THE CORNELL LAB OF ORNITHOLOGY

HANDBOOK OF BIRD BIOLOGY

THIRD EDITION

EDITED BY
IRBY J. LOVETTE AND JOHN W. FITZPATRICK

TheCornellLab of Ornithology

WILEY

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Preface

At this very moment, somewhere on earth, the sun is rising and a dawn chorus of birdsong welcomes the new day. This never-ending avian symphony has been performed non-stop for millions of years, yet our scientific understanding of avian biology still improves with every passing year. This third edition of the *Handbook of Bird Biology* is intended as a current and helpful guide into the spectacular richness of bird diversity and the wonderful and varied ways that birds look, behave, display, function, and evolve.

The third edition of the *Handbook* extends a tradition that began in 1972 when the Cornell Lab of Ornithology first offered a Home Study Course in Ornithology to the general public. That early correspondence course comprised nine seminars on different topics, all written by the Cornell Lab's Director at the time, Dr. Olin Sewall Pettingill, Jr, an ornithologist known for helping connect recreational birdwatchers with scientific advances in avian biology. The first Home Study Course students received nine units of mimeographed sheets sent through the mail. Over the subsequent two decades, the materials increased in length and sophistication as the Home Study Course evolved and expanded. More than 10,000 students successfully passed their mailed-in exams and completed the course.

This material was expanded and modernized as it was incorporated into the 2004 second edition of the *Handbook*, which was produced as an impressively hefty single-volume book co-published by the Cornell Lab of Ornithology and Princeton University Press. It became a multi-authored endeavor with 11 chapters written by experts in their respective fields, each of whom lent their own personal style to explaining why birds look, act, and function in the ways that they do. The second edition remained the foundation of the continuing Home Study Course, used by an additional 5000 students from 65 countries. The book was likewise adopted as a textbook for many college-level ornithology courses and enjoyed as a general reference by many individuals interested in learning more about birds, even outside of any formal or informal coursework.

This third edition, published in 2016, represents an even more extensive overhaul of the content, presentation, and coverage of the *Handbook of Bird Biology*. The new edition's 15 chapters have been authored by 18 expert ornithologists, including five authors who extensively revised their well-regarded chapters from the second edition and 13 who contributed entirely new material. The new content includes extensive and expanded coverage of hundreds of recent discoveries and insights about avian ecology, behavior, evolution, physiology, anatomy, and conservation.

Given that birds are so visually appealing, it is appropriate that the new edition be presented in full color, a first for any general textbook of Ornithology. The 1150 photographs, illustrations, and figure elements depict hundreds of bird species, along with graphs and tables that explain intriguing facets of their underlying biology. The *Handbook* editors and authors express their deep thanks to the many individuals—credited in the figure legends—who generously contributed photographs or artwork to this edition.

Readers familiar with the earlier editions may notice that this edition is now global in its coverage of the world's birds and the people who study and conserve them. It includes examples featuring bird species that are collectively found literally everywhere on earth that birds occur. In addition to the venerable traditions of ornithological research in North America and Europe, exciting new discoveries are now constantly being made by ornithologists from the rest of the Americas, Africa, Asia, Australia, and islands around the world. Our hope is that readers of this book—wherever they might be—will enjoy finding out more about some of the most familiar birds that live around their homes, while also being inspired by learning about species that occur in far-away places.

A special new feature of the third edition is that it is complemented and supplemented by a wealth of online materials found on the Bird Academy website of the Cornell Lab of Ornithology (web link: **birdbiology.org**). These resources include interactive learning modules on topics ranging from feathers to sexual selection; high-quality video and audio clips chosen to represent behaviors or phenomena discussed in the text; animations that illustrate fundamental concepts in ornithology; longer feature-length coverage of special topics; and much more. The resources are conveniently organized in reference to the corresponding chapters of this *Handbook*. We encourage all readers to use this online material to supplement their readings here. This is especially helpful for the chapters on bird song (Chapter 10) and mating behavior (Chapter 9) where there is no better way to understand these behaviors than to hear or see examples of living birds in action.

In addition to the 18 chapter authors, the creation of this third edition was possible only through the dedicated efforts of the skilled editorial and production teams at the Cornell Lab of Ornithology and Wiley. The Editors express a debt of gratitude to their Cornell colleagues whose expertise and energy brought this book to completion, including Myrah Bridwell (Permissions Editor), Rebecca Brunner (Development Editor), Alexandra Class Freeman (Art Program Editor), Kevin McGowan (Advising Science Editor), Nancy Trautmann (Education Program Director), Mya Thompson (Online Content Manager), Melissa Walker (Citation Manager), and Megan Whitman (Project Manager). We are likewise deeply appreciative of the wise input and skillful management of this project from the editorial group at Wiley, from our initial discussions with Alan Crowden and Ward Cooper and ultimate project oversight by Kelvin Matthews, through to the production oversight by Emma Strickland and David McDade, hundreds of artistic contributions to figures by Debbie Maizels, production management by Rosie Hayden, skillful project management by Jane Andrew and indexing by Terrence Halliday. We feel extremely fortunate to have had the opportunity to work with such dedicated and professional individuals and teams from both organizations.

About the Cornell Lab of Ornithology

This *Handbook* is an educational resource created by the Cornell Lab of Ornithology, a unit of Cornell University located in Ithaca, New York, USA. The Cornell Lab is a world leader in the study, appreciation, and conservation of birds. Our hallmarks are scientific excellence and technological innovation to advance the understanding of nature and to engage people of all ages in learning about birds and protecting the planet. Our mission—which we take to heart and which guides all of our endeavors—is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds*.

Founded in 1915, the Cornell Lab has grown over the past century into an unusual amalgam of a university department, conservation organization, technology and engineering think-tank, and communications agency. Our staff and faculty number nearly 200 individuals, complemented by almost as many undergraduates, graduate students, and postdoctoral scholars from Cornell and from visiting institutions worldwide. Our vibrant broader community includes 400,000 citizen science participants from all walks of life and 14+ million bird enthusiasts of all ages who connect with us online at birds.cornell.edu.

