Grzimek's
Animal Life Encyclopedia

Second Edition

Grzimek's
Animal Life Encyclopedia

Second Edition

Volume 8
Birds I

Jerome A. Jackson, Advisory Editor
Walter J. Bock, Taxonomic Editor
Donna Olendorf, Project Editor

Joseph E. Trumpey, Chief Scientific Illustrator

Michael Hutchins, Series Editor
In association with the American Zoo and Aquarium Association

GALE®

THOMSON GALE™

Detroit • New York • San Diego • San Francisco • Cleveland • New Haven, Conn. • Waterville, Maine • London • Munich

Grzimek's Animal Life Encyclopedia, Second Edition
Volume 8: Birds I

Project Editor
Donna Olendorf

Editorial
Deirdre Blanchfield, Madeline Harris, Christine Jeryan, Kristine M. Krapp, Kate Kretschmann, Melissa C. McDade, Mark Springer

Permissions
Kim Davis

Imaging and Multimedia
Mary K. Grimes, Lezlie Light, Christine O'Bryan, Barbara Yarrow, Robyn V. Young

Product Design
Tracey Rowens, Jennifer Wahi

Manufacturing
Dorothy Maki, Evi Seoud, Mary Beth Trimper

© 2003 by Gale. Gale is an imprint of The Gale Group, Inc., a division of Thomson Learning Inc.

Gale and Design™ and Thomson Learning™ are trademarks used herein under license.

For more information, contact
The Gale Group, Inc.
27500 Drake Rd.
Farmington Hills, MI 48331–3535
Or you can visit our Internet site at http://www.gale.com

ALL RIGHTS RESERVED
No part of this work covered by the copyright hereon may be reproduced or used in any form or by any means—graphic, electronic, or mechanical, including photocopying, recording, taping, Web distribution, or information storage retrieval systems—without the written permission of the publisher.

For permission to use material from this product, submit your request via Web at http://www.gale-edit.com/permissions, or you may download our Permissions Request form and submit your request by fax or mail to: The Gale Group, Inc., Permissions Department, 27500 Drake Road, Farmington Hills, MI, 48331-3535, Permissions hotline: 248-699-8074 or 800-877-4253, ext. 8006, Fax: 248-699-8074 or 800-762-4058.

Cover photo of great egret (*Casmerodius albus*) by M.H. Sharp, Photo Researchers, Inc. Back cover photos of sea anemone by AP/Wide World Photos/University of Wisconsin-Superior; land snail, lionfish, golden frog, and green python by JLM Visuals; red-legged locust © 2001 Susan Sam; hornbill by Margaret F. Kinnaird; and tiger by Jeff Lepore/Photo Researchers. All reproduced by permission.

While every effort has been made to ensure the reliability of the information presented in this publication, The Gale Group, Inc. does not guarantee the accuracy of the data contained herein. The Gale Group, Inc. accepts no payment for listing; and inclusion in the publication of any organization, agency, institution, publication, service, or individual does not imply endorsement of the editors and publisher. Errors brought to the attention of the publisher and verified to the satisfaction of the publisher will be corrected in future editions.

ISBN 0-7876-5362-4 (vols. 1-17 set)
0-7876-6571-1 (vols. 8-11 set)
0-7876-5784-0 (vol. 8)
0-7876-5785-9 (vol. 9)
0-7876-5786-7 (vol. 10)
0-7876-5787-5 (vol. 11)

LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA

Grzimek, Bernhard.
[Tierleben. English]
Grzimek's animal life encyclopedia.— 2nd ed.
v. cm.
Includes bibliographical references.
Contents: v. 1. Lower metazoans and lesser deuterosomes / Neil Schlager, editor — v. 2. Protostomes / Neil Schlager, editor — v. 3. Insects / Neil Schlager, editor — v. 4-5. Fishes I-II / Neil Schlager, editor — v. 6. Amphibians / Neil Schlager, editor — v. 7. Reptiles / Neil Schlager, editor — v. 8-11. Birds I-IV / Donna Olendorf, editor — v. 12-16. Mammals I-V / Melissa C. McDade, editor — v. 17. Cumulative index / Melissa C. McDade, editor.
ISBN 0-7876-5362-4 (set hardcover : alk. paper)
1. Zoology—Encyclopedias. I. Title: Animal life encyclopedia. II. Schlager, Neil, 1966- III. Olendorf, Donna IV. McDade, Melissa C. V. American Zoo and Aquarium Association. VI. Title.
QL7 .G7813 2004
590′.3—dc21
2002003351

