includes humans plus their closest extinct relatives.

Based on currently known fossils, the paths of hominids and other apes split in Africa between five million and ten million years ago. Nearly all early hominid fossils come a narrow rift zone in eastern Africa that extends from Ethiopia south through Kenya, Tanzania, and into South Africa. Evidently, three distinct hominid species lived contemporaneously in east Africa. Among the oldest fossil hominids is *Australopithecus anamensis*, from the Awash district of Ethiopia, which is around 4.4 million years old[3]. A second species, *Australopithecus afarensis*, from the Fejej district of Ethiopia is 3.9 to 4.1 million years old. A more recently discovered hominid named *Ardipithecus ramidus* was collected from Kenyan rocks that are between 3.9 million and 4.2 million years old. A short trackway of footprints made by someone walking bipedally across wet muddy ash along a lake shore in east Africa dates to about 3.7 million years old. These prints belong to a creature whose feet resemble human feet and whose hands were freed from their primitive role in locomotion. A modest adaptive radiation had begun long before the Pleistocene[4].

The oldest hominids were bipedal and their brains were slightly enlarged, compared with the brains of chimps. The earliest are called australopithecines (a group of doubtful monophyly). They were just over three feet tall and weighed about 65 pounds--less than modern chimps. The volume of their brains measured just under a pint

(400 to 450 cubic centimeters)[5], which represents a real increase in brain size for the first hominids.

These hominids occur in rocks between about 4.4 and 1.0 million years old. By about 2.5 million years ago, fossils document a distinctive new species named *Homo habilis*. Its brain grew to more than a pint in volume (500 to 600 cubic centimeters). Almost four feet tall, and it weighed about 70 pounds. *Homo habilis* survived until 1.5 million years ago.



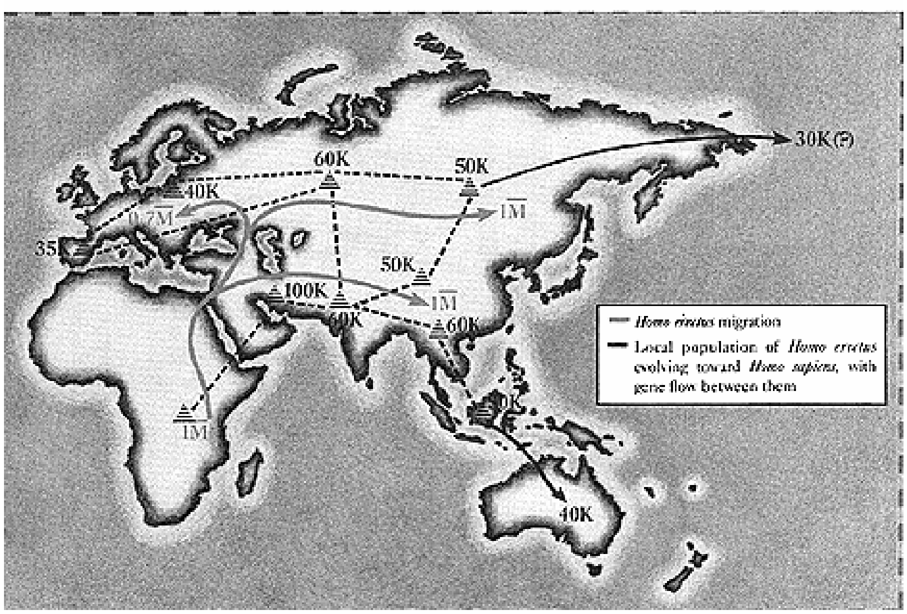


Figure 17.02 Alternative models to explain the distribution of humans over the globe. In the top figure, two migrations out of Africa are proposed, the first by *Homo erectus* and the second by *Homo sapiens*, following their separate origins in Africa. In the bottom map, *Homo erectus* moved out of Africa and locally evolved into *Homo sapiens*. (From R. Lewin, 1993. The Origin of Modern Humans. Scientific American Library, New York).

About 1.6 million years ago, fossils of still another species appear, named *Homo erectus*. Its brain averaged nearly a quart (935 cubic centimeters) in volume. This species is larger, averaging about 130 pounds. Brain size is partly a function of body size, but even correcting for the difference in size, a real increase in brain size and computing power evolved in *Homo erectus*. This was evidently the first hominid to disperse out of Africa, extending its range to Asia and Java by about one million years ago (fig. 17.02). By about 500,000 years ago it was living in Europe as well. Stone tools extend back about two million years, but so far there is no direct evidence about which of our relatives made and used them. Some of the Java sites were recently re-dated to between 27,000 and 53,000 years old, suggesting that *Homo erectus* survived much longer in southeast Asia than previously thought[6]. If so, it overlapped with our own species in time.

Homo sapiens, our own species, appears in the fossil record between 400,000 and 150,000 years ago. The exact date of the oldest *Homo sapiens* fossil is in dispute, as anthropologists argue over the identities of certain incomplete European fossils. But there is no mistaking the identity of more complete fossils, because *Homo sapiens* has a huge brain, with a volume approaching 1.5 quarts (between 1200 and 1600 cc)[7], and a body mass still around 130 pounds. With the emergence of *Homo sapiens'* huge brain came the accouterments of humans and human societies. The first evidence of 'domestic' fire is about 500,000 years old. Art goes back about 35,000 years, and agriculture arose about 10,000 years ago[8]. The relationships among world populations are now being mapped out in detail, using information from both genetics and linguistic characteristics (fig. 17.03).