The Cornell Lab is located in the Johnson Center for Birds and Biodiversity and surrounded by the Sapsucker Woods preserve. We invite all readers of this book to come and enjoy our visitor center and to go birding on our trails. If you cannot visit us in person, be sure to take advantage

The Cornell Lab of Ornithology. Located in the Johnson Center for Birds and Biodiversity, the Cornell Lab is both a unit of Cornell University and an international membership organization. Our mission is *to interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds*. (Photograph by Diane Tessaglia-Hymes © Cornell Lab of Ornithology.)

of our web resources, not only the companion site to this book but also our All About Birds website (**allaboutbirds.org**), our live cameras at active bird nests around the world (**cams.allaboutbirds.org**), our award-winning magazine *Living Bird* (**allaboutbirds.org/living-bird-latest-issue**), and our many citizen science projects (**birds.cornell.edu/citsci**) where you can get involved in collecting information that adds to our ornithological knowledge base to inform bird conservation and management.

We especially encourage all birders—from beginners to experts—to discover and use eBird. At ebird.org you can upload your own checklists and access a rich suite of resources designed to enhance your ability to find and identify birds, all at no cost. eBird is a truly global resource with web portals and partners in many languages and most countries.

We also invite all users of this book to become members of the Cornell Lab at **birds.cornell.edu**. As a non-profit organization, we depend on our members, donors, research, and our other programs for 99% of our operating budget. These resources support the continued development of this *Handbook* and its online enhancements, along with our many other endeavors in science, conservation, education, and outreach. Your engagement supports the advancement of ornithological science and the informed conservation of birds and their habitats worldwide.

Irby J. Lovette
Fuller Professor of Ornithology
Cornell Lab of Ornithology

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**

Bird Academy Web Resources

This *Handbook* is complemented by extensive online learning resources hosted on the Bird Academy site of the Cornell Lab of Ornithology. Be sure to visit **birdbiology.org** to access the web content associated with each *Handbook* chapter. These include hundreds of videos of wild birds, interactive learning modules and features, animated and annotated sound recordings, and in-depth articles on topics of particular importance about birds and their conservation.

We particularly encourage all readers to use the Bird Academy site when reading *Handbook* Chapter 10 on Avian Vocal Behavior. The spectrogram figures seen as static images in the printed chapter are playable on the Bird Academy site as animated recordings: you can hear the actual sounds and watch the visual display of the sonogram. The direct link to that enhanced Chapter 10 content is: **birdbiology.org/vocalbehavior**.

How to report errors and offer suggestions

We encourage all readers of this *Handbook* to visit **birdbiology.org/suggestions** to let us know if you find errors in the text or have other critiques to offer. At that same web link we also welcome suggestions about additional content that could be covered in future editions, newly published studies with relevant findings and discoveries, and all other kinds of feedback that can help the *Handbook* remain a useful and current resource for individuals interested in avian biology. We pay close attention to this feedback and thank all respondents for offering their input.

For additional online material please visit the
Bird Academy website of the Cornell Lab of Ornithology at **birdbiology.org**

Chapter 1 Why Study Birds?

Irby J. Lovette and John W. Fitzpatrick
Cornell Lab of Ornithology

Chapter contents

Birds have a special place in human science and culture: they capture our hearts, arouse our curiosities, and inspire a sense of wonder. We may revel in the diversity and simple beauty of their forms, but birds also fuel fascinations that drive us towards deeper scientific inquiries into their varied ways of life. Every student of ornithology—from recreational birders to career scientists—will find much to learn and appreciate in the extraordinary physical and behavioral adaptations of birds, their rich evolutionary history, and their commanding global presence.

One of the wonderful aspects of enjoying birds is that they are found nearly everywhere. Given that these outwardly delicate creatures must maintain an internal body temperature even higher than our own, their capacity to live in almost every environment on earth is staggering. Birds occupy windswept arctic tundra and harsh antarctic ice, fog-shrouded mountaintops and tropical rainforest understories, the world's driest deserts, and storm-swept high seas. They live amongst us in the most urbanized cities, in suburban backyards, and in the most remote wildernesses. Wherever we travel, birds are our constant companions, and by discovering more about the birds we find around us, we can come to understand many other aspects of the natural world and our relationship to it.

Birds are endlessly fascinating partly because they are so diverse. Birds make use of their myriad habitats with an almost bewildering array of foraging strategies, performing important ecological functions in the process. Many birds capture and eat other animals, from tiny insects to large vertebrates, sometimes including other birds. Some birds hunt by night, and a few even navigate by echolocation. Others hunt high in the sky with eyes far keener than our own, diving down with incredible speed and agility at a moment's notice; many are equally skilled in detecting insects on leaves or worms under the ground. Still others specialize in scavenging, thus speeding up the process of decomposition. Many birds eat nectar, seeds, or fruits, sometimes aiding in plant reproduction by serving as pollinators and seed dispersers.

The breeding strategies of birds are just as varied as their ecological roles. Many engage in complex choreography as a precursor to mating, often presenting highly decorative displays and intricate vocal performances. Some birds pair together for many years or live in extended families, while others mate only for an instant, never to see one another again. Some bird chicks are raised by groups of relatives, some by both parents, others by only their father or their mother, and a few receive no parental care at all. Some birds attempt to raise just one offspring in every alternate year, while other species can raise large broods of chicks several times within a single season. Bird nests come in a dazzling variety of forms, from simple scrapes on the ground, to intricately woven baskets, to messy piles of sticks that may weigh several tons.

Birds flap, hover, soar, glide, stoop, swim, dive, burrow, walk, hop, and even sprint. To us, they often appear—and quickly vanish—as a burst of motion and color. Through their longer movements, birds create living links among the

Opposite: This flock of Greater Flamingos (*Phoenicopterus roseus*) includes both colorful adult birds and whiter juveniles. (Photograph by Ian Davies.)

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Companion website: birdbiology.org

Fig. 1.01 Conifer needles are the principal food of the Spruce Grouse (*Falcipennis canadensis*). (Photograph by Christopher Wood.)

earth's continents, oceans, and hemispheres. Migratory species know the planet as a north-south stage to be traversed twice each year, generating one of the most remarkable global migration spectacles on earth. The annual return of individual birds to their precise breeding or winter territory seems almost miraculous, and this homing ability is a testament to their underlying adaptations for orientation as birds move across vast distances. Other kinds of birds are nomadic, sometimes wandering in great flocks in search of super-abundant food or prime breeding sites; yet other birds are home-bodies, remaining very close to their hatching site throughout their entire adult lives.