Printed in the United States of America
10 9 8 7 6 5 4 3 2 1

Recommended citation: *Grzimek's Animal Life Encyclopedia*, 2nd edition. Volumes 8–11, *Birds I–IV*, edited by Michael Hutchins, Jerome A. Jackson, Walter J. Bock, and Donna Olendorf. Farmington Hills, MI: Gale Group, 2002.

Contents

Foreword viii
How to use this book xi
Advisory boards xiii
Contributing writers xv
Contributing illustrators xviii

Volume 8: Birds I
What is a bird? 3
Birds and humans 19
Avian migration and navigation 29
Avian song 37
Avian flight 45

Order STRUTHIONIFORMES
Tinamous and ratites 53
Family: Tinamous 57
Family: Rheas 69
Family: Cassowaries 75
Family: Emus 83
Family: Kiwis 89
Family: Moas 95
Family: Ostriches 99
Family: Elephant birds 103

Order PROCELLARIIFORMES
Tubenosed seabirds 107
Family: Albatrosses 113
Family: Shearwaters, petrels, and fulmars 123
Family: Storm-petrels 135
Family: Diving-petrels 143

Order SPHENISCIFORMES
Penguins
Family: Penguins 147

Order GAVIIFORMES
Loons
Family: Loons 159

Order PODICIPEDIFORMES
Grebes
Family: Grebes 169

Order PELECANIFORMES
Pelicans and cormorants 183
Family: Tropicbirds 187
Family: Frigatebirds 193
Family: Cormorants and anhingas 201
Family: Boobies and gannets 211
Family: Pelicans 225

Order CICONIIFORMES
Herons, storks, spoonbills, ibis, and New World vultures 233
Family: Herons and bitterns 239
Family: Hammerheads 261
Family: Storks 265
Family: New World vultures 275
Family: Shoebills 287
Family: Ibises and spoonbills 291

Order PHOENICOPTERIFORMES
Flamingos
Family: Flamingos 303

Order FALCONIFORMES
Diurnal birds of prey 313
Family: Hawks and eagles 317
Family: Secretary birds 343
Family: Falcons and caracaras 347

Order ANSERIFORMES
Ducks, geese, swans, and screamers 363
Family: Ducks, geese, and swans 369
Family: Screamers 393

Order GALLIFORMES
Chicken-like birds 399
Family: Moundbuilders 403
Family: Curassows, guans, and chachalacas 413
Family: Guineafowl 425
Family: Fowls and pheasants 433
Family: New World quails 455

Order OPISTHOCOMIFORMES
Hoatzins
Family: Hoatzins 465

For further reading 469
Organizations 474
Contributors to the first edition 479
Glossary 486
Aves species list 497
Geologic time scale 560
Index 561

Volume 9: Birds II
Order GRUIFORMES
Cranes, rails, and relatives 1
Family: Mesites and roatelos 5
Family: Buttonquails 11
Family: Cranes 23
Family: Limpkins 37
Family: Kagus 41
Family: Rails, coots, and moorhens 45
Family: Sungrebes 69
Family: Sunbitterns 73
Family: Trumpeters 77
Family: Seriemas 85
Family: Bustards 91

Order CHARADRIIFORMES
Gulls, terns, plovers, and other shorebirds 101
Family: Jacanas 107
Family: Painted snipes 115
Family: Crab plovers 121
Family: Oystercatchers 125
Family: Stilts and avocets 133
Family: Thick-knees 143
Family: Pratincoles and coursers 151
Family: Plovers and lapwings 161
Family: Sandpipers 175
Family: Seedsnipes 189
Family: Sheathbills 197
Family: Gulls and terns 203
Family: Auks, puffins, and murres 219

Order PTEROCLIFORMES
Sandgrouse
Family: Sandgrouse 231

Order COLUMBIFORMES
Pigeons, doves, and dodos 241
Family: Pigeons and doves 247
Family: Dodos and solitaires 269

