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1

In the Light of Evolution

BIRDS AND EVOLUTIONARY SCIENCE

A few years ago, I joined a birding tour of Ghana. After several days of enjoying such exotic species as drongos, hornbills, and pratincoles, we encountered a beautiful red and black finch, the Black-bellied Seedcracker (*Pyrenestes ostrinus*).[1] I was delighted to see this species because I had long known, and had described in my textbook of evolutionary biology, a study of this species by Thomas Smith,[2] a professor at University of California–Los Angeles. Smith had followed the life of members of a population in Cameroon by fitting each individual with a unique combination of colored leg bands. Bill size is highly variable in seedcracker populations; most birds have either small or large bills, although a minority are intermediate (plate 1). Smith found that large-billed birds feed more efficiently on the large, hard seeds of one species of sedge and small-billed birds handle the small seeds of another sedge more efficiently. Large-billed and small-billed birds both had higher rates of survival than intermediate birds: a striking example of natural selection in action. By occupying somewhat different "ecological niches," birds with different genotypes (specific combinations of genes) persist. Years later, when the study of genomes had advanced, Smith and his collaborators determined that the inherited difference in bill size is caused by different forms of a single gene (called *IGF1*, or insulin-like growth factor 1).[3] As we admired the seedcracker, I told my companions this story. One of them exclaimed, "So that's why it doesn't look like the picture in the field guide! I wondered if the book was wrong." He was intrigued by the idea that different members of a species have different diets and ways of life.

Some birders are focused on seeing and listing species; others are curious about the lives and features of the birds they see. Once in a while a fellow

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birder, knowing that I'm a biologist, will ask me a question. Sometimes it is along the lines of "how can birds fly so fast through dense vegetation without hitting it?" or "how can a tiny Blackpoll Warbler (*Setophaga striata*) fly nonstop from New England to Venezuela?" I awkwardly answer that I don't know much about how birds achieve these amazing feats because those are topics studied by biologists who specialize in bird physiology or brain function, and I haven't followed those fields since I was a student. Some other questions, though, tempt me to say more than they may want to hear. (And I can resist anything but temptation.[4]) Why do some bird species have different color morphs? Why are males more brightly colored than females in some species but not others? Why do albatrosses and many other sea birds lay only one egg? How come I can see more bird species in a two-week birding tour in Peru than in an entire year in eastern North America? Why do they keep changing bird classifications, and how do they know falcons are closer to parrots than to hawks?

Most questions about birds fall into two categories—*how* and *why*—that correspond to two major kinds of biological research. Much of biology poses "how" questions: it aims to understand how organisms function—how the molecular, cellular, and organ components of an organism work, here and now, without reference to how they came to be. "Why" questions are the province of evolutionary biology. We ask why a Eurasian Golden Oriole (*Oriolus oriolus*) or an American Baltimore Oriole (*Icterus galbula*) is brightly colored because we understand that it could have been otherwise: something in its history—in its evolution—caused it to be bright rather than drab. For every characteristic of every species, we can ask "how" questions about its functional role (if any) in an organism's lifetime, complemented by "why" questions about its origin. All species of birds have evolved from a single ancestral species ("common ancestor"), which was one of a great many species of vertebrates that all evolved from a single, more ancient, common ancestor; this, in turn, was a descendant of the ur-ancestor of all animals, from sponges to primates. And so every feature of every bird, from its DNA sequences to its behaviors, has come into existence—has evolved—during this history of descent.

Evolutionary biologists attempt to develop broad principles that can explain all these features of all species. Evolutionary biology illuminates every area of biological research and every group of organisms. The geneticist Theodosius Dobzhansky, who helped to shape modern evolutionary biology, rightly wrote that "nothing in biology makes sense except in the light of

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evolution."[5] There are biologists who study biochemical processes within cells and biologists who study how these processes evolved—and likewise for the structure and function of genomes, brains, and hormones. Among ornithologists, some take a mostly functional approach, and others a more evolutionary approach, to bird physiology, morphology,[6] behavior, and life histories. Others are devoted to understanding the history of bird evolution—how and when birds' form, behavior, habitat use, and geographical distribution diversified during their descent from their common ancestor. The amount of research that bears on bird evolution is immense: when I entered "evolution and bird*" in a search engine (Web of Science), it yielded 73,200 articles in scientific journals.[7] Variant search terms would add many more.