The songs of some birds are among nature's most evocative sounds. Birds make sounds primarily to communicate with other birds, but they do so in a great variety of ways and across a great range of auditory frequencies. For human birders and scientists, learning bird calls and songs is often the key to discovering what species are present in a habitat or location. Going further, we can eavesdrop on the more detailed lives of birds by learning how they use songs to defend territories, advertise to mates, warn of potential dangers, and communicate about their own status.

Beneath all this behavioral and ecological diversity of birds lies a remarkable vertebrate body structure and physiological potential. Birds have unique skeletons: every bird is equipped with specialized forelimbs and fused hand bones that together form a wing. Some birds' wings are proportionally too small for flight; others have wings that are modified into flippers for swimming. All birds have beaks, lay eggs, and breathe via a system of one-way airflow, which permits more efficient capture of oxygen than the in-and-out breathing pattern of mammals. Yet despite these similarities, birds have a wondrous variety of physical forms—from the smallest of hummingbirds to the towering ostriches—that are adapted to different ways of life. Their internal body processes are similarly multifarious: some birds can dive deep into water and remain submerged for minutes, others can fly at great heights where the air is thin and oxygen correspondingly poor. Different birds can extract energy and nutrients by digesting a great range of foods, from tough leaves to fluid nectar, and from tiny invertebrates to rodents swallowed whole. Some birds time their breeding based on subtle shifts in day length that cause cascading effects on their hormones and reproductive systems. Others use specialized areas of their brains to remember the locations of thousands of seeds that they have hidden for later consumption.

The external beauty of birds is enriched by their variety of feathers, which are magnificent in function as well as form.

Fig. 1.02 Scimitar-billed Woodcreepers (*Drymornis bridgesii*) are among the many bird species in which male–female pairs coordinate their songs to produce a synchronized duet. (Photograph by Ian Davies.)

Fig. 1.03 The Rufous-tailed Jacamar (*Galbula ruficauda*) uses its long bill to capture butterflies and other agile flying insects. (Photograph by Benjamin G. Freeman.)

Fig. 1.04 Penguins, like this Gentoo Penguin (*Pygoscelis papua*), have many morphological and physiological adaptations for their aquatic lifestyle. (Photograph by Christopher Wood.)

Feathers are an adaptation found in no other animal group today, but we now know that birds are the living descendants of otherwise extinct dinosaurs that also sported a great variety of feathered plumage. Feathers provide birds with thermal insulation, waterproofing, and, in many cases, facilitate their flight. Feathers come in bold or cryptic patterns, ornamental shapes, incredible shades of color, pure tones, impressive lengths, or, in just the right light, brilliant iridescence. Many birds offer a combination of these features that play a large role in both mate choice and camouflage.

There are enough species of living birds—10,000 or so—to keep the most ardent birders questing after new sightings throughout their lives. This rich diversity has evolved over 150 million years, creating the panoply of avian orders and families that populates our field guides. Over the smaller timescales that can be addressed in field studies, birds have provided some of the best examples of how evolutionary forces play out in time. Scientists have carefully documented how natural selection can change bird populations in just a few generations, and how intense sexual selection can drive the evolution of gaudy plumage and elaborate displays. Birds have therefore played a central role in our general understanding of these most basic processes by which species arise and change through time.

Birds have a similarly influential standing in our efforts to conserve the natural world. Birds serve as flagships for imperiled habitats and ecosystems, and as early warning systems for environmental toxins or other destructive forces. Conservation efforts focused on birds often help preserve many other less conspicuous organisms. And owing to their charisma and popularity with humans, birds can help inspire all of us towards being better stewards of natural systems and biodiversity.

This book is about all of these aspects of avian biology, and more. Thanks to a fortuitous combination of diversity, accessibility, and charisma, birds through the ages have taught humans an extraordinary amount about natural history. Nearly everyone on earth has seen and wondered about a bird, and this familiarity helps give birds their special inspirational power—birds capture our imagination and curiosity by simply being in our presence. Researchers over the years have harnessed this same accessibility of birds to answer questions in the laboratory and in the field with relative ease, especially compared with the challenges of studying most other animals. Dozens of principles in evolution, ecology, biogeography, behavior, neurobiology, life history theory, natural resource management, and conservation biology have been—and continue to be—discovered and refined through studies of birds. This book is intended as a tool to help all of its readers find further inspiration in the birds that form an important part of our lives.

1.1 Engaging with birds in the twenty-first century

Whether we study them as students, casual observers, lifelong learners, or professional scientists, birds can be mesmerizing any time we stop and simply watch them. At the bird feeder, at the city park, in a parking lot, at the beach, or in the woods, these creatures share the planet with us largely in disregard of our fascination with them. Pausing to observe birds employ their adaptations—those that allow them to fly, catch a fish in a flash, or show off gorgeous songs and plumage—is one of the most satisfying ways to connect personally with the details and the larger workings of the natural world. The more we watch them, the more we are likely to want to know about birds.

Today our intrinsic interest in birds can go further than ever before. We can learn, observe, and contribute to a dynamic and unprecedented collection of knowledge about birds. Significant gaps still exist in our understanding, but by simply watching and recording birds—even the most common ones—individuals and communities can make a big difference. Birds are extremely sensitive indicators of ecosystem conditions and quality. As humans continue to alter the natural world, the status of bird populations can provide clues about the type and scale of our impacts. Which bird species are declining, and which are increasing? Which species are successfully adapting to human-modified habitats, and why? As the planet warms, are birds changing their migratory routes, or spending the winter in different places?

Among all of the ways that we can engage with birds, "citizen science" projects deserve special mention owing to the benefits they generate for both their human participants and the avian subjects of their observations. Many local and regional citizen science endeavors provide enjoyable ways to enhance your engagement with the birds in your area. On a global scale, eBird (**ebird.org**) is the most geographically widespread avian citizen science initiative of all; it is based at the Cornell Lab of Ornithology, the same organization that developed this book, with partnering organizations in many countries and resources available in most of the world's major languages. The eBird project involves simple checklists of bird sightings submitted online by birders from every country in the world. The aggregation of this vast amount of information on bird distributions allows researchers to address questions that have, until now, been impossible to pursue. By sharing observations in the same database, people from all professions and walks of life directly increase global understanding of bird populations, movements, use of habitats, and relationships with humans.

