

TEN THOUSAND BIRDS



ORNITHOLOGY
SINCE DARWIN

TIM BIRKHEAD
JO WIMPENNY
BOB MONTGOMERIE

Ten Thousand Birds

TEN
THOUSAND
BIRDS

Ornithology since Darwin

TIM BIRKHEAD JO WIMPENNY BOB MONTGOMERIE

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PREFACE

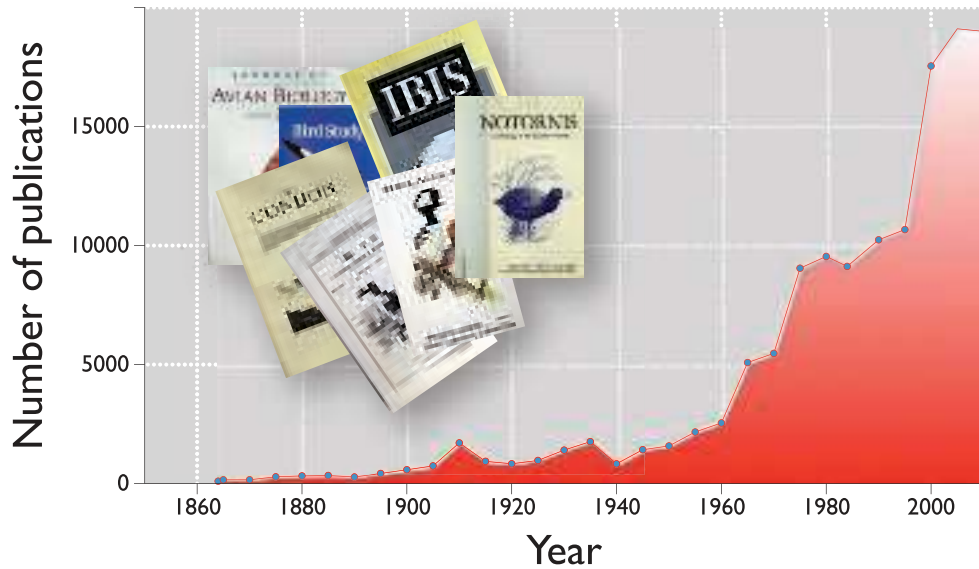
The body of a bird is not just a prodigiously complicated machine, with its trillions of cells—each one in itself a marvel of miniaturized complexity—all conspiring together to make muscle or bone, kidney or brain. Its interlocking parts also conspire to make it good for something—in the case of most birds, good for flying. An aero-engineer is struck dumb with admiration for the bird as flying machine: its feathered flight-surfaces and ailerons sensitively adjusted in real time by the on-board computer which is the brain; the breast muscles, which are the engines, the ligaments, tendons and lightweight bony struts all exactly suited to the task. And the whole machine is immensely improbable in the sense that, if you randomly shook up the parts over and over again, never in a million years would they fall into the right shape to fly like a swallow, soar like a vulture, or ride the oceanic up-draughts like a wandering albatross.

—RICHARD DAWKINS, IN *THE WASHINGTON POST* ON 23
AUGUST 2011, IN RESPONSE TO TEXAS GOVERNOR PERRY'S
CLAIM THAT “EVOLUTION IS JUST A THEORY”

THERE ARE CURRENTLY VERY CLOSE TO TEN thousand species of birds in the world, both beautiful and improbable, and they have contributed more to the study of zoology than almost any other group of animals (Konishi et al. 1989). The reasons are obvious: birds are diurnal, they are often easily observed and studied, and we like them. As a result, the study of birds goes back at least as far as ancient Greece, although it is generally recognized that scientific ornithology began in the mid-1600s with the publication of John Ray's *Ornithology of Francis Willughby* (Ray 1676). Since then, the study of birds has continued apace, with by far the greatest increase in ornithological knowledge occurring since the middle of the twentieth century. We estimate that there have been no fewer than 380,000 ornithological publications since Darwin published *The Origin of Species* in 1859.¹ The

temporal pattern reflects the change in numbers of ornithologists: increasing slowly between 1860 and 1960, but then more rapidly as more academic positions for zoologists became available in the 1960s. In 2011 there were as many papers on birds published as there had been during the entire period between Darwin's *Origin* and 1955.

Several “histories of ornithology” have been written (appendix 1)—especially in the last few years, suggesting that the subject has come of age. Few of these, however, have included the twentieth century, possibly because of the sheer volume of information. Yet residing within this enormous mass of literature is a small number of wonderful, groundbreaking discoveries, and it is these that form the basis for this book. This isn't to say that most of what has been done is of little value but rather that, as in most areas of



The number of scientific publications about birds published each year since 1850; data from the Zoological Record and Google Scholar. Inset shows some covers of ornithological journals.

science, the few individuals that make major breakthroughs have relied consciously or unconsciously on the substantial foundations provided by generations of ornithological foot soldiers.