So for almost any question we might ask about how birds evolved, there is plenty of research on which to draw. Nevertheless, the known is far less than the unknown. Questions such as "how do new species form?" and "why do female birds prefer flashy males?" are debated and are the subjects of active research. And while we may be able to provide a general answer to a question (e.g., why do birds' bills differ in shape?), there may not be a definitive answer for a particular species. (I don't know of any research about why the bill of the Groove-billed Ani [*Crotophaga sulcirostris*] is grooved.) Evolutionary biologists strive, instead, to develop theories that should apply to a wide range of species but which require detailed information to explain particular cases. For example, there are several models[8] to account for genetic polymorphism—the persistence of two or more genetically different types within a population, such as the color "phases" of the Tawny Owl (*Strix aluco*) and the Eastern Screech Owl (*Megascops asio*). Information about the survival and reproduction of each form, under several environmental conditions, may be needed to match a particular instance to one of the models.

I can imagine someone thinking, at this point, "I watch birds because I'm entranced by their beauty and their behavior or because I enjoy the challenge of finding and identifying as many species as I can. It's an aesthetic, emotionally rewarding experience. Doesn't looking at a bird with the cold analytical eye of science ruin the experience?" Of course, I can't speak for everyone, but for me, birding certainly has those rewards, and the more I know, the more my appreciation is enhanced. As many as I have seen, I still am overwhelmed by a peacock's beauty, but it also spurs me to ask why and how it came to be, and having an answer enlarges and makes whole my experience. We integrate intellectual and aesthetic appreciation when we want to know the names of the birds we encounter and to which family or group a species belongs.

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With knowledge of their biology, the most common, everyday birds take on new interest. Take the ubiquitous House Sparrow (*Passer domesticus*).[9] When I stop to look at a House Sparrow, I sometimes think of its broader evolutionary context: other species in the genus *Passer*. For example, the Italian Sparrow (*Passer italiae*) originated as a hybrid between House and Spanish Sparrows (*Passer hispaniolensis*) (see chapter 10), and the Eurasian Tree Sparrow (*Passer montanus*) replaces the House Sparrow as a human associate in southeastern Asia. The House Sparrow itself shows interesting geographical variation in Europe: northern birds are bigger than birds in the south. This is one of many species of birds and mammals that have this pattern due to adaptive evolution: larger bodies lose heat more slowly than smaller ones and are advantageous in colder regions. What is more, since House Sparrows were introduced from Europe into North America in 1851, they have spread widely, and northern populations have evolved larger size. This was one of the first examples of how rapid evolution can be; Darwin never imagined that evolutionary changes could happen within a few human lifetimes.

The Superb Fairywren (*Malurus cyaneus*) in Australia (plate 2) is another example of a common bird that poses interesting questions. A group usually has two or more bright blue and black males and several brown birds that include both males and females. Biologist Andrew Cockburn and his associates studied the extraordinary breeding behavior of fairywrens for more than twenty-five years.[10] The bright-plumaged and brown males all cooperate to rear nestlings. Cooperative breeding is known in many birds, and why it has evolved poses a very interesting question (chapter 7). But there is more: female fairywrens, to a greater extent than any other bird yet known, engage in “extra-pair copulation,” or adultery: they will travel across intervening territories to mate with a “hotshot” male. The female’s male associates dutifully help raise babies that usually aren’t their own offspring. Why are females so unfaithful, and why do males stay and rear the offspring?