Such studies are particularly crucial as we develop strategies to facilitate the coexistence of human cultures with stable and functioning natural systems. When we take the time to listen and understand them, birds become more than captivating creatures—they reveal themselves as indicators of environmental health. All over the world, humans are taking the pulse of the planet through their interactions with birds.

1.2 A short note on the names of birds

Depending on your place of origin, you may find that some familiar birds mentioned in this book have unfamiliar names, as there is some regional variation in the "official" English names of birds, and even greater variation in their colloquial names. Similarly, there are several authoritative lists of the world's bird species that are generally in high agreement with one another, but that differ in the way they "lump" or "split" a handful of species or higher taxonomic groups. All English and scientific names of birds used in this book follow the eBird/Clements Checklist version 6.9, which includes taxonomic updates through to August 2014. This Checklist and its more recent updates are freely accessible at **birds.cornell.edu/clementschecklist/**.

In this book, we treat the full English names of bird species as capitalized proper nouns. Group names and other variants are regular nouns and not capitalized. Thus you might read a sentence like: "Among all of the world's species of chickadees and tits, the Great Tit (*Parus major*) is one of the most widely distributed and best studied." The two-word Linnaean name (*Genus species*) is included every time a bird species is mentioned within the text in a new context or as a new example.

1.3 Birds and ornithology are both worldwide

This book is international in scope: birds are found worldwide, and ornithologists have conducted important studies of thousands of species in all of the major habitats and biomes of the earth. The discipline of ornithology is similarly global, as the scientific process of investigation is unconstrained by national boundaries and new discoveries about birds are constantly being published in scientific journals by researchers from all parts of the world.

In choosing examples to be included in this book, the authors and editors have purposefully selected species and studies that span this global breadth. If a particular example

Fig. 1.05 The Red-billed Leiothrix (*Leiothrix lutea*) is native to Asia, but its popularity as a cage-bird has led to introduced populations in other areas of the world. (Photograph by Ian Davies.)

treats a bird that is unfamiliar to you, consider whether any of the species that you know from your own region might exemplify a similar trait or phenomenon. More generally, we hope that this global breadth of examples helps inspire you to learn about the full range of avian diversity in all of its worldwide glory.

Although ornithological expertise is now truly global, in past times the scientific study of birds was centered largely in Europe and North America, and these regions still have more academic ornithologists than do some other areas of the world. The editors and authors of this book are primarily based in North America, with a few from Europe, although most of us have done field studies elsewhere. For these two reasons—ornithological history and our own familiarity—North American and European birds are somewhat overrepresented in this book in comparison to their total fraction of avian diversity. Nonetheless, readers from every other corner of the globe are sure to find examples in this book featuring birds found in their local area.

1.4 Web resources beyond this handbook

We hope that you feel excited and empowered with this book in your hands. We encourage you to treat it as an entry point into the lives of birds, for there is so much more to bird biology than we could squeeze into these chapters. This book is a product of the Cornell Lab of Ornithology, where our scientists and outreach experts have assembled a wealth of supplemental materials that accompany this book and which are free to access online. Using this book in combination with these web resources will enhance your learning about avian biology and simultaneously be a lot of fun. These online resources include video and audio files related to the material covered in each chapter; interactive, visually compelling modules that bring to life many of the principles outlined here; and much more.

Before reading further, be sure to access additional online content for this book at birdbiology.org.






Chapter 2 Avian Diversity and Classification

Irby J. Lovette
Cornell Lab of Ornithology

Chapter contents

The more than 10,000 species of modern birds share a common ancestor, birds that probably lived about 130 million years ago (Fig. 2.01). The evolutionary tree that stretches back through time to connect present-day birds with their avian ancestors provides the basis for classifying birds into a series of hierarchical groups, from the Class Aves, which includes all birds, down to the species that form the tips of the tree's branches. These nested groups are important because they provide a system of classification that helps organize avian diversity in a way that is both evolutionarily correct and useful to birders and ornithologists.

This is a particularly exciting time for people interested in the evolutionary relationships of birds. Rapid advances in genetic technologies make it possible to access the entirety of avian genomes, providing a wealth of comparative information about living birds that can be used to reconstruct their evolutionary relationships and learn how their genes control aspects of avian physiology, behavior, and ecology. Meanwhile, spectacular fossil discoveries continue to expand our understanding of ancient birds and their affinities both to one another and to other dinosaurs. A comprehensive picture of the relationships of all living birds, and a good understanding of where they came from, is now within reach.

This chapter concludes with an overview of all orders and families of living birds. These categories are essential tools for organizing avian diversity for both scientists and birders.

2.1 Classifying avian diversity

Today there are slightly more than 10,000 species of living birds, according to the most commonly accepted classifications of worldwide avian diversity. The scientists who study this diversity are called systematists. The field of systematics involves two general pursuits. One is the **classification** of birds and other organisms into a hierarchy of taxonomic levels, such as species and families. This endeavor focuses on describing newly discovered species and on understanding the distinctions between species. The other task of systematics is to uncover the relationships between taxonomic groups and to look back through time to reconstruct their evolutionary histories. Most commonly, this historical investigation involves creating an underlying evolutionary tree, or **phylogeny**.

Classification: in an evolutionary context, the process by which scientists name organisms and assign them into larger groups based on their evolutionary relatedness.

Phylogeny (or phylogenetic tree): a diagram that depicts the evolutionary relationships connecting a set of organisms.

Opposite: Stunning *Tangara* tanager diversity. Many species in this neotropical genus frequently forage together in mixed flocks. Species, clockwise from top left: Black-capped Tanager (*T. heinei*), Brassy-breasted Tanager (*T. desmaresti*), Black-backed Tanager (*T. peruviana*), Green-headed Tanager (*T. seledon*), Silver-throated Tanager (*T. icterocephala*), Red-necked Tanager (*T. cyanocephala*). (Photographers, clockwise from top left: Andy Johnson, João Sérgio Barros Freitas de Souza, Almir Cândido de Almeida, Dario Sanches, Juan Ignacio Zamora Mora, Frank Shufelt.)

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Companion website: birdbiology.org

Fig. 2.01 All living birds share a common ancestor. Despite their incredible diversity in forms and ways of life, all living birds—including the (A) African Wood-Owl (*Strix woodfordii*), (B) Orange-headed Thrush (*Geokichla citrina*), and (C) Tufted Puffin (*Fratercula cirrhata*)—descend from a common avian ancestor. (Photographs by: A, Roger Wasley; B, Shashi Shankar Hosur; C, Christopher Wood.)