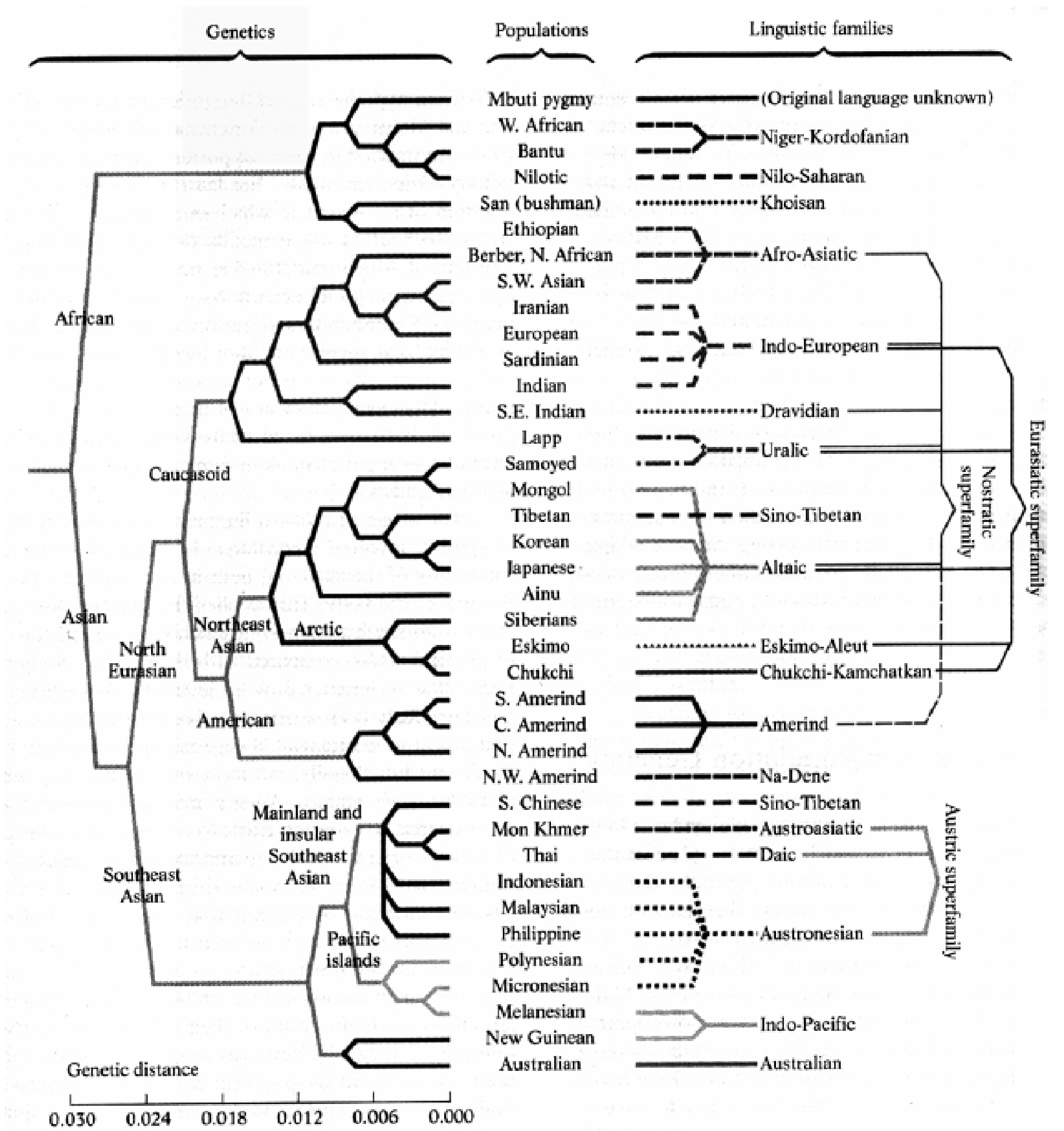


Figure 17.03 Information from genetics (left) and linguistic characteristics (right) lead to very similar conclusions on the relationships among world populations. (From R. Lewin, 1993. The Origin of Modern Humans. Scientific American Library, New York).

Elizabeth Vrba (Yale University) and a group of colleagues document an episode of climatic deterioration, begining in the Miocene and culminating in the Pleistocene, that corresponded with a major turnover in the fauna of the African Rift Valley[9] during early hominoid history. A rapidly shifting environment may have been the substrate for human origins. Steven Stanley (Johns Hopkins University) calls humans the children of the Ice Age[10], arguing that a confluence of environmental and developmental factors sparked the emergence of *Homo*. However they did it, humans survived the Pleistocene extinctions to achieve unprecedented success by many measures of the term.

Measures of Human Success

One distinguishing feature of *Homo sapiens* is our repertoire and extensive use of tools. Tools and their effects leave an archeological record, and they document a rich history of human activity before there were written records. Intensive use of tools began sometime before 100,000 years ago. Demographer Joel Cohen (Rockefeller University) has suggested that the discovery of how to make and use tools led to one of the first great spurts of human population growth, which peaked about 100,000 years ago[11]. Between 400,000 and 100,000 years ago, he estimates the combined population of the human species grew to 100,000 (fig. 17.04).

Cohen describes that over the next few thousand years a drop in population levels may have occurred, based on analyses of the variability of DNA sequences in modern human populations. Human populations may have fallen to about 10,000 people, producing a bottleneck in DNA sequence variability that is still discernible in people today. The reduction had probably occurred by about 80,000 years ago, during the last of the Pleistocene Ice ages. The survivors lived in Africa and slowly expanded across the Old World. By 40,000 years ago, human populations had spread to Europe, Asia, and Australia. Before the end of the Pleistocene, by 12,000 years ago, people had discovered the New World and traveled through North America to the forests of South America.

A second surge in human population size began as people in different parts of the world discovered agricultural techniques and grew some of their own food. From about 10,000 to about 6000 years ago, the global population rose to somewhere around five million people. Cohen estimates that before this surge, human populations grew at a rate that would lead them to double in approximately 40,000 years or more. Following the agricultural surge, global populations grew at a rate in which they doubled every 2000 to 3000 years.

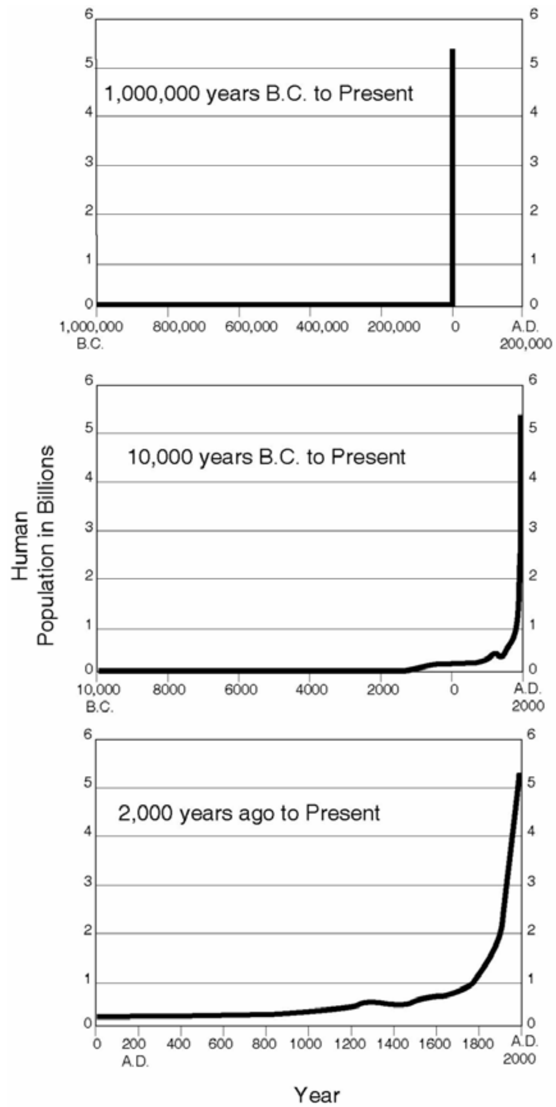


Figure 17.04. Human population growth shown on three different time scales (From J. E. Cohen, 1995. How Many People Can the Earth Support? W. W. Norton & Co., New York).

A third surge in population growth began in the early 18th century. This episode coincided with the discovery of science and technology in Europe, and the renaissance of global navigation that distributed agricultural species cultivated by different peoples throughout the world. The global human population surged to 750,000,000 people, and the population now doubled about every century. When Richard Owen named Dinosauria in 1842, the human census had just passed the one billion mark (fig. 17.04).

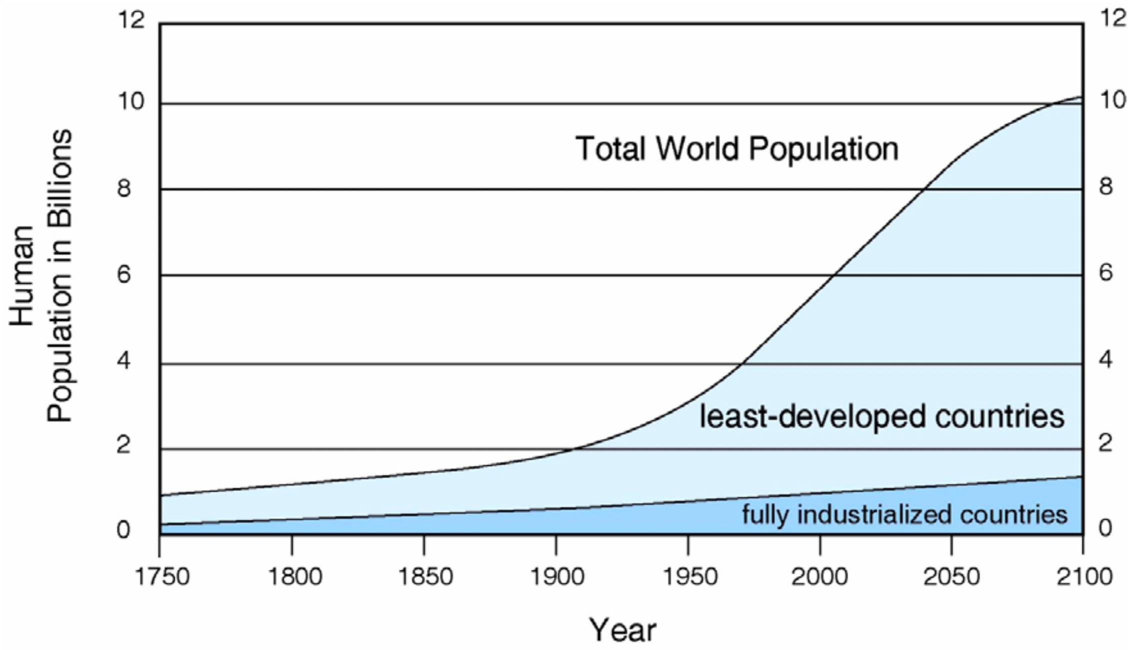


Figure 17.05 The projected peak human population will reach close to 10 billion people early in the 22nd Century, most of whom will be born in under-developed countries in the next century. (From: A. P. Dobson, 1996. Conservation and Biodiversity. Scientific American Library, New York).