These are fascinating questions that evolutionary biology can help to answer—as it can shed light on countless other aspects of birds, ranging from their coloration and structure to their geographic distribution and diversity. My aim in this book is to pose such questions and show how insights from evolutionary biology can answer them. Also, research into these topics has revealed features of many species that I think will amaze and delight anyone who likes birds and help them appreciate birds all the more. And if some readers learn more about evolution and how it is studied, the book will have served

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another purpose—sharing some of the richness of evolutionary science that I have found so rewarding.

By "evolution," biologists usually mean change in the features of a single species over time (that is, across generations) as well as the division of a single species into two or more descendant species, both of which undergo change. The alterations of a feature must be inherited to count as evolutionary change. Some features can be affected by an individual's environment, but these changes are generally not inherited. A generation of people might be lighter skinned than their grandparents because they work in offices instead of fields and so are less suntanned, but this doesn't count as evolution. As inheritance is a defining feature of evolution, evolutionary change of organisms' features (their *phenotype*) is accompanied by evolution at the level of the genes. There is also evolution at the genetic (DNA) level that may not affect any features of the organism.

In *The Origin of Species,* Darwin developed two main themes: that all living things have descended, with modification, from common ancestors; and that the chief cause of modification is natural selection of inherited variations. The wealth of insights, hypotheses, and information in Darwin's writings is staggering. Every time I read a few pages of *The Origin of Species,* I'm simply floored by the questions he thought to ask, the possible answers he advanced, and the evidence he found in an extraordinary range of facts, some of them seemingly trivial. During his voyage on the *Beagle,* he notices, in South America, that a flycatcher, the Great Kiskadee (*Pitangus sulphuratus*) (figure 1.1), sometimes acts like kestrels and kingfishers when foraging. Later he cites this, in *The Origin of Species,* to illustrate that species might change and perhaps become adapted to new ways of life. Not everyone can see a world in a grain of sand, but Darwin realized that a coherent explanation or theory must be able to accommodate, and build on, every fact, however trivial it might seem.

Evolutionary biology today is devoted to Darwin's two great themes: what has happened in the evolution of the world's organisms, and what have been the causes of these evolutionary events?

In studying the history of evolution, biologists today draw mostly on two sources of information (the subject of chapters 2 and 3). One is the fossil record. The other is the similarities and differences among living species in their characteristics and DNA sequences. This information enables biologists to

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FIGURE 1.1. A Great Kiskadee (*Pitangus sulphuratus*), a common flycatcher in much of tropical America, north to the border of Texas. (Art, Luci Betti-Nash.)

piece together species' relationships, to infer their family tree, or phylogeny (chapter 2). Both phylogenies and fossils can yield information on how features have changed; for instance, they tell us that flightless birds like kiwis and penguins have evolved from flying ancestors and that the same transition has happened independently in kiwis, penguins, and many other lineages. Often, such phylogenetic information can help us understand how certain features that differ among species, such as bill shape, are adaptive.

How does evolution happen? Darwin's greatest idea, one of the most important ideas in human history, was natural selection. (The philosopher Daniel Dennett called evolution by natural selection "the single best idea anyone has ever had."[11]) *If* a character (meaning a feature or trait) varies among individuals of a species, and *if* the variation is at least partly hereditary (i.e., genetic), and *if* individuals with a certain variant condition tend to survive or

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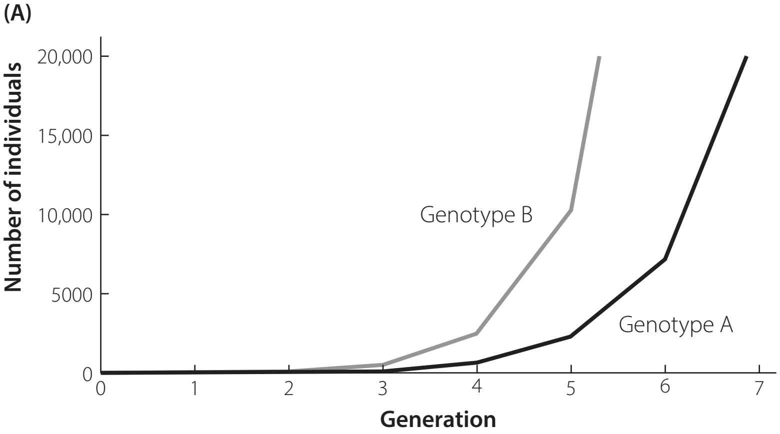