These two endeavors are fundamentally linked to one another. For example, an avian systematist who discovers a bird that could be a new species will likely describe the particular characteristics that help define it as a distinct entity, while also placing the new species within a broader evolutionary tree that includes other related species. Our understanding of both the classification and phylogeny of birds has improved greatly in recent years, in part because of new discoveries and in part because of technological advances.

2.1.1 Avian classification

A quick flip through a typical bird field guide will reveal that the birds in it are organized meaningfully: for example, the ducks and geese are grouped together, and they are clustered separately from other superficially similar waterbirds such as loons, grebes, or cormorants (Fig. 2.02). These groupings are based primarily on studies of museum specimens over the past 150 years (Boxes 2.01 and 2.02; Chapter 6), and they reflect our understanding of bird evolution and the way it has played out over time as a branching, hierarchical process. For example, the ducks and typical geese are all more related to one another than they are to any members of other groups, and they are therefore classified together in the family Anatidae. Within this family, species that are even more closely related to each other are then placed within the same genus; for example, the genus *Anas* includes several dozen species of dabbling ducks, including the Mallard (*Anas platyrhynchos*) and related species of teals, wigeons, shovelers, and pintails. This classification structure allows us to place birds into increasingly inclusive categories, as shown in Fig. 2.03, in which each level includes all the members of the previous ranks, going back to the common shared ancestor of all birds. Most field guides and other references on bird diversity follow this organizational practice of putting the most closely related species together, usually by grouping together birds in the same family.

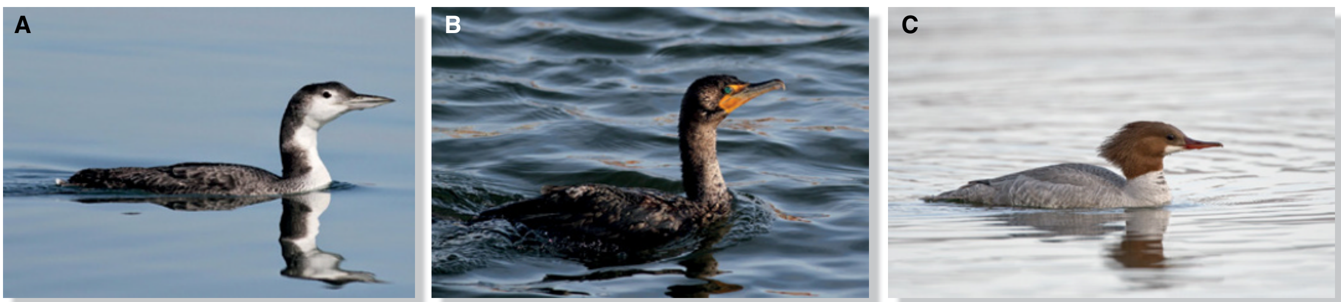

Fig. 2.02 Similar-looking birds in different taxonomic groups. Despite their superficially similar appearances, the (A) Common Loon (*Gavia immer*), (B) Double-crested Cormorant (*Phalacrocorax auritus*), and (C) Common Merganser (*Mergus merganser*) are only distantly related—each belongs to a different order. (Photographs by: A and B, Jay McGowan; C, Christopher Wood.)

Box 2.01 The importance of scientific collecting

Our understanding of living birds is founded on studies of specimens that have been collected and prepared over the past two centuries, and which now are curated in museums around the world. Some of the largest museums hold more than 1 million bird specimens, others only a handful, but all are important for the record of avian diversity they preserve.

A collection of specimens is a physical archive of actual biodiversity that records which birds were present in particular times and places, along with a great variety of information about the birds themselves, such as the habitat they were found in, detailed features of their internal and external anatomy, and the DNA content of each bird's genome. Bird specimen collections therefore are an irreplaceable resource used by a wide range of ornithological researchers and conservation professionals, as well as by students, teachers, and artists.

Although museum curators frequently salvage birds that die from other causes—such as birds that hit windows or cars, or that are caught in commercial fishing nets—and turn them into specimens, most specimens in the world's museums were collected intentionally for that purpose. The era of intense scientific collecting spanned the late 1800s into the mid-1900s, but this endeavor continues today. No ornithologist enjoys intentionally sacrificing birds, but many would argue that when done responsibly, the value of new specimens is high enough to justify the endeavor. Others disagree, and emotions can run high on both sides of the pro-collecting and anti-collecting debate.

One question often asked by first-time visitors to a large museum collection is: "Why do you need so many specimens? Wouldn't one or a few specimens of each species be enough?" For some kinds of research, one specimen is adequate, but for most studies it is important to be able to measure the degree of variation within each species. This broader sampling is especially essential in any study that uses statistics to compare different groups of birds.

A natural related question is: "You have so many specimens already; why do you keep collecting more?" One answer is that birds and their distributions change over time, and having new specimens allows researchers to study these changes. Another answer is that we can glean more data from new specimens than from older material. Current specimen preparators are careful to record every aspect they can about a bird they convert into a specimen, whereas a label on a specimen from the nineteenth century might indicate only the country in which it was obtained. Modern specimens also are accompanied by new types of materials, such as frozen tissue samples, which allow types of analyses that are impossible with older samples.