Order PSITTACIFORMES
Parrots
Family: Parrots 275

Order MUSOPHAGIFORMES
Turacos and plantain eaters
Family: Turacos and plantain eaters 299

Order CUCULIFORMES
Cuckoos, anis, and roadrunners
Family: Cuckoos, anis, and roadrunners 311

Order STRIGIFORMES
Owls 331
Family: Barn owls 335
Family: Owls 345

Order CAPRIMULGIFORMES
Nightjars 367
Family: Oilbirds 373
Family: Frogmouths 377
Family: Owlet-nightjars 387
Family: Potoos 395
Family: Nightjars 401

Order APODIFORMES
Swifts and hummingbirds 415
Family: Swifts 421
Family: Tree swifts 433
Family: Hummingbirds 437

Order COLIIFORMES
Mousebirds
Family: Mousebirds 469

Order TROGONIFORMES
Trogons
Family: Trogons 477

For further reading 487
Organizations 492
Contributors to the first edition 497
Glossary 504
Aves species list 515
Geologic time scale 578
Index 579

Volume 10: Birds III
Order CORACIIFORMES
Kingfishers, todies, hoopoes, and relatives 1
Family: Kingfishers 5
Family: Todies 25
Family: Motmots 31
Family: Bee-eaters 39
Family: Rollers 51
Family: Hoopoes 61
Family: Woodhoopoes 65
Family: Hornbills 71

Order PICIFORMES
Woodpeckers and relatives 85
Family: Jacamars 91
Family: Puffbirds 101
Family: Barbets 113
Family: Toucans 125
Family: Honeyguides 137
Family: Woodpeckers, wrynecks, and piculets 147

Order PASSERIFORMES
Perching birds 169
Family: Broadbills 177
Family: False sunbirds and asities 187

Family: Pittas 193
Family: New Zealand wrens 203
Family: Ovenbirds 209
Family: Woodcreepers 229
Family: Ant thrushes 239
Family: Tapaculos 257
Family: Tyrant flycatchers 269
Family: Sharpbills 291
Family: Manakins 295
Family: Cotingas 305
Family: Plantcutters 325
Family: Lyrebirds 329
Family: Scrub-birds 337
Family: Larks 341
Family: Swallows 357
Family: Pipits and wagtails 371
Family: Cuckoo-shrikes 385
Family: Bulbuls 395
Family: Fairy bluebirds and leafbirds 415
Family: Shrikes 425
Family: Vanga shrikes 439
Family: Waxwings and silky flycatchers 447
Family: Palmchats 455
Family: Hedge sparrows 459
Family: Thrashers and mockingbirds 465
Family: Dippers 475
Family: Thrushes and chats 483
Family: Babblers 505
Family: Wrens 525

For further reading 539
Organizations 544
Contributors to the first edition 549
Glossary 556
Aves species list 567
Geologic time scale 630
Index 631

Volume 11: Birds IV

Family: Old World warblers 1
Family: Old World flycatchers 25
Family: Australian fairy-wrens 45
Family: Australian warblers 55
Family: Australian chats 65
Family: Logrunners and chowchillas 69
Family: Quail thrushes and whipbirds 75
Family: Fantails 83
Family: Monarch flycatchers 97
Family: Australian robins 105
Family: Whistlers 115
Family: Pseudo babblers 127
Family: Australian creepers 133
Family: Long-tailed titmice 141
Family: Penduline titmice 147
Family: Titmice and chickadees 155
Family: Nuthatches and wall creepers 167
Family: Treecreepers 177
Family: Philippine creepers 183
Family: Flowerpeckers 189
Family: Pardalotes 201
Family: Sunbirds 207
Family: White-eyes 227
Family: Australian honeyeaters 235
Family: Vireos and peppershrikes 255
Family: New World finches 263
Family: New World warblers 285
Family: New World blackbirds and orioles 301
Family: Finches 323
Family: Hawaiian honeycreepers 341
Family: Waxbills and grassfinches 353
Family: Weavers 375
Family: Sparrows 397
Family: Starlings and mynas 407
Family: Old World orioles and figbirds 427
Family: Drongos 437
Family: New Zealand wattle birds 447
Family: Mudnest builders 453
Family: Woodswallows 459
Family: Magpie-shrikes 467
Family: Bowerbirds 477
Family: Birds of paradise 489
Family: Crows and jays 503