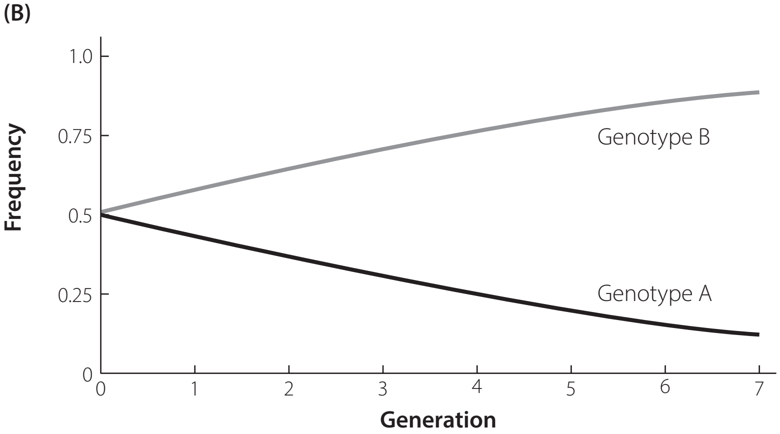

FIGURE 1.2. A simple model of genetic change by natural selection. Two genotypes (groups of organisms with specific combinations of genes) differ in a characteristic that affects survival or reproduction. Genotype A has an average fitness equal to 3, meaning than an average newborn A leaves 3 offspring. Genotype B has an average fitness of 4, because it is more likely to survive and reproduce or because females lay more eggs. In the upper diagram, the number of B individuals grows faster than the number of As. It therefore makes up an increasing proportion (frequency) of the population, as shown in the lower diagram. (From Futuyma and Kirkpatrick 2017.)

reproduce more than others, *then* the proportion of that variant type in the species population will increase from one generation to the next, and it may ultimately replace all other variants (figure 1.2). Natural selection, then, is simply an average difference in the survival and reproduction of genetically different types of organisms. Darwin postulated that this process is the chief

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cause of evolution, and certainly of adaptive evolution—the origin and alteration of characteristics that enhance survival and reproduction. He likened natural selection to human selection of domesticated animals and plants, in which breeders propagate their stock from individuals that have particularly desirable features.

The Origin of Species was first published in 1859. Seven years later, an obscure monk, Gregor Mendel, published an obscure paper on inheritance in peas that was not widely noticed until 1900, when it became the foundation of the modern science of genetics. Since then, genetic knowledge has become the chief framework for describing the processes of evolution within species. This framework, expressed in both words and equations, describes the factors that cause genetic changes in species. In the simplest terms: a new version of a gene (an *allele*) comes into existence by *mutation* (usually a change of one of the units of a DNA sequence). At first it is very rare—only one or a few individuals carry the allele. If this allele alters a characteristic in such a way as to increase an individual's chance of survival or reproduction, it is said to be *naturally selected* and may become more common because such individuals survive or reproduce more than those that lack the allele and the advantageous feature. Perhaps the allele entirely replaces the original form of the gene (the new allele is *fixed*), and the population as a whole has a somewhat altered *phenotype* (i.e., characteristic: shorter legs, differently colored bill, different display behavior—whatever feature the gene affects).