Shortly after World War II, Cohen has measured another surge in population growth, and this one was the most significant surge so far. It was prompted primarily by several developments in medicine and public health, which reduced mortality and prolonged life, and the global human population reached 2.5 billion.

In the next 36 years, the global population doubled. A last surge occurred in the late 1960's, reaching an all-time peak in population growth rates. It was also prompted by medical developments that led to increased human reproductive fertility. Today there are about 5.6 billion people on Earth. In the last 100 years, more people have been born than in all the rest of human history. Current human populations are growing at the rate of two percent per year--one billion people every twelve years. Current projections estimate that the all-time high will be reached in 2135 AD, with eleven to twelve billion people crammed on the Earth (fig. 17.05). So successful are humans that we have already become 100 times more numerous than any other land animal in the history of Life in our 100 pound (50-kilo) weight class. Through our agricultural practices, it is estimated that humans capture 20 to 40% of the solar energy reaching the Earth's surface and consume it exclusively for our own needs[12]. *Homo sapiens* is one of Nature's greatest success stories, but at what cost?

The Specter of 1662

About 300 miles west off the eastern coast of Madagascar in the Indian Ocean are three islands now called Mauritius, Réunion, and Rodriguez, which together form the Mascarene Islands. Mauritius was the first to be discovered, in the first half of the 16th century by a Portuguese navigator, but the entire chain remained uninhabited until 1598 when the Dutch took possession and established a colony on Mauritius. The colonists found birds that "...were of large size and grotesque proportions, the wings too short and feeble for flight, the plumage loose and decomposed, and the general aspect suggestive of gigantic immaturity."[13] Little did these colonists realize that their encounter with the Dodo bird (fig. 17.06) would prove infamous.

Figure 17.06 The Dodo of Mauritius. This engraving was taken from a painting made before the Dodo went extinct. (From: H.E. Strickland and A. G. Melville, 1848. The Dodo and its Kindred. London).

Before Europeans landed on Mauritius, it was pristine, spectacularly beautiful, and uninhabited. Early Dutch, French, and English travelers described it as a Garden of Eden. Besides the Dodo, there were evidently flightless relatives on each of the other two Mascarene Islands. A second species known as the Rodriguez Solitaire lived on Rodriguez Island, but became extinct by the end of the 18th century. A third species, known as the White Dodo, may have lived on Réunion Island at the time of European settlement. This creature has been given several names, including *Raphus solitarius* and *Victoriornis imperialis*, but our entire record of it consists of a couple of oil paintings reportedly made from a live bird displayed in Amsterdam and contradictory tales by 16th and 17th century travelers[14, 15]. If it ever existed, this bird had become extinct by the end of the 17th century. So far, no bones of it have been recovered.

The first great chronicler of the Dodo, H. E. Strickland, described in 1848 that "The history of these birds was as remarkable as their organization. About 2 centuries ago their native isles were first colonized by Man, by whom these strange creatures were speedily exterminated. So rapid and so complete was their extinction that the vague descriptions given them by early navigators were long regarded as fabulous or exaggerated, and these birds, almost contemporaries of our great grandfathers, became associated in the minds of many persons with the Griffin and the Phoenix of mythological Antiquity."[16]

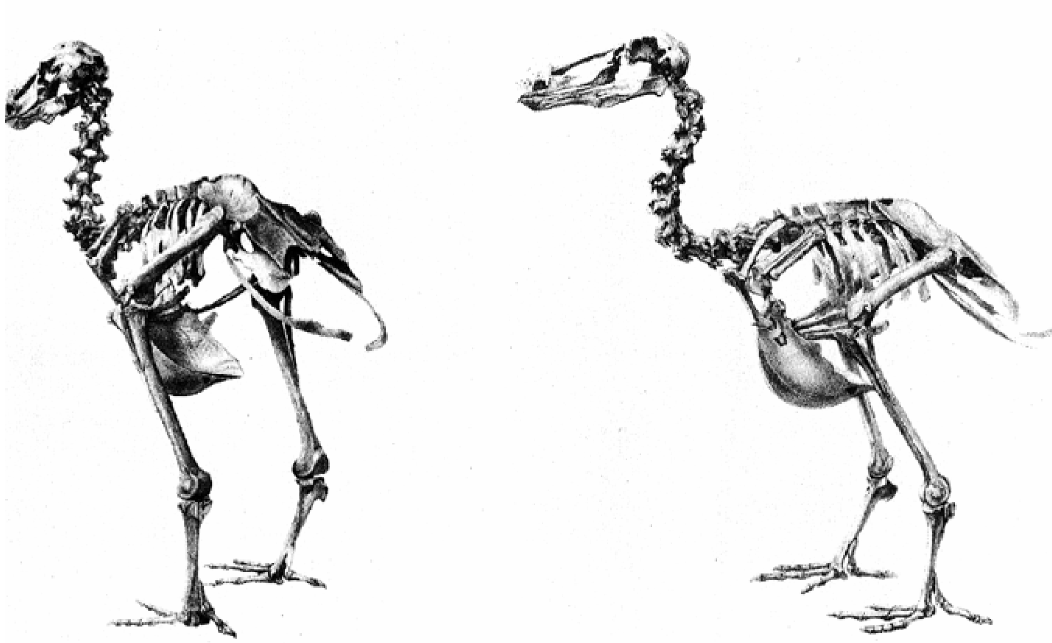


Figure 17.07 Two views of the skeleton of the Dodo, from a study by Richard Owen (R. Owen 1971. Notes on the articulated skeleton of the Dodo in the British Museum. Transactions of the Zoological Society of London, 7: 513-525.)

The extinction of the Dodo went unnoticed at first, and the bird was quickly lost from human recollection when the Dutch evacuated the island in 1712. The French later occupied the island, but there was no one left alive on Mauritius who knew of the Dodo. Years would pass before European naturalists, investigating reports of 'mythical' birds, recovered physical evidence verifying that the Dodo had indeed existed. In 1740, naturalists visiting the Mascarenes conducted an intense search for the Dodo, but no trace was found. Specimens eventually came into the possession of European naturalists (fig. 17.07 - 17.09). In 1758 Linnaeus named the species *Raphus cucullatus,* although he probably did not realize that the Dodo was extinct. Repeated attempts to locate a living Dodo on Mauritius failed, and by the mid-18th century, it was all too evident that the bird was gone.

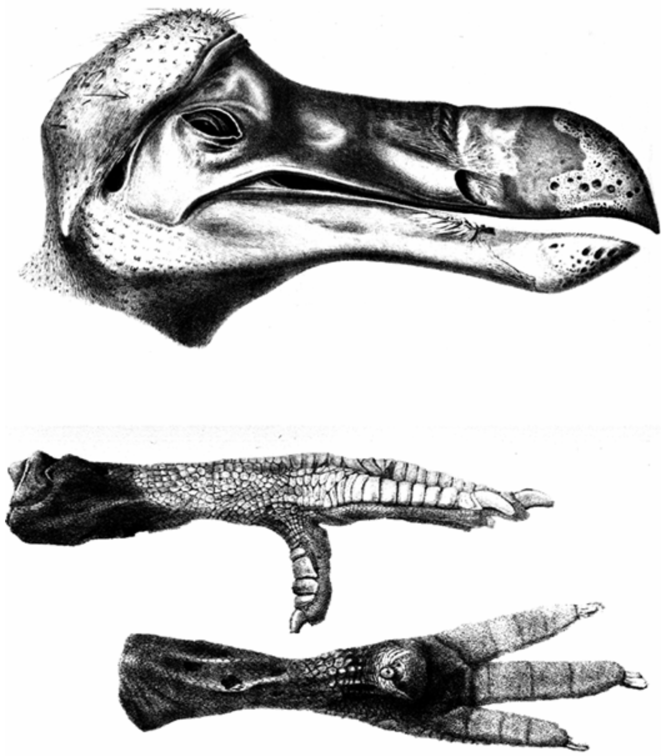


Figure 17.09 The head and foot of a Dodo specimen now in the British Museum (Natural History). (From: H.E. Strickland and A. G. Melville, 1848. The Dodo and its Kindred. London).