Science in its broadest sense has a long history, but modern science began only in the seventeenth century, with the scientific revolution, as logic and experimentation gradually swept away the folklore, alchemy, and old wives' tales that had persisted since the time of Aristotle. As Jürgen Haffer (2007a) points out, the renaissance in science in the mid-1600s—and the work of Francis Willughby and John Ray in particular—provided not only a firm scientific foundation for ornithology but initiated what were to become the two major strands in the study of birds: systematics and field ornithology.

The first of these strands, beginning with the naming and description of all known

bird species—which at the time was thought to number about five hundred—formed the basis for Ray's *Ornithology of Francis Willughby* (1676, 1678), so named because Willughby, Ray's protégé and patron, died at just thirty-six years of age, before their book was completed. Ray's second, field-based approach was presented later in his book *The Wisdom of God*, published in 1691, long after Willughby's death. Here Ray introduced the concept of physicotheology (later known as “natural theology”), which used the exquisite fit between an animal's design and its lifestyle as evidence of God's wisdom. In modern terms, *The Wisdom of God* is about adaptation, which for Ray was mediated through God. The book caused a revolution both in religious thinking and in natural history. With extraordinary prescience Ray asked, for example, why some birds produce a clutch of one egg, while

others produce clutches of ten or more; why some birds breed early in the year, while others breed later. Not only did Ray pose important biological questions, he anticipated their answers with uncanny insight and common sense (Birkhead 2008).

Ray's ingenious ideas were appreciated by others, most notably William Paley, whose *Natural Theology* (1802) became essential reading for nineteenth-century Cambridge undergraduates intending to enter the church—as was Darwin before he went off on his *Beagle* voyage in December 1831. Paley's rich examples captivated Darwin, who went on to call them adaptations. Paley is best known now—thanks to Richard Dawkins's *Blind Watchmaker* (1986)—for his parable of the watch. Imagine finding a watch, he said: its intricate design tells you that it must have a designer. Now look at nature: the exquisite fit between an organism and its environment tells you that it too must have had its designer, and that designer could only have been God. Paley's writings shaped Darwin's thinking, not about God but about adaptation, and as he later said, “The old argument from design in Nature [natural theology], as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered.”²

Despite the genius of Ray's double-barreled approach, the next two hundred years of ornithology were dominated by systematics: the naming and describing of species, as well as determining their position in God's grand scheme of things. Only after Darwin seeded the idea that the behavior and ecology of animals might have evolved through natural selection did Ray's second idea begin to take hold. But it was a slow change. Until the 1920s, ornithology, like

the rest of zoology, consisted almost exclusively of museum work—the study of skins, skeletons, and eggs—and the museum ornithologist's idea of “fieldwork” was the killing and collecting of specimens for study. In the late nineteenth century, Elliott Coues (1896) identified the shotgun as the ornithologist's most important piece of field equipment. His contemporaries—like Edmund Selous, who opposed museum-based ornithology and attempted to promote the study of the living bird—were castigated. As we'll see, genuine field ornithology was not reunited with museum ornithology until the period from 1920 to 1940—a union that pulled ornithology from the sidelines into mainstream biology (Birkhead 2008). This revolution, which forms an important part of the current book, transformed zoology and fueled the extraordinary explosion in ornithological knowledge.

We take Darwin as our starting point because “nothing in biology makes sense, except in the light of evolution,”³ and because Darwin made so many perceptive observations and comments on birds that inspired a number of pioneers to test his ideas. In constructing our overview of ornithology since Darwin, how did we decide what to include—and what to omit? It is quite clearly impossible to summarize every relevant person or idea in a book of this (already large) size. Instead, we decided to focus on a selection of the major contributions of ornithology to general science—that is, on areas where the endeavors of ornithologists have influenced the course of scientific progress. In doing so, we had to identify what we considered the most exciting and interesting findings in ornithology and how those subjects and the people that worked on them helped to

transform biology. Deciding how best to do this occupied us for several months.