Two of the factors that affect genetic evolution are mutation and natural selection. But there are others. Suppose a local population of the species is flooded with immigrants from another population with a different allele, and the immigrants interbreed with the residents. The proportion (or *frequency*) of the residents' original allele is lower and the frequency of the immigrants' allele is higher than before. This process, called *gene flow*, can change a population's genetic composition. Finally, and very importantly, the frequencies of two alleles (say, old allele and new mutation) are affected by pure chance.[12] Some individuals suffer accidental deaths, or are unlucky in love, no matter how genetically vigorous and reproductively potent they are—and their failure to pass on their genes changes the allele frequencies in the next generation, however slightly. This purely random change is called *genetic drift*. Over the course of generations, the frequency of an allele will fluctuate, and since there is no reason for the ups to precisely equal the downs, the frequency will eventually go to 0.0 or 1.0: the allele will be lost altogether or it will completely replace other alleles (figure 1.3). If the population is very small, each individual's bad versus

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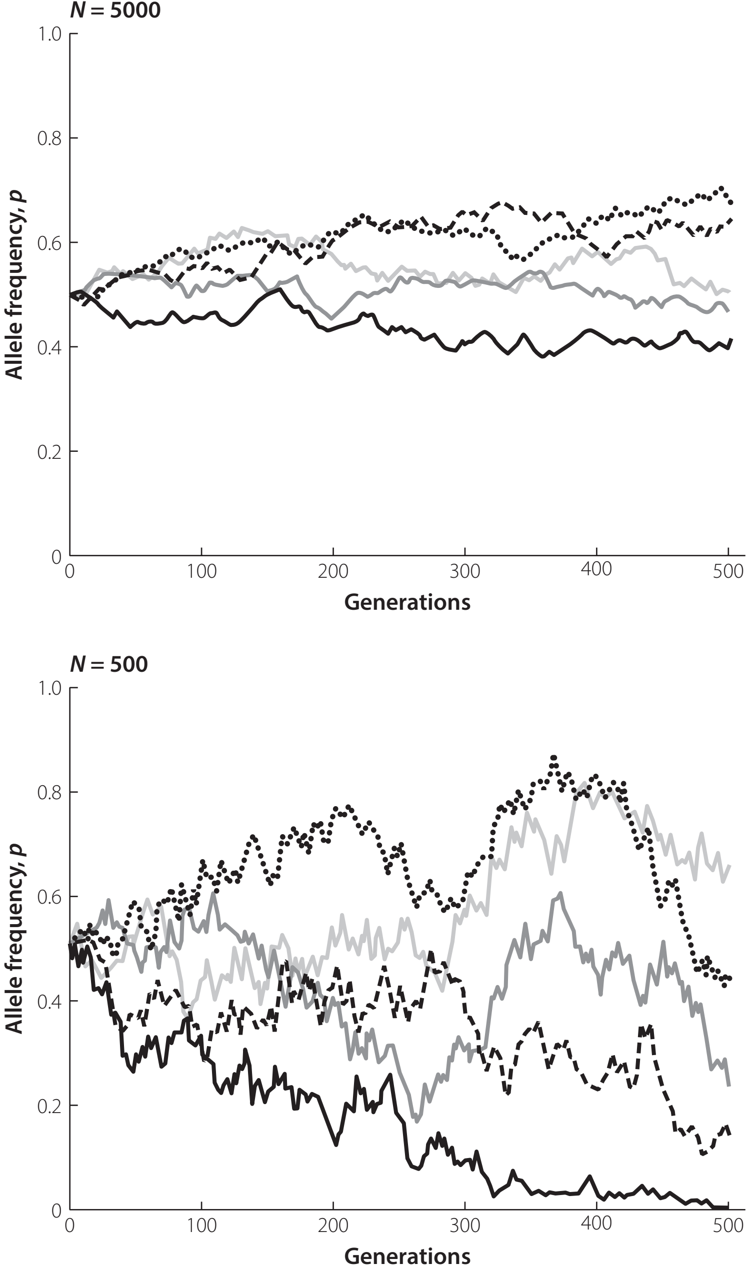

FIGURE 1.3. Evolution by chance: computer simulations of random fluctuations in the proportion (frequency) of one of two alleles (forms of a certain gene). Individuals that carry one allele or the other do not differ in fitness. In the top diagram, five populations, each of 5,000 individuals in each generation, evolve over the course of 500 generations. The frequency of one of the alleles is shown to fluctuate in each of the five populations, which come to differ even though all started with the same frequency (with both alleles equally common). The bottom diagram shows the same kind of history, but the populations are smaller (500 individuals in each generation). The fluctuations are greater, and the populations become different faster. In one of the populations, the one allele has dropped to zero frequency—so the other allele has reached a frequency of one (100% of the gene copies). That allele has taken over that population not because it is better but because it was lucky. (From Futuyma and Kirkpatrick 2017.)