Once this was realized and the timing of events reconstructed, the culprits were obvious. In 1644, while the Dodo was still alive, a resident observed that "Here [in Mauritius] are Hogs of the China kind. These beasts do a great deal of damage to the inhabitants, by devouring all the young animals they can catch."[17] As Strickland was able to reconstruct, in the few short years following Dutch colonization, "This unfortunate and defenseless bird was slaughtered by the hundred by the sailors who often for months lived on its flesh, but also often killed it for pure mischief, while finally the work of extermination was completed by the pigs, goats, and monkeys, introduced into the islands." The effects of domestic mammals may have exceeded the casualties inflicted directly by the colonists and sailors, who wrote that the birds were not especially tasty. The advent of domesticated animals proved more than the large flightless bird could withstand. The last reliable sighting[18] of a Dodo was in 1662. Since then, two-thirds of the other endemic birds of Mauritius have also disappeared.

Georges Cuvier had shown decades earlier that species once living in the distant geologic past had become extinct. By Richard Owen's day, thanks largely to Owen himself, it was established that species now alive could become extinct as well. And by that time, scientists were already pointing a finger at human culprits in the Holocene island extinction. In a textbook on paleontology published in 1860, Owen described the phenomenon of extinction this way:

> "That species, or forms so recognized by their distinctive characters and the power of propagating them, have ceased to exist, and have successively passed away, is a fact no longer questioned. That they have been exterminated by exceptional cataclysmic changes of the earth's surface has not been proved. That their limitations in time, in some instances or in some measure, may be due to constitutional changes accumulating by slow degrees in the long course of generations, is possible. But all hitherto observed causes of extirpation point either to continuous slowly operating geological changes, or to no greater sudden cause than the, so to speak, spectral appearance of mankind on a limited tract of land not before inhabited."[19]

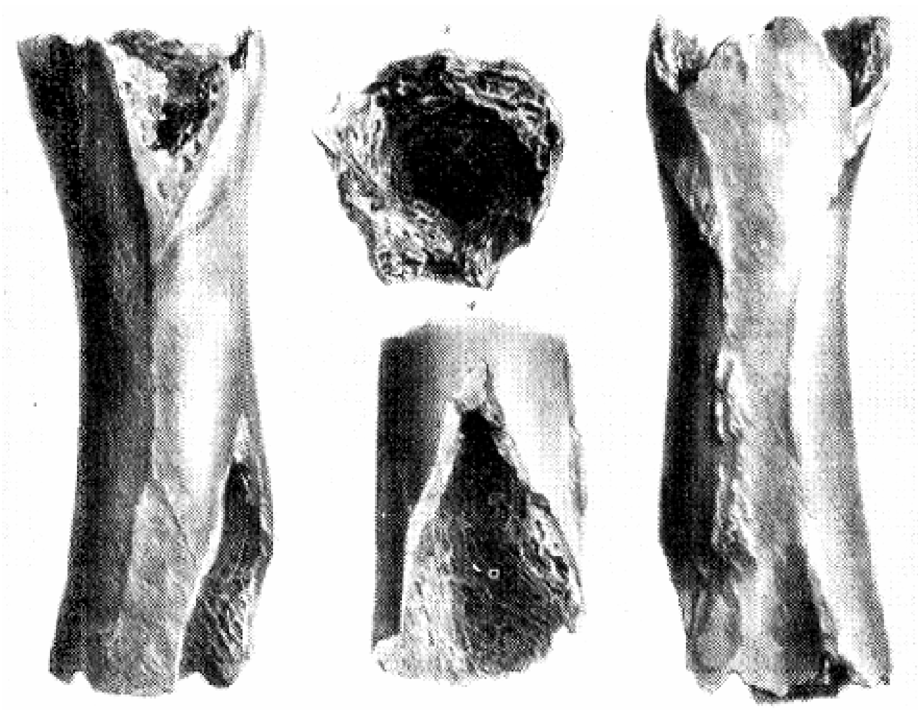


Figure 17.10 The fragment of a thigh bone from which Richard Owen first deduced that large ostrich-like birds, now extinct, once lived in New Zealand. (From R. Owen 1842. Notice of a fragment of a fragment of the femur of a gigantic bird from New Zealand. Transactions of the Zoological Society of London 3, 29-33.)

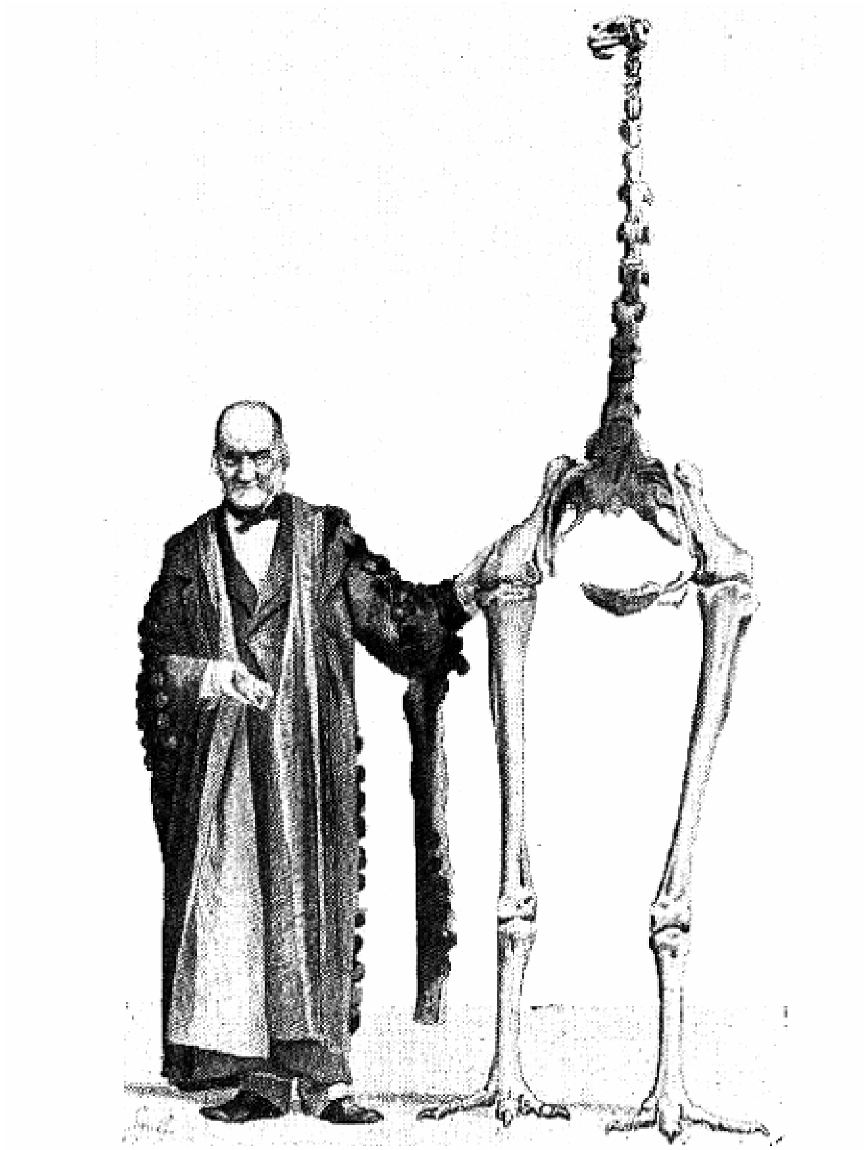


Figure 17.11 Richard Owen, standing 6'1" tall, next to the skeleton of *Dinornis*, one of largest moas. In his right hand, Owen holds the first fragmentary thigh bone that indicated the presence of extinct moas in New Zealand. (From: R. Owen, 1879. Memoirs on the extinct wingless birds of New Zealand, with an appendix on those of England, Australia, Newfoundland, Mauritius and Rodriguez, 2 volumes, London.)