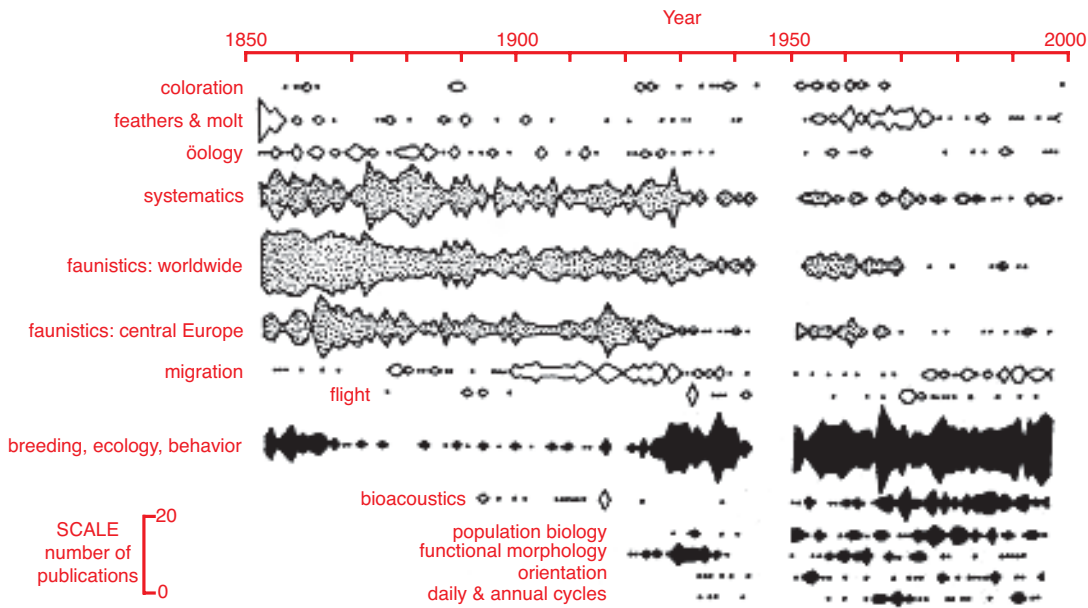
To help us decide on the book's scope we did two things. First, we made a database of 325 ornithologists who were prominent since the 1960s, and for each of these we created a citation report from the Web of Science (citation reports were not available for earlier ornithologists). We ranked these reports according to the total number of times that each ornithologist's work had been cited in scientific publications (excluding self-citations). Second, we conducted a survey of thirty-one senior ornithologists—from a variety of countries and with diverse research interests—asking them to name both the most influential ornithologists and books written by ornithologists since Darwin.⁴ Why books, you might ask? Obviously, there are many fewer books than scientific papers, but books provide authors with the intellectual freedom to express their ideas in a way that is usually impossible in scientific, peer-reviewed papers. Furthermore, while today's researchers concentrate on publishing research papers, this was less often the case in the middle of the twentieth century; thus, relying solely on citation reports based on scientific papers biased our survey in favor of "modern" researchers. Books also have the potential to make authors an "authority" because they provide a synthesis of old and new ideas and, deliberately or inadvertently, often point the way forward.

Of the ornithologists considered to be the most influential, David Lack was the clear leader (30 votes), followed by Ernst Mayr (23), Niko Tinbergen (21), Robert MacArthur (11), Peter Grant (11), Nick Davies (11), Erwin Stresemann (11), Charles Sibley (11), Konrad Lorenz (9), and Donald Farner (8).

Of the books considered to be most influential, David Lack's again came out on top, taking the first three places: *Ecological Adaptations for Breeding in Birds* (1968), *The Natural Regulation of Animal Numbers* (1954), and *Population Studies of Birds* (1966). In chronological order, the others in the top-ten list of books were *Systematics and the Origin of Species* (Mayr 1942), *The Study of Instinct* (Tinbergen 1951), *The Herring Gull's World* (Tinbergen 1953b), *Animal Species and Evolution* (Mayr 1963), *The Theory of Island Biogeography* (MacArthur and Wilson 1967), *Ecology and Evolution of Darwin's Finches* (Grant 1986), and *Sperm Competition in Birds* (Birkhead and Møller 1992).

We initially considered the straightforward option of writing a chapter on each of our top ten ornithologists, or of adopting a chronological approach, recounting the major ornithological discoveries by each of those individuals decade by decade. Both of these alternatives seemed a bit tedious, so we decided instead that a topic-based series of chapters was more interesting for both us and our readers, and more meaningful in a broader biological sense. Using the achievements of our top ten ornithologists and books as a guide—but also consulting colleagues and relying upon our own experiences as professional ornithologists—we identified eleven topics that encompass much of ornithology since Darwin.

We had several criteria for deciding what kinds of discoveries to include. Discoveries had either to have broad biological relevance, to change the course of ornithology, to make an important point, or simply to appeal to our interests. Our account comprises what we consider to be the major advances in scientific ornithology over the past 150



The number of publications per year in different areas of ornithology from 1850 to 2000 published in *Journal für Ornithologie*.

years: a broad introduction that includes an overview of the main discoveries and those who made them, as well as myriad other research programs that extended, refined, and built upon those major advances. We expect that most knowledgeable readers will agree with the major discoveries that we cover, but the others that we describe here are personal choices that we thought were both interesting and informative about the voyage of discovery, the people involved, or the scientific findings themselves. In a way, then, what we have written is a set of essays on key ornithological topics whose development we explore from Darwin to today. Darwin was more than an ornithologist—he was too broad for that—but he had good credentials as an ornithologist because he raised birds and he wrote extensively about their biology. Many of today’s ideas have their genesis in his writings.