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good luck will have a bigger impact than if the population is large. So genetic drift changes allele frequencies faster in small than in large populations. Now suppose a particular allele enhances the chance of survival (it is advantageous) but only slightly. (Selection is said to be weak.) Both natural selection and genetic drift are operating, and if the population is small enough, random drift will be more influential than weak natural selection, and the advantageous allele may not become a fixed feature of the population. Whether natural selection or genetic drift rules depends on the strength of natural selection compared with the population size.

Mutation, natural selection, genetic drift, and gene flow affect evolution within the various local populations of a species and in a species as a whole. When gene flow between populations of a species is curtailed, the other three processes continue more independently in each of the separated populations, enabling them to become more different from each other. Under some conditions, the populations may ultimately become different species (chapter 10).

These processes underlie evolutionary changes within a species; they are very generic (and genetic) ideas that can be used to describe changes in everything from DNA sequences to biochemical, anatomical, and behavioral characteristics. And these concepts pervade all of evolutionary biology, including phylogenetic and paleontological studies of the history of evolution of birds (and everything else). A lot of evolutionary research involves trying to interpret differences within and among species in these terms. Chapters 4 and 5 include some fascinating examples of how biologists try to study these factors, especially natural selection, as they apply to specific characteristics of birds.

Birds have been and continue to be immensely important in the development of evolutionary science.[13] To be sure, they have been less useful than insects, plants, and bacteria in the study of the genetic foundations of evolution, partly because they don't reproduce as rapidly (although they are playing a larger role in genetic studies today with the growth of genomics). But birds have contributed more to studies of the evolution of physical characteristics, behavior, life histories, ecology, speciation, and geographic distribution than almost any other major group of organisms. My examples start with Darwin (of course!). In *The Voyage of the Beagle* (1839),[14] he refers to more than fifty species of birds that drew his attention, some of which he later used as evidence in *The Origin*

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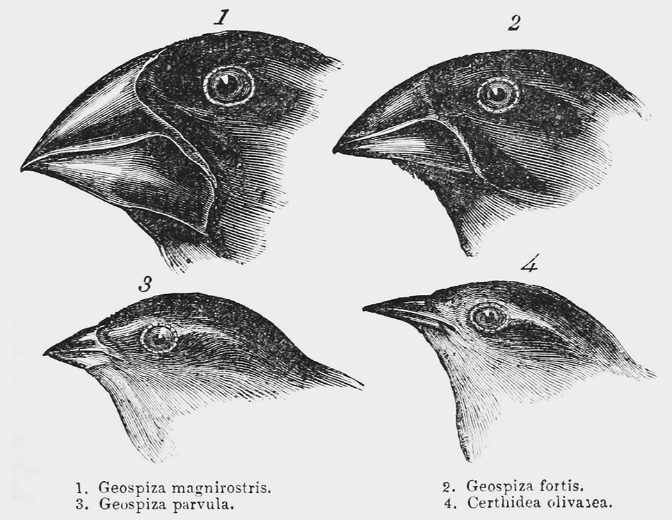

FIGURE 1.4. A drawing by the ornithologist John Gould in Darwin's *The Voyage of the Beagle,* showing several of the finches that are now often referred to as "Darwin's finches."

of Species. The most striking passage describes the finches of the Galápagos Islands: "Seeing this gradation and diversity of structure [of bills] in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends" (figure 1.4). This was his first published hint of what he had been thinking.