For further reading 525
Organizations 530
Contributors to the first edition 535
Glossary 542
Aves species list 553
Geologic time scale 616
Index 617

Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E.O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa—regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in super markets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"—places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade—the hunting of endangered wild animals for large scale human consumption—is pushing many species, including our closest relatives, the gorillas, bonobos, and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought specialists from various disciplines to write the sections with

which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 205 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Gzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909–1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series is being completely revised and updated for the first time in over 30 years. Gale is expanding the series from 13 to 17 volumes, commissioning new color images, and updating the information while also making the set easier to use. The order of revisions is:

Vol 8–11: Birds I–IV
Vol 6: Amphibians
Vol 7: Reptiles
Vol 4–5: Fishes I–II
Vol 12–16: Mammals I–V
Vol 1: Lower Metazoans and Lesser Deuterostomes
Vol 2: Protostomes
Vol 3: Insects
Vol 17: Cumulative Index

Organized by order and family

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science through which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the protostomes, in Vol. 1, the series progresses through the more complex animal classes, culminating with the mammals in Vols. 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. Opening chapters introduce the class of animal, followed by chapters dedicated to order and family. Species accounts appear at the end of family chapters. To help the reader grasp the scientific arrangement, each type of chapter has a distinctive color and symbol:

▲ = Family Chapter (yellow background)

● = Order Chapter (blue background)

⏢ = Monotypic Order Chapter (green background)

As chapters narrow in focus, they become more tightly formatted. General chapters have a loose structure, reminiscent of the first edition. While not strictly formatted, order chapters are carefully structured to cover basic information about member families. Monotypic orders, comprised of a single family, utilize family chapter organization. Family chapters are most tightly structured, following a prescribed format of standard rubrics that make information easy to find and understand. Family chapters typically include:

Thumbnail introduction
- Common name
- Scientific name
- Class
- Order
- Suborder
- Family
- Thumbnail description
- Size
- Number of genera, species
- Habitat
- Conservation status

Main essay
- Evolution and systematics
- Physical characteristics
- Distribution
- Habitat
- Behavior
- Feeding ecology and diet
- Reproductive biology
- Conservation status
- Significance to humans

Species accounts
- Common name
- Scientific name
- Subfamily
- Taxonomy
- Other common names
- Physical characteristics
- Distribution
- Habitat
- Behavior
- Feeding ecology and diet
- Reproductive biology

Conservation status
Significance to humans
Resources
Books
Periodicals
Organizations
Other

Color graphics enhance understanding

Grzimek's features approximately 3,500 color photos, including approximately 480 in four Birds volumes; 3,500 total color maps, including almost 1,500 in the four Birds volumes; and approximately 5,500 total color illustrations, including 1,385 in four Birds volumes. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges, and are color coded to show resident, breeding, and nonbreeding locations (where appropriate).

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal skins from University of Michgan Zoological Museum library. In addition to species illustrations, *Grzimek's* features conceptual drawings that illustrate characteristic traits and behaviors.

About the contributors

The essays were written by expert contributors, including ornithologists, curators, professors, zookeepers, and other reputable professionals. *Grzimek's* subject advisors reviewed the completed essays to insure that they are appropriate, accurate, and up-to-date.

Standards employed

In preparing these volumes, the editors adopted a conservative approach to taxonomy, relying primarily on Peters Checklist (1934–1986)—a traditional classification scheme. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, Gale consulted with noted taxonomist Professor Walter J. Bock as well as other specialists to obtain the most up-to-date information possible. When scientific controversy over the classification of a particular animal or group of animals existed, the text makes this clear.

Grzimek's has been designed with ready reference in mind and the editors have standardized information wherever feasible. For ***Conservation status,*** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN web page at http://www.iucn.org/themes/ssc/redlists/categor.htm

In addition to IUCN ratings, essays may contain other conservation information, such as a species' inclusion on one of three Convention on International Trade in Endangered Species (CITES) appendices. Adopted in 1975, CITES is a global treaty whose focus is the protection of plant and animal species from unregulated international trade.