It is inevitable that some readers will consider our account biased—and it is, for bias is unavoidable. An obvious bias is that much of the ornithological knowledge acquired since Darwin has come from Europe and North America, far less from other parts of the world, although wherever possible we have identified important people and advances from Australasia, Africa, Asia, and South America. Our account is also biased by our choice of topics, of stories, and of the people involved in those stories, all of which reflect our own interests and our interpretation of the available information. Others with different backgrounds and expertise would have undoubtedly written a different account—indeed, we hope they will.

For us, ornithology is the *scientific* study of birds, and an ornithologist is someone who studies birds and writes up their findings for publication in scientific journals (Haffer

2001). Although bird watching was a precursor of scientific ornithology and many ornithologists began their careers as bird watchers (Fisher 1940; Weidensaul 2007), this book is not a history of bird watching.

Histories can be dull. But our experiences teaching undergraduates show us that histories are brought to life by stories about the people that populate them. The history of ornithology is overflowing with extraordinary individuals and intriguing stories. Science—ornithological or otherwise—is conducted by real people with real human attributes, including ambition, integrity, jealousy, obsession, and deception. In telling their stories we encounter the full gamut of human frailties from fraud to murder. Some individuals make a name for themselves from a single moment of insight, whereas for others fame emerges only after decades of labor. Our emphasis here is on people—the ornithologists who created the wonderful and extraordinary body of knowledge that we so often take for granted. Michael Brooks, author of *Free Radicals: The Secret Anarchy of Science* (2011), perfectly captures our view: “Scientists have a habit of airbrushing science’s great moments to smooth out the human wrinkles and flaws in the process of discovery. Ultimately, though, scientists did themselves a disservice when they dehumanised their field. No wonder we have had such trouble keeping schoolchildren interested in science.”⁵ Knowing about history is important too. As the nineteenth-century French philosopher Auguste Comte said, “It is true that a science cannot be completely understood without a knowledge of how it arose.”⁶ Many great biologists have said the same. Here’s the evolutionary biologist, R. A. Fisher, writing in 1959:

More attention to the History of Science is needed, as much by scientists as by historians, and especially by biologists, and this should mean a deliberate attempt to understand the thoughts of the great masters of the past, to see in what circumstances or intellectual *milieu* their ideas were formed, where they took the wrong turning or stopped short on the right track. A sense of the *continuity* and the progressive and cumulative character of an advancing science is the best prophylactic I can suggest against the manic-depressive alternations of the cult of *vogue* and *boost*, which threatens to smother the scientific efforts, gigantic as they are, of at least one great nation.⁷

The value of an historical perspective on a scientific discipline like ornithology is not always immediately obvious. Many young researchers feel they do not have sufficient time to plough through the original texts and so do not bother. We believe very strongly that an understanding of the history of a topic has several advantages. First, it allows researchers to see their own work in context: scientists search for “the truth,” but what seems to be the truth can change in the light of new evidence—evinced by the ongoing refinements in avian taxonomy and systematics that we describe in chapter 3—and hence the more appropriate description of science as “truth for now.” In other words, on the basis of what we know, this is what we currently believe to be true, but as scientists we are prepared to change our minds if convincing alternative evidence comes to light. Looking back on his career, this was one of the traits that Darwin felt had contributed to his success (Darwin 1887; Barlow 1958).⁸

Second, knowing “the literature”—what one’s predecessors have done—is an essential

part of scholarship and at the very least helps to avoid reinventing the wheel. The problem, of course, is how much of the previous literature can a researcher be expected to know. As we've already indicated, the volume of ornithological articles from the twentieth century is overwhelming. For this reason most young biologists assume that going back as far as the year 2000 is far enough. It isn't, but such a strategy is perhaps the only way to survive in the current academic environment where the acquisition of research grants is so essential for a scientist's career. It is precisely because most scientists cannot afford the luxury of learning history that we hope our synthesis of ornithology will be useful and at the very least provide a guide to the literature of a recently passed era.

But there's a third reason why history is of value: it can be a crucible of creation, triggering new ideas and new ways of looking at old problems. Thus it can be immensely stimulating to see how our ornithological predecessors grappled with particular topics; how they behaved or misbehaved; how they organized their lives; how they failed to recognize the significance of certain facts or data because they had no useful frame of reference at the time. Scientists get their inspiration from a variety of sources, but looking at the history of one's own discipline can be the most rewarding of all.

The topics we have chosen to cover in this book each have their own chronology, their own characters, ideas, and stories. There's no particular logic to the order of chapters other than what we thought would make an interesting read, which means that, in a way, each chapter can be read in isolation. Having said that, the influence of some ornithologists—David Lack and Ernst Mayr, for

example—is so far reaching they appear in several chapters.