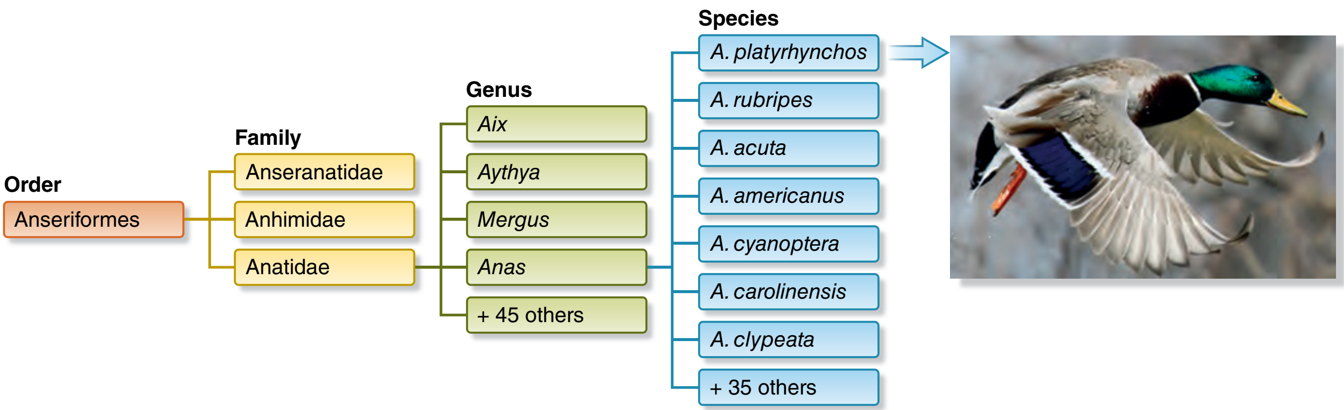

Fig. 2.03 Avian classification. The Linnaean system categorizes organisms within hierarchical levels based on their relatedness to other taxa, down to the principal unit of species—as illustrated here with the Mallard (*Anas platyrhynchos*). (© Cornell Lab of Ornithology; photograph by Randy E. Crisp.)

Box 2.02 Preparing bird specimens

When people think of bird specimens in a museum, they often envision the taxidermy mounts in exhibit displays that show birds in realistic postures. Specimens made for research purposes, however, almost never take on this lifelike appearance. Instead, scientific bird specimens traditionally have been prepared in one of three ways: round skins, wet specimens, or skeletons.

Most specimens are in the form of round skins, in which most of the bird's internal parts are removed and replaced with stuffing (Fig. 2.B2.01). The specimen then is dried in a standard stretched-out orientation, with the wings folded at the side and the bill pointing forward. Advantages of round skins include the ease of taking many standard measurements of structures such as the bill, wing, and tail, and the practical utility of fitting many specimens together in one museum drawer.

Making a beautiful round skin requires practice and skill. The parts of the bird that could rot must be removed, and, in the process, the entire skin is turned inside-out, stuffed, and then sewn back together. Once dried, round skins are generally stable: on opening a specimen drawer, it can be difficult to distinguish round skins that are more than a century old from those that were recently collected. Moisture and insects are the greatest threats to round skins.

Museum collections also may include wet specimens, entire birds that are first fixed using formalin—which helps keep their tissues hard—and then stored in jars full of alcohol. Wet specimens are particularly useful for studies of avian anatomy because they preserve the internal structures and organs that are destroyed when making a round skin.

Skeletons are a third common type of bird specimen (Chapter 6). To make a skeleton, first the skin and feathers are removed, along with the organs and largest muscles. Then the remaining carcass often is put into a bin containing dermestid beetles that eat the remaining fleshy tissues but not the bones. The cleaned bones later are numbered and stored in a small box.

Most specimen preparators try to maximize the information that can be gleaned from each specimen, so they also freeze bits of tissue for genetic and other biochemical analyses, and they may also preserve the contents of the crop and stomach for diet analysis.

Laws about possessing and transporting dead birds vary widely around the world. Although some museums are happy to receive carcasses of birds that have died from natural causes, it is critically important to check with them in advance to ensure that no regulations are violated in the process. In any situation in which a dead bird might become a specimen, it is essential to record exactly where and when the dead bird was found. This procedure usually is done by writing these data on a slip of paper and bagging it securely together with the bird before placing it in a freezer.

Fig. 2.B2.01 Round skins in avian research collections. This common type of museum specimen preserves the bird's external anatomy, including the plumage. When kept dry and away from destructive insects, round skins remain useful indefinitely. These specimens—including some that are more than a century old—are from the Cornell University Museum of Vertebrates collection. (Photograph by Jennifer Campbell-Smith.)

Fig. 2.04 Distinctive variants of the same species. Despite their different coloration, these two male Asian Paradise-Flycatchers (*Terpsiphone paradisi*) are members of the same species. Individuals of both forms often occur and interbreed at the same location. (Photographs by: left, Manish Panchal; right, Dr. George Mothi Justin.)

Within this classification system, the **species** is the most fundamental and broadly used unit of avian diversity. As covered later in this chapter, ornithologists have devised many definitions for what exactly constitutes a bird species, but in general terms each bird species looks or behaves differently from related species, tends not to interbreed with members of other species, and has a past history of being evolutionarily distinct from other species.

Below the species level, ornithologists may describe **subspecies**, populations that differ in subtle attributes from other populations of the species. In situations where subspecies are readily distinguished by plumage differences or other distinctive traits, they may be illustrated separately in field guides. For example, the single Barn Swallow subspecies that breeds in North America (*Hirundo rustica erythrogaster*) has reddish underparts, whereas the subspecies that breeds across much of Europe and Asia (*Hirundo rustica rustica*) has snowy white underparts (Chapter 3). Although some bird subspecies have been defined carefully and show distinctive traits, such regional variants are not sufficiently different to cause them to be treated as fully separate species. Many named subspecies, however, are the result of older studies that do not meet modern standards because of limited sampling, obsolete criteria, or a focus on subjective differences among the subspecies. Still other subspecies are known to have fuzzy boundaries, with one subspecies blending into the next where their ranges overlap; sometimes birds showing this kind of geographical variation are instead referred to as being of different *races* of the same species. Often it is convenient to be able to give a name to a truly distinctive bird population, but many birds can be assigned to a particular subspecies or race only by knowing where they were observed. At an even finer scale, some birds show distinctive variants even within a single location; the forms of these species with distinctive plumage or markings are termed *morphs* (Fig. 2.04).

Above the species level, avian taxonomy is somewhat more straightforward. When the classification is correctly assigned, every higher grouping, from a particular genus—such as the genus *Anas* into which the Mallard falls—all the way to the Class Aves—which includes all birds—includes an ancestral bird species and all of its descendants. This important criterion means that every named group of birds reflects a true evolutionary unit and that these units can be assembled into a hierarchy representative of the underlying evolutionary tree of all birds. In technical terms, these categories each represent **monophyletic groups**, or **clades**. These interchangeable terms refer to the complete

Species: the basic unit of biological classification for birds. Criteria for defining bird species vary, but they generally group into a single species the individuals and populations with very similar traits, a history of recently shared ancestors, and the continued ability to fully interbreed.

Subspecies: in birds, a distinct population or group of populations within a more widespread species that is distinguishable from other subspecies on the basis of one or more diagnostic traits.