Birds figure in eleven of the fourteen chapters of *The Origin of Species*. Darwin had taken up pigeon breeding in order to learn how the diverse varieties of domestic pigeons had been formed by human selection of native Rock Doves (*Columba livia*). Pigeons dominate chapter 1 and recur throughout the book.[15] He describes how novel, inherited variations gave rise to breeds that differ more than whole genera and families of birds: "the Jacobin has the feathers so much reversed along the back of the neck that they form a hood"; the fantail has "thirty or even forty tail-feathers, instead of twelve or fourteen—the normal number in all the members of the great pigeon family" (and in many other bird families as well). In developing the idea of a "struggle for existence," he points out that the (Northern) Fulmar (*Fulmarus glacialis*) lays only one egg but is "the most numerous bird in the world"—showing that most species,

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which lay more eggs but are rarer, must suffer immense mortality. Writers on "natural theology" cited species' adaptations as evidence of the wisdom and beneficence of the Creator, but Darwin saw that many species have features that serve no function and instead show evidence of their ancestry. Referring to the Campo Flicker (*Colaptes campestris*; plate 3), he writes that "on the plains of La Plata, where not a tree grows, there is a woodpecker, which in every essential part of its organisation, even in its colouring, in the harsh tone of its voice, and undulatory flight, told me plainly of its close blood-relationship to our common species; yet it is a woodpecker which never climbs a tree!" Likewise, "what can be plainer," he asks, "than that the webbed feet of ducks and geese are formed for swimming? Yet there are upland geese with webbed feet which rarely go near the water," which he had seen in Chile.

In pondering human evolution, Darwin ventured that some human features could best be explained by what he called sexual selection, the subject of more than half of *The Descent of Man, and Selection in Relation to Sex* (1871). Sexual selection, meaning variation in mating success, was Darwin's explanation for many of the colors, crests, exaggerated tail feathers, wattles, behavioral displays, and other features (especially of males) that delight and intrigue everyone who has any interest in birds. Drawing on both his own observations and natural history literature, Darwin devotes four full chapters to birds and cites at least 170 species. Birds provided more evidence for his ideas about sexual selection than any other group of animals (figure 1.5).

I'll mention just a few later ornithological contributions to evolutionary science. Let's start in 1899. Darwin had presented massive evidence for descent with modification—the fact of evolution—but no direct evidence of natural selection. Apparently, neither he nor anyone else, for almost forty years after *The Origin of Species*, thought it would be possible to detect and measure natural selection, which Darwin thought would work extremely slowly, like the uplift of mountain ranges. Hermon Bumpus, in 1899, was one of the first to report natural selection. He made measurements of 136 distressed House Sparrows that were collected near Woods Hole, Massachusetts, after a severe winter storm. About half died and half recovered. Bumpus reported that those that deviated most from the average succumbed,[16] a pattern that we now call "stabilizing selection," which will maintain the status quo. Since then, similar measurements on hundreds of species have shown natural selection on many characteristics.

David Lack, whose career was mostly at Oxford University, christened the finches in the Galápagos Islands "Darwin's finches" in the 1940s and was the

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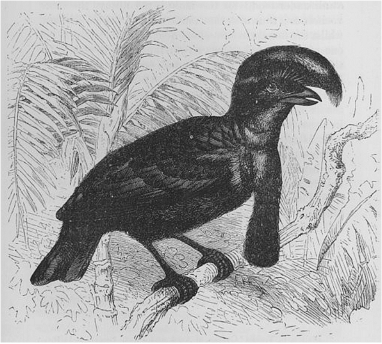

FIGURE 1.5. A South American Long-wattled Umbrellabird (*Cephalopterus penduliger*), in Darwin's *The Descent of Man, and Selection in Relation to Sex*. The male's wattle is one of many examples that Darwin proposed had evolved by sexual selection.

first to propose that they formed an "adaptive radiation," in which the related species had become adapted by natural selection to specialize on different food items. He suggested that they illustrated Darwin's idea that species diverge—become different—because specialization enables them to escape competition with other species.[17] This principle later became a major focus of ecologists who wanted to understand how species can coexist. Lack made an even more important contribution when he proposed and verified an explanation for why birds lay a certain number of eggs and no more. This was the start of a whole field of study: understanding why species have evolved differences in their reproductive rate and other aspects of their life history. I'll describe Lack's study in chapter 7.