For consistency, and because the common names of birds can vary from country to country, we have used the International Ornithological Congress (IOC) list of world bird names (Gill and Donsker 2012) for the vernacular names of birds, capitalized for full species names—such as American Robin and Common Cuckoo—but lower-cased when referring to robins or cuckoos in general. For scientific names refer to the latest online version⁹ of that IOC world list. We have made every effort to be scientifically correct and to document all our sources, citing references in the text in the standard scientific manner. To avoid cluttering the text we tried to use no more than two key references at a time, and these should provide the reader with a portal into the relevant literature. This means that we included references in the text—such as “Lack (1954)” —in part because this is the convention in the scientific literature. We recognize that this style can sometimes seem intrusive to the reader, but its advantage is that it allows one to instantly attribute information to a particular person or a particular publication; giving credit where credit is due is an important feature of scientific practice. A list of all the references is provided at the back of the book. We have also included additional notes at the back of the book, identified by superscripts in the main text. We have kept these notes brief to save space, but we provide more scholarly detail on the book's website at <http://myriadbirds.com>. At the end of each chapter we have also written a “coda” to present a summary of the historical significance of the topic, as well as our own speculations and opinions.

The graphical timelines in each chapter are an important feature of the book. At a glance, these provide a chronological summary of events, key concepts, discoveries, publications, and so on. The late Jürgen Haffer, a superb historian of ornithology—a geologist by profession—urged us to use the geologist’s bottom-up timeline, with the most recent events at the top.

A list of most of the ornithologists that we refer to explicitly in the text is presented in our gallery of five hundred ornithologists at the back of the book. Our aim here is to provide some more details, such as birth and death dates, of those people whose work we describe; it is not intended as a list of the most influential ornithologists since Darwin.



Jürgen Haffer. An oil geologist by profession, Haffer was an amateur ornithologist who undertook pioneering studies of speciation in Amazonian birds (photo in 2008 or 2009 at age 75 or 76).

Each chapter opens with a painting or illustration of a bird or particular group of birds relevant to that chapter. In each case we have chosen an artist whose work we find inspiring, and to highlight the fact that artists have made an enormous contribution to our appreciation of birds.

Our primary goal has been to present the history of modern ornithology in a readable fashion. In doing so we have avoided historical fiction, in that we do not pretend to know what people might have said or thought. Instead we have used direct quotations, either from published sources or from our own interviews, experiences, and interactions with people who study birds. Indeed, one of the most enjoyable aspects of this project was meeting and talking to a wide range of eminent ornithologists. The quotes are important because they constitute empirical information: this is what was said. To maintain the flow of the text, all quotes are referenced with a superscript in the notes at the back of the book.

The audio recordings of those ornithologists that we interviewed are available at <http://myriadbirds.com>. These interviews provided us with a wonderful web of connections between ornithologists of different eras, and we used them both to inform the text and as a source of quotes. We hope that they will be useful to future historians of ornithology. In each chapter we also present some brief autobiographies, featuring key researchers who were involved in the development of each topic. Some of these were constructed from our interviews, but in most cases individuals wrote a brief account for us, detailing what and who influenced their ornithological career as well as a summary of their main achievements. Our instructions



Chestnut-mandibled Toucan, one of several species whose systematic relations Jürgen Haffer explored (e.g., Haffer 1974). Mayr (1983) referred to Haffer's work on this group as the finest research on bird speciation.

were deliberately vague, since we wanted the authors themselves to determine what they wrote—the results speak for themselves.

Between us we have lived through at least half of the twentieth century, and the busiest half at that. Our origins (two in Britain, one in Canada) have helped reduce any geographic bias; our ages (two around sixty, one in her late twenties) have helped minimize any ageism, and our genders (two male, one female) have helped, we hope, to avoid any sexism. We have been practicing ornithologists ourselves for more than a hundred years in total (we started young!), and we know or have known many of the ornithologists mentioned in the book—an enormous privilege that has provided us with an intimate and inspirational view of ornithology.

ACKNOWLEDGMENTS

In 1959, as part of the centenary of the British Ornithologists' Union (BOU), Max Nicholson wrote this: "The recent successes of British ornithology have largely been based on new ideas with new organizations to foster and serve them, but these would not have been enough without the spread of a sense of common purpose and the growth of innumerable friendships which it has brought about."¹⁰ His comment about friendship is as true today as it was then, and in completing this volume we have been overwhelmed by the generosity of our fellow ornithologists across the world in helping us achieve our goals.

We started this project by conducting a survey of the most influential ornithologists

and the most influential ornithological books of the twentieth century. The following kindly provided nominations: Malte Andersson, Peter Berthold, Jacques Blondel, Jerry Brown, Andrew Cockburn, Fred Cooke, John Coulson, John Crook, John Croxall, Nick Davies, André Dhondt, Peter and Rosemary Grant, Jürgen Haffer, Richard Holmes, Ellen Ketterson, Walt Koenig, John Krebs, Kate Lessells, Anders Møller, Pat Monaghan, Ian Newton, Gordon Orians, Chris Perrins, Theunis Piersma, Morné du Plessis, Robert Ricklefs, Uli Reyer, Karl Schulze-Hagen, Claire Spottiswoode, John Wingfield, Roswitha and Wolfgang Wiltschko, and Robert Zink.