From Owen's day to the present, both climate and human predation have been implicated as Pleistocene killing mechanisms. Numerous Pleistocene archeological sites leave no doubt that humans preyed on some now-extinct species. Although it is hard to overestimate the ingenuity and persistence with which humans have pursued other species into oblivion, it remains doubtful that human actions account for all the losses in the first pulse of extinction, owing to small human populations and primitive technology.

But during the second pulse of extinction, in the Holocene, a huge and ominous record of evidence linking humans to catastrophic loss of bird species has accumulated in different parts of the world. One estimate suggests that, on average, one species became extinct every 83 years in the early days of the Holocene[20]. The rate of loss increased so that by the time the Dodo died out, one species became extinct every four years, on average. At least 92 species of birds have become extinct since the Dodo, and the toll for this interval will probably rise as zooarcheologists study the remains of human habitation in Holocene sediments. The most recent studies of threatened and endangered birds suggest that by the end of this century, one species will become extinct every six months. Although human history did not begin this way, what E. O. Wilson calls a “tragic symmetry” arose in the Holocene, between the growth of human populations and the loss of biodiversity. Dinosaurs were especially hard-hit.

Owen’s First Discovery of Extinct Dinosaurs

In 1839, three before publishing his first paper on Dinosauria, Owen reported that giant birds similar to the Ostrich and Emu once lived on New Zealand. Earlier tales had been told of gigantic birds that might still survive in remote areas never trodden by man. Traditions among the elder natives of Atuas held that birds covered with ‘hair’ had waylaid forest travelers, overpowering them before killing and devouring them. But no such birds had ever been seen there by Europeans.

Owen produced the first meager evidence that this wasn’t just a myth. It consisted of only the broken shaft of a thigh bone (fig. 17.10). But with this fragment, Owen performed a feat of scientific deduction that astonished the world and catapulted him into the limelight. He wrote, “So far as my skill in interpreting an osseous fragment may be credited, I am willing to risk the reputation for it on the statement that there has existed, if there does not now exist, in New Zealand, a struthious bird nearly, if not quite, equal in size to the Ostrich, belonging to a heavier and more sluggish species.”[21] From a mere scrap of bone, he reconstructed the whole animal, although he was roundly criticized by other scientists who found such a leap of faith outrageous.

The bone had been brought for sale at a cost of 39 guineas to the College of Royal Surgeons, where Owen's career began. The College's museum committee declined to buy the specimen despite Owen's pleas, but Owen persuaded a donor to purchase it for another natural history collection, so that it could be properly studied and published upon. In a paper that had met strong editorial resistance, announced the discovery of a giant extinct New Zealand bird[22]. His critics demanded more substantial proof.

Recounting the story forty years later, Owen had 100 extra copies of his article "distributed in every quarter of the islands of New Zealand where attention to such evidences was likely to be attracted."[23] In 1843, he received two shipments of bones in response. Pictured first in his imagination, Owen finally saw the bones whose existence he had predicted. They became the type specimen of *Dinornis struthoides*, and Owen launched a series of papers on the extinct birds of New Zealand. As additional specimens arrived, he described more than a dozen species of extinct moas. Many years later, having risen to the Directorship of the British Museum (Natural History), Owen obtained the original scrap of moa bone for the national collections (fig. 17.11).

Even in 1843, New Zealand was largely unexplored by competent naturalists. It took several years to determine that all the moas were in fact extinct. As the European population there grew, it became impossible to deny that they were gone. But evidently, they hadn't been gone long. In 1878 a dried head with neck, legs, and skin with ligaments and feathers attached was found in a cave (fig. 17.12). These were purchased by Owen for the British Museum and became the type specimens of his new species *Megalapteryx didinus*. The feathers are described as very hair-like, some grayish-brown, some with a rust tinge and others tipped in white. Several other pieces of mummified carcasses have been found since then.

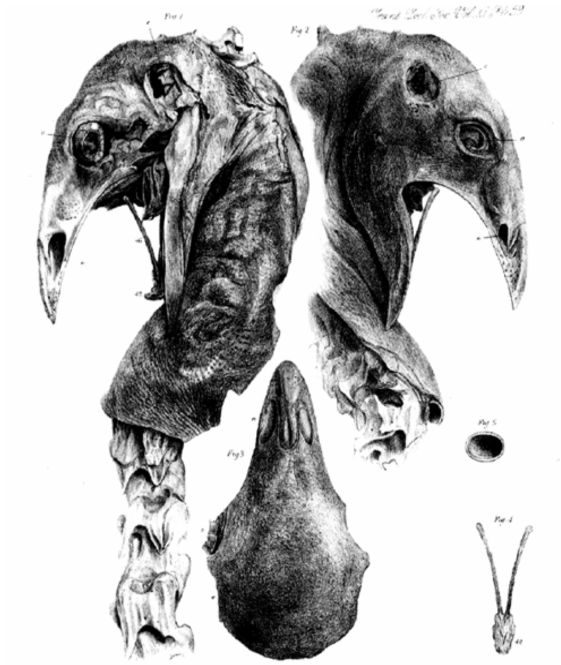


Figure 17.12 The mummified head of a moa. This specimen still exists in the Natural History Museum, London. (From: R. Owen, 1879. Memoirs on the extinct wingless birds of New Zealand, with an appendix on those of England, Australia, Newfoundland, Mauritius and Rodriguez, 2 volumes, London.)

Fossil moas as old as the Miocene or Pliocene have now been recovered, but the tectonic history of New Zealand suggests that their flightless ancestors may have rafted away on the island during the Cretaceous. Long before the arrival of humans, moas had adaptively radiated on the islands of New Zealand. It has been argued that some species became extinct as the climate changed from being drier to much more rainy at the end of the Pleistocene. But there is much evidence that human hunters encountered the last of New Zealand's moas during the Holocene.

Before human habitation, there were approximately thirteen moa species, ranging from the size of a turkey to the tallest bird known--a towering twelve feet (3.6 meters)[24]. This is far more diversified than any living ratite lineage. The adaptive radiation of moas covered both islands of New Zealand, and the birds were abundant when the Maoris first landed on the North Island about 1000 years ago (fig. 17.13).

The moa's flesh may be what convinced the Maoris to stay. Recent dating methods and finely calibrated chronological studies of the sites have enabled us to reconstruct a detailed crime scene[25]. At numerous archaeological sites, moa bones have been found with Maori kitchen refuse, along with bones of domestic dogs that were brought from their home to the north in Polynesia. Fires set by the Maoris in the grasses and brush near the beaches destroyed moa breeding colonies, and other evidence suggests heavy human predation on these birds. The Maoris hunted the moas for food and killed them in great numbers, leaving their butchered bones scattered all over New Zealand. The killing of large numbers of birds began around 1100 A. D., and over the next two hundred years, the diet of Maoris must have consisted predominantly of moas. The hunting sites slowly spread to the South Island, where the last were extirpated. Seeds, twigs, and other stomach contents preserved in one moa carcass provided a radiocarbon date of about 1330 A.D. for the moa's last meal. How much later they survived is unclear. The colonization of New Zealand began in the decades following the visit by Captain James Cook in 1769. There are reports by Europeans claiming to have seen live moas, but these are unverified. There are also some claims of butcher marks on moa bones that appear to have been made with iron blades. Although hard to substantiate, this could represent evidence that Europeans were among the last humans to dine on moas.