Grzimek's provides the following standard information on avian lineage in ***Taxonomy*** rubric of each Species account: [First described as] *Muscicapa rufifrons* [by] Latham, [in] 1801, [based on a specimen from] Sydney, New South Wales, Australia. The person's name and date refer to earliest identification of a species, although the species name may have changed since first identification. However, the organism described is the same.

Other common names in English, French, German, and Spanish are given when an accepted common name is available.

Appendices and index

For further reading directs readers to additional sources of information about birds. Valuable contact information for ***Organizations*** is also included in an appendix. While the encyclopedia minimizes scientific jargon, it also provides a ***Glossary*** at the back of the book to define unfamiliar terms. An exhaustive ***Aves species list*** records all known species of birds, categorized according to Peters Checklist (1934–1986). And a full-color ***Geologic time scale*** helps readers understand prehistoric time periods. Additionally, each of the four volumes contains a full ***Subject index*** for the Birds subset.

Acknowledgements

Gale would like to thank several individuals for their important contributions to the series. Michael Souza, Program Assistant, Department of Conservation and Science, American Zoo and Aquarium Association, provided valuable behind-the-scenes research and reliable support at every juncture of the project. Also deserving of recognition are Christine Sheppard, Curator of Ornithology at Bronx Zoo, and Barry Taylor, professor at the University of Natal, in Pietermaritzburg, South Africa, who assisted subject advisors in reviewing manuscripts for accuracy and currency. And, last but not least, Janet Hinshaw, Bird Division Collection Manager at the University of Michigan Museum of Zoology, who opened her collections to *Grzimek's* artists and staff and also compiled the "For Further Reading" bibliography at the back of the book.

Advisory boards

Series advisor

Michael Hutchins, PhD
Director of Conservation and William Conway Chair
American Zoo and Aquarium Association
Silver Spring, Maryland

Subject advisors

Volume 1: Lower Metazoans and Lesser Deuterostomes
Dennis Thoney, PhD
Director, Marine Laboratory & Facilities
Humboldt State University
Arcata, California

Volume 2: Protostomes
Dennis Thoney, PhD
Director, Marine Laboratory & Facilities
Humboldt State University
Arcata, California

Sean F. Craig, PhD
Assistant Professor, Department of Biological Sciences
Humboldt State University
Arcata, California

Volume 3: Insects
Art Evans, PhD
Entomologist
Richmond, Virginia

Rosser W. Garrison, PhD
Systematic Entomologist, Los Angeles County
Los Angeles, California

Volumes 4–5: Fishes I–II
Paul Loiselle, PhD
Curator, Freshwater Fishes
New York Aquarium
Brooklyn, New York

Dennis Thoney, PhD
Director, Marine Laboratory & Facilities
Humboldt State University
Arcata, California

Volume 6: Amphibians
William E. Duellman, PhD
Curator of Herpetology Emeritus
Natural History Museum and Biodiversity Research Center
University of Kansas
Lawrence, Kansas

Volume 7: Reptiles
James B. Murphy, PhD
Smithsonian Research Associate
Department of Herpetology
National Zoological Park
Washington, DC

Volumes 8–11: Birds I–IV
Walter J. Bock, PhD
Permanent secretary, International Ornithological Congress
Professor of Evolutionary Biology
Department of Biological Sciences,
Columbia University
New York, New York

Jerome A. Jackson, PhD
Program Director, Whitaker Center for Science,
Mathematics, and Technology Education
Florida Gulf Coast University
Ft. Myers, Florida

Volumes 12–16: Mammals I–V
Valerius Geist, PhD
Professor Emeritus of Environmental Science
University of Calgary
Calgary, Alberta
Canada

Devra Gail Kleiman, PhD
Smithsonian Research Associate
National Zoological Park
Washington, DC

Library advisors

James Bobick
Head, Science & Technology Department
Carnegie Library of Pittsburgh
Pittsburgh, Pennsylvania

Linda L. Coates
Associate Director of Libraries
Zoological Society of San Diego Library
San Diego, California

Lloyd Davidson, PhD
Life Sciences bibliographer and head, Access Services
Seeley G. Mudd Library for Science and Engineering
Evanston, Illinois