We also interviewed and/or obtained autobiographies from Thomas Alerstam, Pat Bateson, Peter Berthold, Walter Bock, Terry Burke, Nicky Clayton, Andrew Cockburn, Nigel Collar, Joel Cracraft, Nick Davies, Steve Emlen, John Fitzpatrick, Brian Follett, Rosemary and Peter Grant, Jack Hailman, Mike Harris, Ben Hatchwell, Geoff Hill, Robert Hinde, Peter Hudson, Alex Kacelnik, Ellen Ketterson, Walt Koenig, Kate Lessells, Ian Newton, Fernando Nottebohm, Peter O'Donald, Colin Pennycuick, Chris Perrins, Richard Prum, Robert Ricklefs, Wolfgang Schleidt, Peter Stettenheim, Bridget Stutchbury, Arie van Noordwijk, Sarah Wanless, Adam Watson, Roswitha and Wolfgang Wiltschko, John Wingfield, and Amotz Zahavi.

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Other colleagues read and commented on either entire chapters or parts of chapters. We are most grateful to Thomas Alerstam, Malte Andersson, Allan Baker, Jerry Brown, Alan Brush, Joel Cracraft, Nick Davies, Scott Edwards, John Fitzpatrick, Jim Flegg, Brian Follett, Frank Gill, Rhys Green, John Harshman, Geoff Hill, Robert Hinde, Pat Monaghan, Ian Newton, Trevor Price, Jens Rolff, Wolfgang Schleidt, Ben Sheldon, Peter Stettenheim, Bill Sutherland, Brian Switek, Charles Wellman, and Tony Williams. We are especially grateful to Frank Gill, Jeremy Mynott, and Ian Newton, who read and commented on the entire manuscript.

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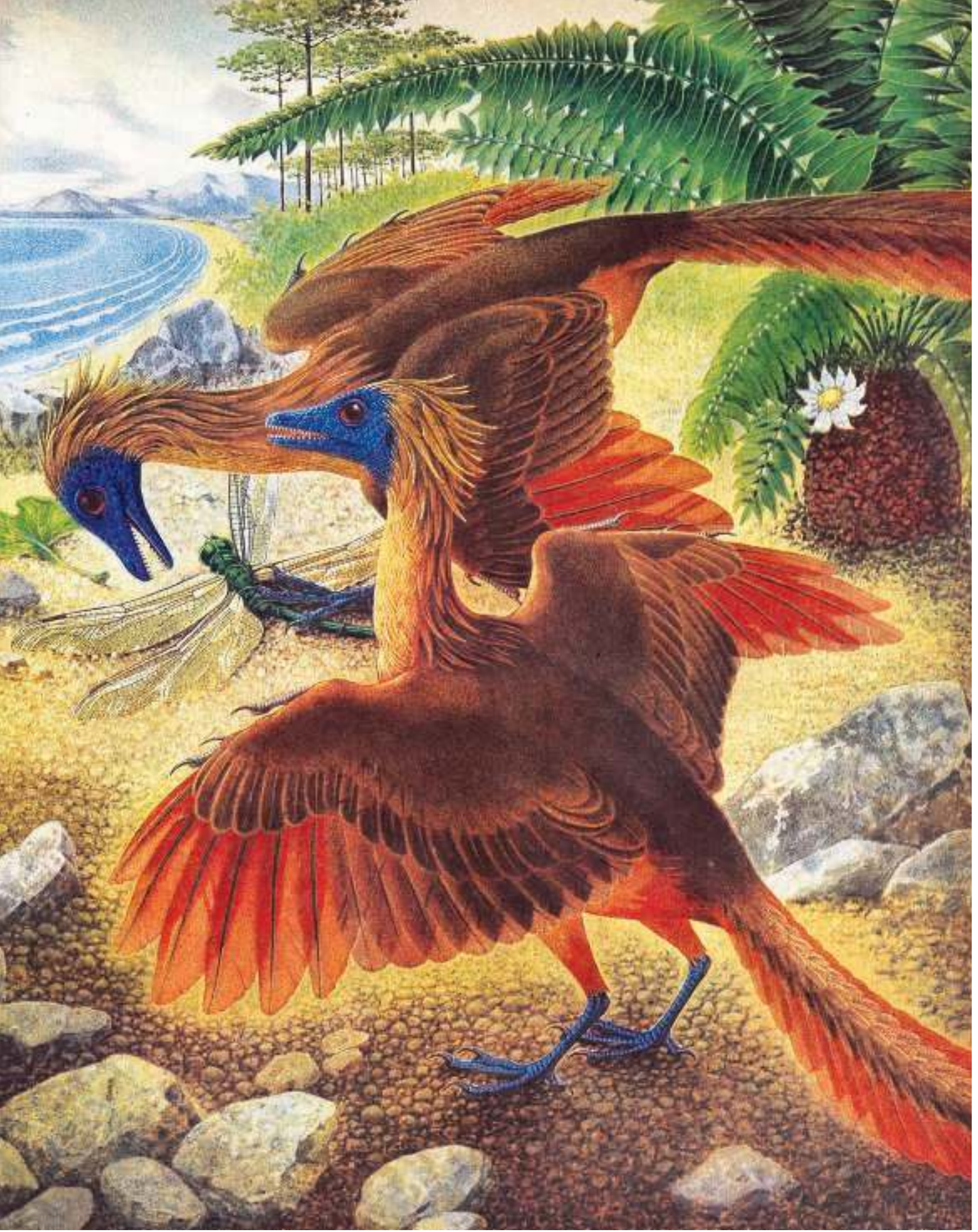
Wilson. We are especially grateful to those individuals and organizations that provided us with images with a minimum of hassle—they know who they are.