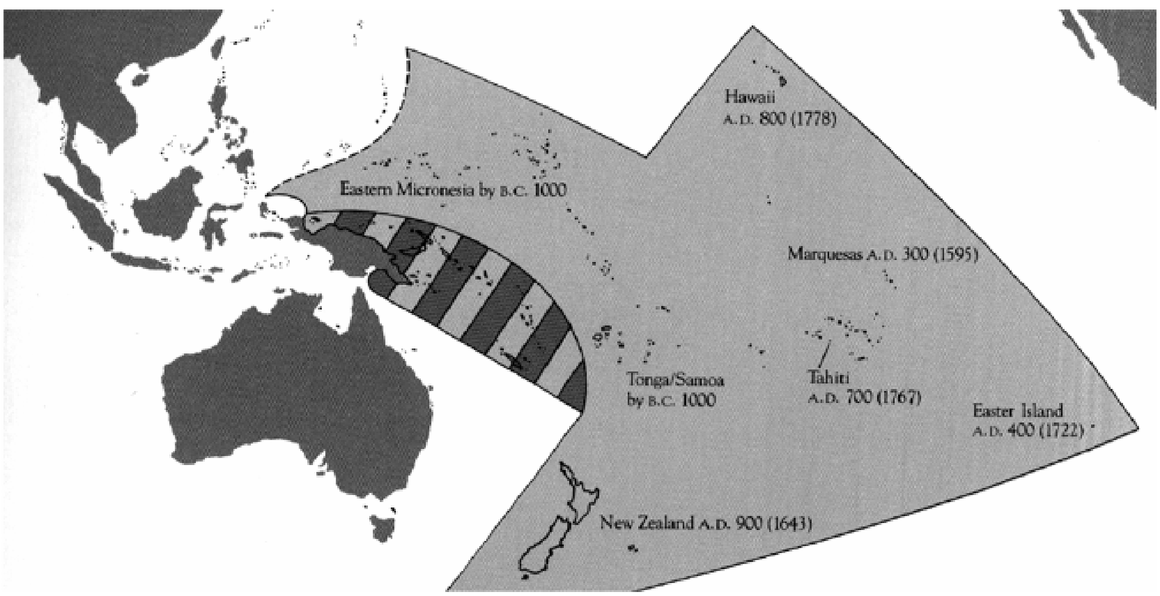


Figure 17.13 The dates of discovery of the western Pacific islands by Polynesians and Europeans. Dates of discovery for the latter are in parentheses. (From W. H. Menard 1986. Islands. Scientific American Library, New York).

Maori traditions recall the moa as resembling a cassowary, with a brightly colored neck and a comb on its head. The skulls of at least three different moa species preserve evidence of a crest, which was probably a sexual characteristic like the crests and wattles in their living relatives. Also recalled is that the female incubated the nest while the male supplied her with food[26].

In 1844, Robert Fitzroy, former Captain of Darwin's famous voyage on the *Beagle* and then governor of New Zealand, interviewed an elder Maori named Kawane Paipai. He claimed to have taken part in a moa hunt. Fitzroy's account was later published by extinct bird chronicler Errol Fuller: "He remembered the birds being hounded, encircled and then speared to death, sometimes with weapons designed to snap easily once the body was stuck. Trapped moas defended themselves vigorously with terrible blows from their feet but while administering these, the monstrous bipeds were forced temporarily to support their weight on one leg. A party of hunters would launch a frontal attack - a feint - while another crept behind waiting for the moment when the Moa raised a leg; then the party attacking from the rear would strike, knocking away the supporting leg. Once down, the victim was either dispatched immediately or such grievous wounds were inflicted that the final outcome was no more in doubt."[27]

Other Island Extinctions

The combination of human overkill and environmental destruction by rats, cats, pigs, dogs, and goats devastated native birds on small islands. For ground nesting species, the effects of introduced mammals have been especially devastating. An additional source of pressure is deforestation. Declining diversity in island floras depleted certain food supplies and nesting territories, further reducing the diversity of island bird faunas. Nowhere has this damage been so severe as on the islands of the tropical Pacific, where high levels of avian diversity evolved over the long course of their Cenozoic diversification.

The tragic history of Pacific island birds was recently investigated by David Steadman (Florida Museum of Natural History), Storrs Olson (US National Museum of Natural History), and a group of collaborators. Steadman presented a chilling summary of their findings: "On tropical Pacific islands, a human-caused 'biodiversity crisis' began thousands of years ago and has nearly run its course."[28] The loss of bird life may have totaled between 2000 and 8000 species, representing at least a 20% decline in the number of bird species globally.

The islands of Melanesia were first occupied by humans 30,000 years ago. The islands of western Polynesia and Micronesia remained uninhabited until 3500 years ago. Most islands of the Pacific and Indian Oceans were inhabited at least 1000 years ago. Steadman describes the distinct signatures of human disturbance in the Holocene sediments deposited on and around the islands, including the accumulation of more clays as soils unbounded by vegetation washed off the island. Charcoal also appears in the sediments in abundance. Pollen from forest trees gave way to fern pollen, signaling the beginnings of deforestation. On the island of Mangaia, Steadman found this signature in sediments pre-dating the earliest known cultural sites by 1000 years.

Upon their arrival, the colonists began clearing forests, cultivating crops, and raising domesticated animals. The indigenous forests and grasslands with their many species were cleared and burned to make way for a few domestic crops, further disrupting the local ecology. Seabird colonies vanished from many islands, and numerous species became extinct. Some extinctions were due to human predation; others resulted from the loss of soil that removed all suitable breeding habitat for burrowing species, like the petrels. On some islands, including Ua Huka in the Marquesas, Steadman found evidence that breeding seabird species dropped from 22 to 4 during human occupation. On the whole, however, the landbirds suffered far more extensive losses.

Steadman reports that "Although the rate of extinction varied with ruggedness of terrain and size or performance of the prehistoric human population, we have no evidence that the process for prehistoric extinctions differed fundamentally from those that continue to deplete surviving species today. The differences are mainly technological (snares versus guns and stone adzes and fire versus chain saws and fire, for example)."[29]

On the Hawaiian Islands, 60 native bird species have become extinct since the arrival of Polynesians between 1500 and 2000 years ago. Roughly one-third of those remaining (20 to 25 species) disappeared in the two centuries following the arrival of Europeans, and two-thirds of the surviving species are now endangered. On these and other Pacific islands there is a consistent stratigraphic sequence in the lava tubes, sinkholes, stream and lake deposits that preserve extinct island animals. The oldest deposits contain fossils of only native species, including shorebirds and landbirds. The most common fossils are flightless rails, which had rapidly radiated as their ancestors flew from island to island and populated them with descendant species. Many islands hosted one or more endemic species. In higher and younger sediments, the bones of native species dwindle, and the bones of domestic animals predominate in association with kitchen refuse. Finally, rats and iron appear in the record, indicating the arrival of Europeans, with their greater killing power.

In the first half of this century, biologists thought that Pacific birds were well documented, but they had been unaware of the much higher levels of Holocene diversity. Current zooarcheological explorations of island prehistory are greatly extending our knowledge of organisms that had been prematurely considered to be well documented. Before discovering the great Holocene extinction of Pacific birds, biologists and biogeographers thought that today's distribution patterns for birds were natural. Now they are beginning to reinterpret the patterns in the recognition of human effects. Throughout the Pacific, landbirds suffered much higher species-level extinction, but the seabirds were also affected, and the modern patterns of global seabird distribution are unnatural. Steadman also points out that many ecologists continue to analyze these birds as if the modern ecosystems are natural. While some of the range losses for living species might be restored through conservation efforts, it is increasingly apparent that we are centuries too late to preserve any true reflection of the original Pacific avifaunas.

Funk

To understand the full effects of humans on island birds, and the complex interplay between human and natural factors in recent extinctions, we consider one last example: the Great Auk or Garefowl, that disappeared early in the 19th century. Auks are seabirds that resemble penguins, although they are allied with shorebirds like gulls. Auks have a large head, short tail and chunky body that is covered by a dense, waterproof, black and white plumage. They dive and swim for food, and all, save the Great Auk, can fly. They spend their entire lives in the sea and, unlike most island species, they seem to have wide geographic ranges. But once a year they congregate on islands to breed.

The Great Auk stood three feet tall with an ungainly upright stance on land (fig. 17.14). It occupied a niche in northern waters much like that of the penguins in the southern oceans. It hunted in coastal and open waters, mostly following schools of small fish. When swimming the Great Auks had penguin-like speed and dexterity. Their legs were short and powerful with a piston-like motion, and while swimming on the surface their large, webbed feet provided strong thrust. Underwater, they used their short, pointed wings to "fly" and steered with their feet as they pursued fish and other prey (fig. 17.15). The Great Auk was the largest species of auk known at any time in the Quaternary. It is said to have issued a croaking and a gurgling noise[30].