Monophyletic group: in evolutionary terms, any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

Clade: a synonym for a monophyletic group, referring therefore to any group of organisms that includes the most recent common ancestor of that group and all of its past and present descendants.

collection of evolutionary lineages past and present that share a common ancestor.

In theory, every split in the evolutionary tree of birds could be used to define one of these taxonomic categories, and some avian systematists argue for exactly this approach. Unfortunately, giving a name to every such split would result in many thousands of avian groups, and the names would change with every advance in our understanding of the evolutionary tree of birds. Instead, most traditional and current avian classifications use a much smaller group of hierarchical categories, such as the familiar levels of genera, families, and orders. Although the placement of the boundaries between these higher ranks is somewhat arbitrary and is highly influenced by past practices and our own organizational convenience, this approach leads to a manageable number of taxonomic categories. As described later in this chapter, our understanding of avian relationships is improving rapidly, so even the traditional taxonomic hierarchy of birds is being modified to reflect new discoveries about how these groups and their constituents are related to one another.

2.1.2 Naming bird species

The concept of hierarchical classification actually predates our modern understanding of evolution. The hierarchical classification system still in use today—the Linnaean System—is named after Carl Linnaeus, the Swedish biologist who in the 1730s developed and popularized a system of nomenclature in which each organism is given a two-word scientific name indicating its genus and species. For example, the scientific name of the House Sparrow is *Passer domesticus*. The first word in this type of **binomial name** refers to the genus in which the species is placed: the House Sparrow is in the genus *Passer* along with more than 20 other Old World sparrow species with which it shares a common ancestor (Fig. 2.05). In a Linnaean binomial name, the first letter of the genus name is capitalized. The second word in the name—*domesticus*—is the species name, which refers only to the House Sparrow; the species part of the binomial is never capitalized.

Although birds are most commonly referred to using this two-word naming system, technical publications on avian diversity sometimes use more elaborate versions with additional levels. For example, a reference to "*Passer domesticus rufidorsalis* Brehm 1855" includes an additional word—*rufidorsalis*—that refers specifically to the subspecies of House Sparrow found in the Nile Valley of Africa, as well as a reference indicating that this subspecies was formally described in an 1855 paper by the German ornithologist Alfred Brehm.

Every bird species is given a scientific binomial name when it is first described formally in a publication. A standardized set of rules set by the International Commission on Zoological Nomenclature (ICZN), the governing body charged with setting the criteria for animal nomenclature, must be followed by the person or team describing the new species. As explorers penetrate the last remote areas of the world, the naming of new bird species is becoming increasingly rare, with only a few such discoveries each year. Sometimes, however, new birds are found in less remote areas, as in the recent discovery of the Cambodian Tailorbird (*Orthotomus chaktomuk*) in the highly populated floodplain of the Mekong River (Mahood et al. 2013) (Fig. 2.06). In contrast to the earlier days of exploration, when it was common to name a species for oneself or in recognition of a sponsor, the scientific names of new species now are based most often on the new bird's region, the local language, a distinctive trait of the species, or the name

Binomial name: a naming system in biology in which each species is assigned a unique name consisting of two parts, the name of the genus and the name of the species, as in the scientific name of the House Sparrow: *Passer domesticus*.

Fig. 2.05 Binomial nomenclature. As indicated by their scientific names, (A) the House Sparrow (*Passer domesticus*), (B) the Eurasian Tree Sparrow (*Passer montanus*), and (C) the Cape Sparrow (*Passer melanurus*) all belong to the same genus, *Passer*. (Photographs by: A, Jay Diaz, KoolPix; B, Johan van Beilen; C, Ian White.)

Fig. 2.06 New birds are still being described. The Cambodian Tailorbird (*Orthotomus chaktomuk*) was first discovered in 2009 as a serendipitous outcome of a research program on avian influenza. (Photograph by James Eaton, Birdtour Asia.)

of an influential scientist. The species name *chaktomuk* of the Cambodian Tailorbird, for example, is based on a Khmer language term for the region near the city of Phnom Penh where the bird was discovered.

In addition to discoveries of previously unknown species, we are steadily gaining a better understanding of variation within and among previously described species. This improved understanding can lead to the **lumping** together of two species formerly considered distinct species into one single species. More commonly, however, populations within a described species are found to be more different than previously thought, leading to the **splitting** of one former species into two or more species. For example, the widespread bird known in Eurasia as simply the Wren and in North America as the Winter Wren was long considered to be the same species (*Troglodytes troglodytes*), but studies of genetic and song differences (Drovetski et al. 2004; Toews and Irwin 2008) recently led to a three-way split that divided the Eurasian Wren (*Troglodytes troglodytes*) from two species in North America, the western Pacific Wren (*Troglodytes pacificus*) and the eastern Winter Wren (*Troglodytes hiemalis*) (Fig. 2.07). As with the split of these wren species, changes in bird classification are usually first motivated by scientific studies that present new information on the underlying biology of the species being lumped or split. Ultimately, the formal decision about which species to recognize (and the names they are given) usually rests with regional committees of professional ornithologists that weigh the evidence for each potential change.

Lumping: informal term for changes in classification that involve merging into one species two or more taxa that were previously each considered to be a separate species.

Splitting: informal term for changes in classification that involve separating into different species populations that were previously considered to be part of a single species.

2.1.3 English and local names

Although every bird species has a formal scientific name, most people who enjoy birds—including professional ornithologists—refer to a bird by its common name in their local language. Although lists of worldwide common bird names exist in several languages, the most comprehensive common name systems for birds are in English. Worldwide, every bird species has a common English name, and occasionally more than one if it has varying names in different parts of the world. For example, the species scientifically known as *Gavia immer* has long been known as the Common Loon in North America but as the Great Northern Diver in Eurasia. An international group of ornithologists has proposed a standardized list of English names for all birds in order to reduce these regional naming discrepancies (Gill and Wright 2006). In their system, for example, the English name of *G. immer* is a compromise between the North American and Eurasian variations: the Great Northern Loon. Although nobody enjoys changing long-standing and familiar names, the general goal of improving worldwide communication about birds through consistent terminology is laudable.

Bird species often have additional names in local dialects or languages that reflect a direct understanding of that bird's ecology or behavior. For example, in Jamaica, the Snowy Egret (*Egretta thula*) is known as "Golden Slippers," a reference to the bright yellow feet at the base of its black legs (Chapter 8). Likewise, several cuckoos from Jamaica are known as "rainbirds," because they often call before or after downpours (Downer and Sutton 1990).