Special thanks to Al Bertrand, our editor, and his team at Princeton University Press (including Hannah Paul, Dimitri Karetnikov, and Ali Parrington) for their efficient and enthusiastic support.

We thank all of those listed above for their help: we couldn't have completed this

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Ten Thousand Birds



CHAPTER I

Yesterday's Birds

The road from Reptiles to Birds is by way of Dinosauria to the Ratitae.

—THOMAS HENRY HUXLEY, IN A LETTER TO ERNST HAECKEL ON 21 JANUARY 1868¹

THE TERRIBLE CLAW

LATE ONE HOT AUGUST EVENING IN 1964, near Bridger, Montana, the paleontologist John Ostrom and his assistant, Greg Meyer, made a discovery that revolutionized the study of ancient birds. Toward the end of a hard day in the field, they spotted, in the slanted light, some claws and bones protruding from the reddish-brown soil. Scrambling to the spot, they began digging with the only tools they had at hand—a jackknife, a small paintbrush, and a whisk broom. Rapidly running out of natural light, they marked the location so they could resume work the next morning. Given the fossil's sickle-like claws, Ostrom was convinced this was a carnivorous dinosaur: "I was almost certain, although still wary, that we had discovered something totally new."² And they had, as the subsequent week of excavation revealed—a

specimen considered by some³ to be the most important dinosaur discovery of the mid-twentieth century, an animal Ostrom called *Deinonychus*, "the terrible claw." This was a seventy-kilogram bipedal runner with sharp claws on all four feet and an especially oversized retractable claw on the second toe of each hindlimb. *Deinonychus* was a killing machine, and its study revolutionized our understanding of how dinosaurs lived and breathed and how birds evolved. *Deinonychus* was a member of the *Dromaeosauridae*, a family of theropod dinosaurs—including *Velociraptor*, made famous by the movie *Jurassic Park*—that proliferated in the Cretaceous.

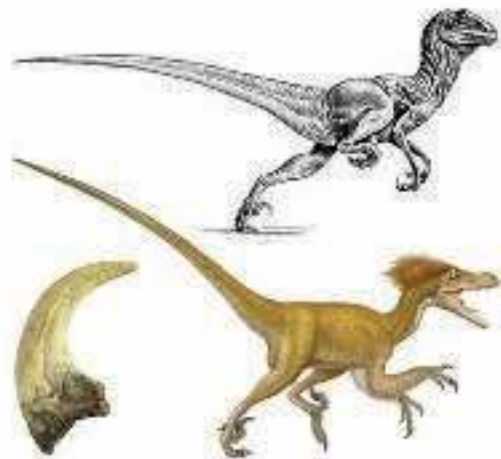
Like so many others who influenced ornithology in the early twentieth century, Ostrom started out studying medicine. Growing up in Schenectady, New York, he began his premed studies there at Union

A pair of *Archaeopteryx lithographica*. Painting by Rudolf Freund for an article in *LIFE* magazine on evolution (Barnett 1959). In 1959 nothing was known about the colors of plumages and bare parts of fossil birds, so Freund was guessing (probably incorrectly, as it turns out).

College in the late 1940s. Prophetically, one of his course requirements was to study evolution, so—keen student that he was—he started to read the course text, Simpson’s (1949) *The Meaning of Evolution*, the night before the first lecture. Enthralled, he spent the night reading, then wrote to the author, the eminent paleontologist George Gaylord Simpson, to say how excited he had been by what he had read. Much to Ostrom’s surprise and delight, Simpson answered right away, inviting Ostrom to come and study the paleontology of mammals with him at Columbia University in New York City. To the chagrin of his parents, Ostrom abandoned his medical studies and moved to the big city, in 1951, to begin a PhD on the paleontology of reptilian dinosaurs, in the end working with a leading dinosaur specialist, Edwin H. Colbert, rather than Simpson. Six years after obtaining his PhD, Yale hired Ostrom as their curator of vertebrate paleontology at the Peabody Museum, a post held a century earlier by one of the great American paleontologists, Othniel Charles Marsh.