Modern thinking about *speciation*—the process by which a species splits into two or more descendant species—starts with Ernst Mayr's studies of birds. Mayr entered biology through bird-watching as a young student in Germany. From 1927 to 1930, he collected birds in New Guinea and the Solomon Islands, and in 1931 he was hired by the American Museum of Natural History in New York to curate its large collection of birds from that region. These were the basis of his many papers on bird taxonomy and of his ideas about speciation. He presented these ideas, and synthesized a vast amount of evidence about what species are and how they are formed, in his 1942 book *Systematics and the Origin of Species*.[18] He continued to publish prolifically on evolution, bird systematics, and the philosophy and history of biology until his death in 2005 at the age of one hundred.

The family tree, or phylogeny, of species is both a basis for classification and a key to understanding the evolutionary history of species and their characteristics. Determining relationships among species is not easy, especially when it is based on similarity in just a few anatomical features. The muscles that operate a bird's sound-producing structure (syrinx) helped to distinguish perching birds (Passeriformes) as a distinct evolutionary branch, but it was hard to be sure that this one characteristic was a reliable index of relationship.

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The development of modern, more reliable methods came with the use of molecular information, especially DNA. Many evolutionary biologists developed (and continue to improve) these methods, but the first person to apply them to a large group of organisms was one of my teachers, the ornithologist Charles Sibley at Cornell University (later at Yale). The best DNA technology in his day, before DNA sequencing on a large scale was feasible, was a crude method, "DNA–DNA hybridization," which Sibley and his long-term collaborator, Jon Ahlquist, used to estimate relationships among thousands of species of birds.[19] Many of Sibley's claims were certainly wrong—but some were both surprising and apparently correct.

Two founders of the science of animal behavior, Konrad Lorenz in Germany and Niko Tinbergen in the Netherlands, developed their ideas partly by studying birds. Tinbergen, whose books included *The Herring Gull's World*, emphasized that one of the most important questions to ask of any animal's behavior is how and why it evolved. This approach has been a dominant theme in animal behavior since the 1960s, led largely by researchers on bird behavior. Similarly, David Lack, Robert MacArthur, Jared Diamond, and other students of birds were among the scientists who shaped an evolutionary approach to ecology, the scientific study of interactions between organisms and their environment.

These are some of the pioneers who drew on birds to develop major areas and ideas in evolutionary biology. A great many other students of birds, then and since, have developed these subject areas and have gained insight into the evolutionary history and causes of birds' characteristics and diversity. Some readers will have noticed that all the biologists I have mentioned so far are (White) men—as in most of biology and other sciences. It was only in 1937 that one of the first major studies by a woman was published: "Studies in the life history of the song sparrow," by Margaret Morse Nice[20]—a study more ecological than evolutionary in nature. Happily, women have more recently contributed many pathbreaking studies, as I describe in later chapters. Biologists throughout the world, including Asia and Latin America, conduct research on bird evolution, but unfortunately fewer people of color in the United States and Europe do so (although this too is changing).

So birds have been major players in all kinds of evolutionary studies—and this research has cast light on almost any aspect of bird biology and diversity you can think of. In the following chapters, I begin with evolutionary relationships among birds and what the fossil record tells of their history (chapters 2 and 3). I then turn to the process of adaptation by natural selection as revealed

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by studies of birds (chapter 4), to variation within bird populations—the raw material of evolution (chapter 5)—and to a few fascinating examples of birds' adaptations and how they are studied (chapter 6). The next three chapters answer questions about how birds' diverse life histories (chapter 7), sex lives (chapter 8), and social behaviors (chapter 9) have evolved by natural selection. After asking what species are and how they evolve (chapter 10), I return to birds' evolutionary history, asking what accounts for the geographic distribution and diversity of different groups of birds (chapter 11). Finally, in chapter 12, I ask what light evolutionary studies might cast on the future of birds: their survival or extinction in a world reshaped by humans.[21]

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