Although usually denizens of open water, Great Auks returned every Spring in enormous flocks to court and breed, probably on the same island where they hatched. They congregated in great numbers for about two months on remote rocky islands in the north Atlantic to enact their courtship rituals. Once the chicks were sea-worthy, they migrated north from their breeding grounds out to sea, where they spent the next nine or ten months.

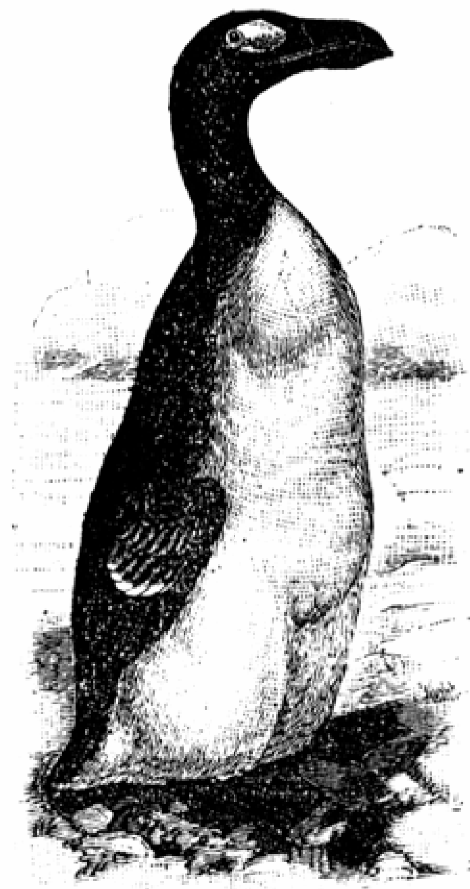


Figure 17.14 The Great Auk stood upright on land, on the rare occasions that it came ashore.

Like many other seabirds, the Great Auk bred only on islands, where their enormous breeding success was probably related to the absence of predatory mammals, birds, snakes, and lizards of the mainland, which prey so successfully on ground-nesting birds. Breeding colonies in the north Atlantic were known on St. Kilda Island of the Outer Hebrides and possibly on the Orkney Islands, Lundy Island, and the Isle of Man. The Great Auks also bred near Iceland's southern coast, on the rocky tips of volcanic islands that rise up from the mid-Atlantic ridge. In the western Atlantic, Great Auks bred on Penguin and Wadham Islands off the south coast of Newfoundland. Their greatest known breeding colony was on Funk Island north of St. Johns, Newfoundland[31, 32].

Figure 17.15 The Great Auk spent most of its life at sea. (From: J. Gould 1832-1837. Birds of Europe. 5 volumes, London.

In a textbook on paleontology published in 1860, Richard Owen alerted his audience to the dire status of this bird, based on the scanty reports to him at that time:

> "The Great Auk (*Alca impennis*, L.) seems to be rapidly verging to extinction. It has not been specially hunted down, like the dodo and dinornis [a moa], but by degrees has become more scarce. Some of the geological changes affecting circumstances favorable to the well-being of the *Alca impennis*, have been matters of observations. The last great auks, known with anything like certainty to have been seen living, were two which were taken in 1844 during a visit made to the high rock, called 'Eldey,' or Meelsoekten,' lying off Cape Reykianes, the S. W. point of Iceland. This is one of three principal rocky islets formerly existing in that direction, of which the one specially named for this rare bird 'Gierfugla Sker' sank to the level of the surface of the sea during a volcanic disturbance in or about the year 1830. Such

disappearances of the fit and favourable breeding-places of the *Alca impennis* must form an important element in its decline toward extinction. The numbers of the bones of *Alca impennis* on the shores of Iceland, Greenland and Denmark attest to the abundance of the bird in former times."[33]

When Owen wrote those words the Great Auk was already extinct. The breeding colony lost as Gierfugla Sker sank beneath the waves was probably the last of its kind. Owen didn't realize that the minor volcanic belch that precipitated the end of the species was simply the last in a series of catastrophes to hit the breeding colonies. Owen was also unaware that in fact the Great Auk *was* "specially hunted down."

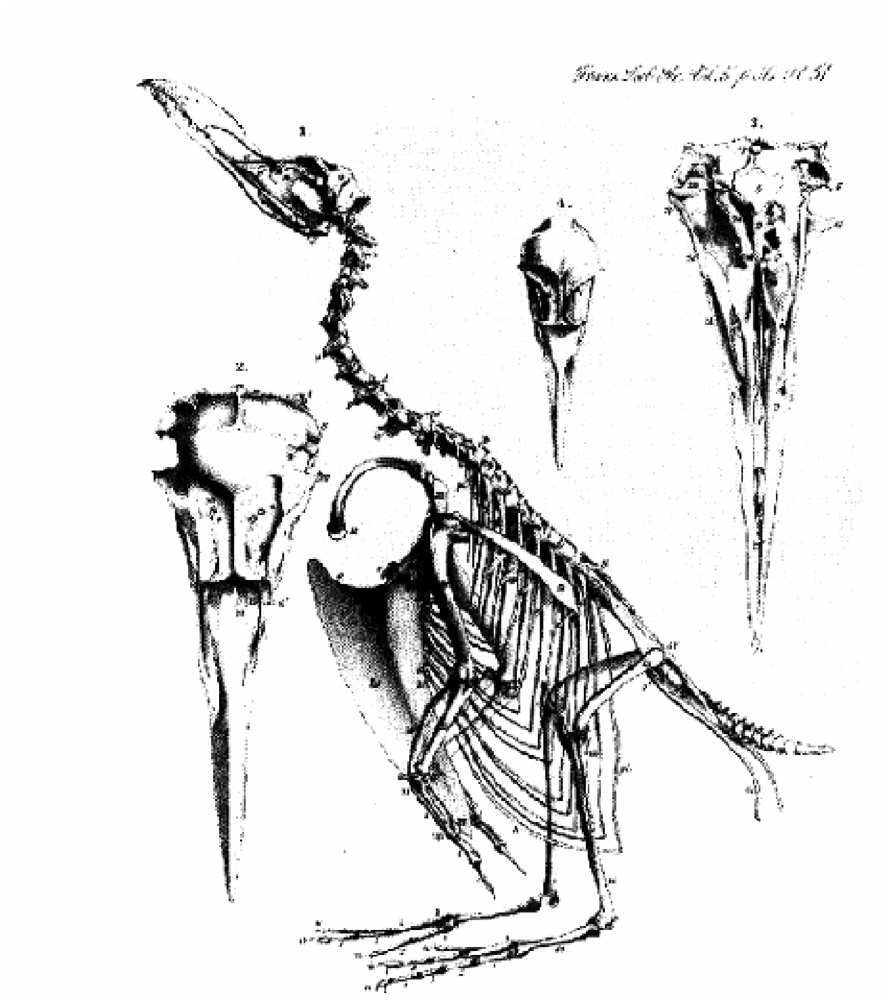


Figure 17.16 The skeleton of a Great Auk, from a study made following its extinction by Richard Owen (From: R. Owen, 1865. Description of the skeleton of a Great Auk or Garefowl. Transactions of the Zoological Society of London 7: 317-335.)

There is a long history of the Great Auk in the Quaternary record, and its bones are usually associated with human artifacts. Evidently, the Great Auk was hunted and eaten by humans for thousands of years before becoming extinct[34]. During the Pleistocene the Great Auk roamed the Mediterranean, where it has been found in fissure deposits at Gibraltar between 70,000 and 90,000 years old. Its bones are also found in 60,000-year- old sediments of southern Italy, in association with artifacts of the Aurignacian culture. The Great Auk reportedly appears in cave paintings of northern Spain, in addition to bones from sediments along the Spanish coast. But the Auk's southern limit retreated northwards as the Quaternary progressed.