Marsh held the first chair of paleontology at Yale, a post created especially for him in 1866. Ever the entrepreneur, he persuaded his wealthy uncle, George Peabody, to donate funds⁴ to establish a museum at Yale so Marsh would have a place to store and display his fossil discoveries. And discover he did—in twenty years of exploration he and his crew found more than a thousand new species of fossil animals, including eighty new dinosaurs,⁵ the first pterosaurs from North America,⁶ and a new group of fossil birds, with teeth, which he called the “Odontornithes.” Marsh’s “Odontornithes,” as presented in his 1880 monograph, included

² *Hesperornis regalis* (“the royal bird of the



Deinonychus antirrhopus was discovered by John Ostrom in 1965. This species was originally depicted as naked (top), but recent evidence suggests that it was covered with “dino-fuzz” as shown here (bottom). A fossil of the sharp hind “killing” claw is also shown (bottom left).

west”) and *Ichthyornis* (“fish bird”), both of which he had described for science.⁷ These new birds were related to *Archaeopteryx*—one of the most famous fossils ever found—and all three of these early birds had teeth, suggesting to Marsh that birds had descended from the toothed reptiles, especially the dinosaurs. Charles Darwin was thrilled: “Your work on these old birds, and on the many fossil animals of N. America, has afforded the best support to the theory of evolution, which has appeared within the last 20 years.”⁸

It was not until Marsh and Edward Drinker Cope (from the Academy of Natural Sciences in Philadelphia) began exploring the western United States in the 1870s that the American badlands began to relinquish their biological secrets.⁹ Cope and Marsh were both brilliant scientists who laid the foundations of modern paleontology. They are probably most famous,

though, for their lifelong feud—aptly called the “Bone Wars”—involving intrigue, chicanery, and insanely intense competition to be first, best, and most famous at everything they attempted, and to have the biggest and most significant collections of discovered-in-America fossils at their home institutions. As we shall see, controversy is a hallmark of paleontology, even today, but the scope, intensity, and nature of the Bone Wars belongs among the great tales of the Wild West, albeit in the name of science. John Ostrom also generated considerable controversy, which continues to this day (2013).

Unlike most of his paleontological predecessors and contemporaries, Ostrom thought about dinosaurs, like *Deinonychus*, as living, breathing animals, not just as a jumble of bonelike rock embedded in a geological stratum. Even his own PhD supervisor, Colbert, considered them to be “sad, slow, stupid creatures that deserved to be extinct.”¹⁰ By focusing on how these animals once lived and evolved—including consideration of their behavior, physiology, development, and ecology—Ostrom’s approach revolutionized paleontology. Ostrom reasoned that *Deinonychus* must have walked on its hind legs—as its forelimbs were built for killing, not walking—and its posture (based on bone and joint reconstruction) was likely upright, bipedal. As a predator, *Deinonychus* would have pounced on its victims, ripping them open with its razor-sharp claws, possibly using the extra-large claws on its back feet to hold its prey down (Fowler et al. 2011), much in the manner of raptorial birds today. Contrary to the standard (albeit Victorian) image of dinosaurs as enormous, plodding, dim-witted beasts, *Deinonychus* was a relatively small—3.4 meters (11 feet) long—nimble

predator with an active lifestyle, and was almost certainly warm blooded.

Just about everything that Ostrom suggested about *Deinonychus* was unorthodox: here was a dinosaur more like a small ostrich than the lumbering giants usually depicted in books. Could it be that birds and dinosaurs were more closely related than had previously been thought? To explore this possibility, Ostrom needed to reexamine both the oldest known fossil bird, *Archaeopteryx*, to learn about the origins of birds, and the pterosaurs, to learn about the origins of flight in the vertebrate animals.

ARCHAEOPTERYX

When Ostrom began his study of *Archaeopteryx* in 1970, only four specimens were known—a lone feather and three partial skeletons—arguably the most important, valuable, famous, and beautiful fossil animal ever found. Ostrom traveled to Europe to study the original specimens kept in London, Berlin, and Maxburg (Germany), and to visit the vast Solnhofen quarries, where the only *Archaeopteryx* specimens ever have been found. To put *Archaeopteryx* into context of the evolution of both reptiles and flight, Ostrom also went to the Teylers Museum in Haarlem, Netherlands, where some of the world’s most complete pterosaur fossils were housed. Pterosaurs—the group that includes the pterodactyls—were flying reptiles, contemporaries of *Archaeopteryx* but not closely related to birds. However, they had several anatomical adaptations for flight that Ostrom wanted to study in detail. With its neoclassic architecture, the Teylers Museum was (and is) a lovely place to work. At the time Ostrom was working, there was

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