Comparisons of local names used by indigenous communities with the scientific names given by ornithologists usually reflect very similar patterns of classification. Both groups of observers recognize very similar sets of species and often distinguish nearly each species with a different name. This suggests that both indigenous and scientific communities fundamentally categorize avian diversity very similarly, probably in response to the real biological differences that separate bird species from one another.

2.1.4 Defining species

Ornithologists who classify bird species follow standard criteria to judge whether two bird populations are members of the same or different species. These boundaries usually are obvious and uncontroversial, but sometimes different scientists reach opposing conclusions about where

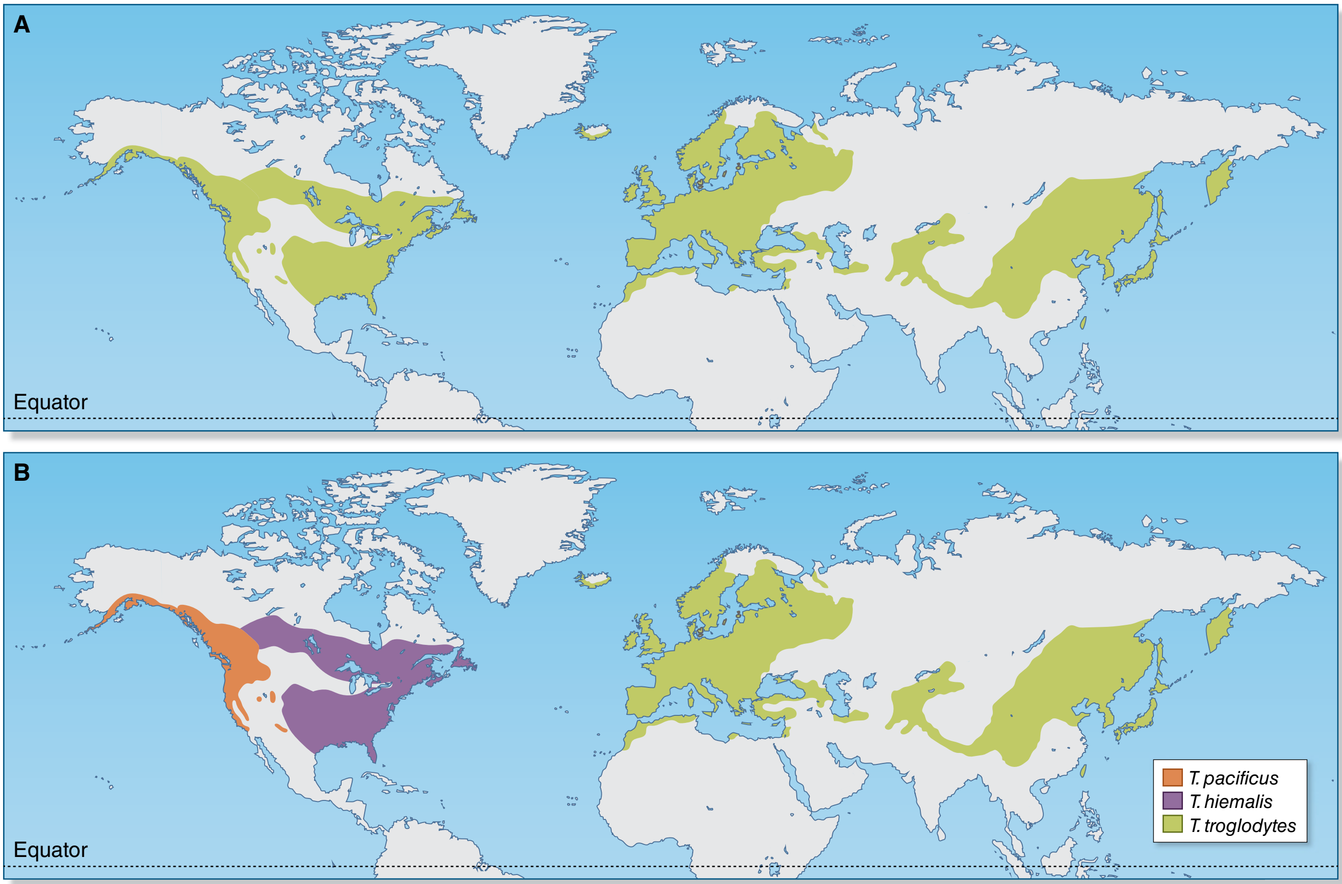

Fig. 2.07 Splitting species based on new evidence. (A) The Winter Wren was once considered to be one species (*Troglodytes troglodytes*) with an extremely broad range (green). (B) On the basis of new behavioral and molecular evidence, these birds have been divided into three separate species: the Eurasian Wren (which kept the original scientific name, *Troglodytes troglodytes*; green), the Pacific Wren (*Troglodytes pacificus*; orange), and the Winter Wren (*Troglodytes hiemalis*; purple). (© Cornell Lab of Ornithology.)

to draw the biological lines delineating different species. In these more complicated scenarios, it is important to remember that the entities we now classify as distinct species all formed over time through the gradual evolutionary process of **speciation** (Chapter 3). Because the speciation process involves one ancestor species gradually splitting into two or more descendant species, it is not surprising that there are points along that evolutionary pathway where conflicting classifications can be drawn, depending on what kind of evidence is considered.

Most birds occur in discrete **populations**, groups of individuals that breed in locations that may be separated in space from other similar populations. Imagine that you have to make a decision about whether the bird populations on two nearby islands belong to the same or different species. The birds from these two islands are generally very similar and clearly closely related, but they also differ in some subtle aspects of their plumage and courtship behavior. What evidence should you examine and what criteria should you use to decide whether they are one or two species?

To define species, biologists refer to **species concepts** that highlight the most important criteria used to decide whether two populations belong to the same or different species. The two most prevalent species concepts in

Speciation: the evolutionary process by which one ancestor lineage splits into two or more descendant species.

Population: in ornithology, a group of interbreeding birds of the same species that live in the same place at the same time.

Species concept: the precise sets of criteria that systematists use when deciding whether two populations are members of the same species, or two separate species. Different species concepts tend to emphasize different such criteria, sometimes leading to disagreements about classification.