The early Holocene record of the Great Auk is well represented in Scandinavia. A Swedish archaeological site contains Great Auk bones that are about 9000 years old. Additional records are found in 6500- year-old sites in Denmark, as well as sites of varying age in Norway and the northern British Isles. A British naturalist visiting the Orkney Islands in 1698 observed live birds and described the Great Auk as being the "stateliest as well as the largest, of all the Fowls here, and above the size of a Solan Goose, of a Black Colour, Red about the Eyes, a large White Spot under each Eye... stands stately, his whole body erected, his wings short; he Flyeth not at all."[35] He also described the egg, which was "twice as big as that of a Solan Goose, and is variously spotted black, green and dark... appears on the first of May and goes away about the middle of June." At most of the historic and prehistoric sites, the bones occur with kitchen refuse and tool marks sometimes scar the bones, providing ample evidence that Great Auks were eaten. But their bones occur in only small numbers compared to other prey species.

By the beginning of the 19th century, the Great Auk had become very rare. Two birds were captured alive in 1812 near the island of Papa Westera in the Orkneys and kept alive for several years in captivity. The skin of one of these is now in the British Museum (Natural History) collections, where it eventually came under the scrutiny of Richard Owen. The last specimen taken in Europe was on the Waterford coast of Ireland in 1834. The last report of a Great Auk in Europe was 1835 at Lundy - the Isle of Puffins. A resident reported seeing two large birds that stood upright-- 'up bold like'-- these might have been Great Auks[36].

Along eastern North America, bones of the Great Auk have been found in middens of American Indians from the Bay of Fundy to Cape Cod. The southern-most record is an American Indian pre-Columbian shell mound in Florida. In New England, 17th century archaeological sites with Great Auk bones contain metal implements of Europeans. British navigators reported that it lived from Cape Cod northwards 300 years ago, but exactly when they disappeared from American waters is uncertain[37].

Despite their wide range across the north Atlantic, their breeding was confined to a small number of sites. At sea the birds were excellent swimmers, reportedly staying submerged as long as a seal. They were extremely evasive, which may account for their rarity in coastal archeological sites. On land, however, the Great Auks were equally awkward, making easy prey for humans and dogs. They were especially vulnerable as they congregated to breed on tiny oceanic islands. Sailors and fishermen took advantage of this and caught large numbers to be salted for food or to bait hooks for the great predatory fish of the north Atlantic. In 1534 Jacques Cartier visited Bird Rocks in the Gulf of St. Lawrence, writing, “These islands were as full of birds as any field or meadow is of grasse, which there do make their nestes.” They killed “above a thousand” and “we put into our boates so many of them as we pleased, for in lesse than one houre we might have filled thirtie such boats of them.”[38]

The north Atlantic sailing routes established by European navigators brought humans to the breeding colonies of the Great Auk with lethal regularity and persistence. One by one, the great breeding colonies were decimated by sailors exploiting the rich waters of the north Atlantic. Hundreds of thousands of birds congregated in one of the largest breeding colonies, on Funk Island. It was among the last to go, and its survival may have resulted from its remote location and inhospitable terrain for landing. But by the late 18th century a market had grown in Europe and America for pillows made of Great Auk feathers, driving hunters to land on Funk Island and harvest a huge cache.

The hunters used a hut built by an earlier sealing crew as their shelter during the Auk’s breeding season. They also built several holding pens. As the wary birds came to shore, they were surprised and herded into the pens. With their powerful bills the auks bit their captors with the tenacity of dogs, but in the end, the flightless birds had no real chance. In the pens, they were clubbed and tossed into cauldrons of boiling water. Parboiling loosened the feathers, rendering them easier to pluck. The fat of the birds was rich in flammable oils that were used to stoke the fires and keep the cauldrons boiling for more birds. The stripped carcasses were tossed aside in great heaps. Before the end of the 18th century the Great Auk had been extirpated on Funk Island.

One final incentive for human predation was the growing value of Great Auk eggs and skins, as they became scarce. The declining Dodo had sparked a collecting fad for skins and eggs among Europe's wealthiest amateur naturalists. Errol Fuller records that 80 skins and 75 eggs of the Great Auk sold for hundreds of pounds at Steven's Auction Rooms in London's Covent Garden during the 19th century[39]. Many late 18th century seamen knew they could fetch a high price for a Great Auk, its skin or its egg. Thus, the remaining adults and their eggs were hunted down, and the few birds that had survived the cataclysmic loss of their breeding grounds finally disappeared.

The last two birds ever seen were spotted by sailors commissioned to find Great Auk specimens for private collectors. They scoured traditional breeding grounds on small islets off the southwest point of Iceland, where the submerged Gierfugla Sker had been specially named for the bird. Landing on Eldey Rock, on the morning of June 3, 1844, they saw among a mass of other seabirds a pair of Great Auks. The sailors immediately set upon the birds, which waddled away as fast as they could. But the birds were clubbed down, and it was rumored that an egg being incubated by the female was crushed underfoot in the excitement. Their carcasses were sold to a collector in Reykjavik. There was one, last, unconfirmed sighting of a Great Auk at the Grand Banks of Newfoundland in 1852, but that was it[40]. The Great Auk had passed from the realm of ornithologists to the realm of archeologists and paleontologists.

In 1864, more than twenty years after the last live specimen was collected, Richard Owen published a monograph on the skeleton of the Great Auk[41]. Remains of the Great Auk were only very poorly represented in natural history museum collections at the time it became extinct. As the basis for much of his description, Owen had to settle for a specimen (fig. 17.16) found by guano miners on some north Atlantic island, which came to him "dried, flattened featherless, and mummified." At the end of the 19th century, naturalists returned to Funk Island to collect a more extensive sample of bones. In a Report of the US National Museum and Smithsonian Institutions, Frederick Lucas described his landing on Funk, July 22, 1887. "Here the Auk bred in peace for ages, undisturbed by man.... Here to day the bones of myriads of Garefowl lie buried in the shallow soil formed above their moldered bodies, and here, in this vast Alcine cemetery, are thickly scattered slabs of weathered granite, like so many crumbling tombstones marking the resting places of the departed Auks."[42]

Lucas described the stratigraphy of the island as having has two distinct layers. The lower and oldest lies directly on granite and weathered pebbles. Formed during the occupancy of the Great Auk, it contains many eggshell fragments, as well as charcoal that had leached down from the overlying layer. "The upper layer of the soil, also from 3 inches to one foot thick, has formed since the extermination of the Auk, principally by the growth and decay of vegetation nourished by their bodies. In fact it is possible, from the character of the plant growth above, to tell something of the probable abundance of Auk remains below; the thickness of the one indicating corresponding plenty of the other."[43]

Excavations in the region of the hut yielded the bones of "thousands of birds mixed together in inextricable confusion." The crania of some birds preserved the marks of cuts and blows, verifying local traditions about how the birds met their end.

The Great Auk was not the only bird to be extirpated on Funk Island. The Gannet, the Puffin, as well as the Common and Arctic Terns also bred there in great abundance in the early 19th century, when Funk Island was described as "a mountain of birds" by naturalists visiting the island in 1844. A few years later the Gannet and Common Tern were gone, and all species of birds breeding on Funk Island, with the exception of the Puffin, were drastically diminished by egg collectors. Puffins found security in their burrows and "to them, at least, the extermination of the Great Auk has provided a decided advantage by providing soil in which to dig their habitations."[44] Lucas and subsequent collectors prospected at the openings of Puffin burrows for the bones of the Great Auk that were unearthed by the burrowing Puffins.

A half-century after the Great Auk disappeared, Frederick Lucas wrote in a Smithsonian Report: "The circumstances that the bird, with suicidal persistence, resorted to the a few chosen breeding places, and that it was there found in great numbers, rendered its destruction not only possible but probable, and when the white man first set foot in America, the extinction of the Great Auk became merely a matter of time."[45] If these words seem overly dramatic, subsequent research on island birds only reinforces the message. A century later David Steadman summed up the second pulse of

Chapter 17, The Mistaken Extinction, by Lowell Dingus and Timothy Rowe, New York, W. H. Freeman, 1998.

Quaternary extinction: “We expect extinction after people arrive on an island. Survival is the exception.”[46]

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