Thane Johnson
Librarian
Oaklahoma City Zoo
Oaklahoma City, Oklahoma

Charles Jones
Library Media Specialist
Plymouth Salem High School
Plymouth, Michigan

Ken Kister
Reviewer/General Reference teacher
Tampa, Florida

Richard Nagler
Reference Librarian
Oakland Community College
Southfield Campus
Southfield, Michigan

Roland Person
Librarian, Science Division
Morris Library
Southern Illinois University
Carbondale, Illinois

Contributing writers

Birds I–IV
Michael Abs, Dr. rer. nat.
Berlin, Germany

George William Archibald, PhD
International Crane Foundation
Baraboo, Wisconsin

Helen Baker, PhD
Joint Nature Conservation Committee
Peterborough, Cambridgeshire
United Kingdom

Cynthia Ann Berger, MS
Pennsylvania State University
State College, Pennsylvania

Matthew A. Bille, MSc
Colorado Springs, Colorado

Walter E. Boles, PhD
Australian Museum
Sydney, New South Wales
Australia

Carlos Bosque, PhD
Universidad Simón Bolivar
Caracas, Venezuela

David Brewer, PhD
Research Associate
Royal Ontario Museum
Toronto, Ontario
Canada

Daniel M. Brooks, PhD
Houston Museum of Natural Science
Houston, Texas

Donald F. Bruning, PhD
Wildlife Conservation Society
Bronx, New York

Joanna Burger, PhD
Rutgers University
Piscataway, New Jersey

Carles Carboneras
SEO/BirdLife
Barcelona, Spain

John Patrick Carroll, PhD
University of Georgia
Athens, Georgia

Robert Alexander Cheke, PhD
Natural Resources Institute
University of Greenwich
Chatham, Kent
United Kingdom

Jay Robert Christie, MBA
Racine Zoological Gardens
Racine, Wisconsin

Charles T. Collins, PhD
California State University
Long Beach, California

Malcolm C. Coulter, PhD
IUCN Specialist Group on Storks,
Ibises and Spoonbills
Chocorua, New Hampshire

Adrian Craig, PhD
Rhodes University
Grahamstown, South Africa

Francis Hugh John Crome, BSc
Consultant
Atheron, Queensland
Australia

Timothy Michael Crowe, PhD
University of Cape Town
Rondebosch, South Africa

H. Sydney Curtis, BSc
Queensland National Parks &
Wildlife Service (Retired)
Brisbane, Queensland
Australia

S. J. J. F. Davies, ScD
Curtin University of Technology
Department of Environmental Biology
Perth, Western Australia
Australia

Gregory J. Davis, PhD
University of Wisconsin-Green Bay
Green Bay, Wisconsin

William E. Davis, Jr., PhD
Boston University
Boston, Massachusetts

Stephen Debus, MSc
University of New England
Armidale, New South Wales
Australia

Michael Colin Double, PhD
Australian National University
Canberra, A.C.T.
Australia

Rachel Ehrenberg, MS
University of Michigan
Ann Arbor, Michigan

Eladio M. Fernandez
Santo Domingo
Dominican Republic

Simon Ferrier, PhD
New South Wales National Parks and Wildlife Service
Armidale, New South Wales
Australia

Kevin F. Fitzgerald, BS
South Windsor, Connecticut

Hugh Alastair Ford, PhD
University of New England
Armidale, New South Wales
Australia

Joseph M. Forshaw
Australian Museum
Sydney, New South Wales
Australia

Bill Freedman, PhD
Department of Biology
Dalhousie University
Halifax, Nova Scotia
Canada

Clifford B. Frith, PhD
Honorary research fellow
Queensland Museum
Brisbane, Australia

Dawn W. Frith, PhD
Honorary research fellow
Queensland Museum
Brisbane, Australia

Peter Jeffery Garson, DPhil
University of Newcastle
Newcastle upon Tyne
United Kingdom

Michael Gochfeld, PhD, MD
UMDNJ-Robert Wood Johnson Medical School
Piscataway, New Jersey

Michelle L. Hall, PhD
Australian National University
School of Botany and Zoology
Canberra, A.C.T.
Australia

Frank Hawkins, PhD
Conservation International
Antananarivo, Madagascar

David G. Hoccom, BSc
Royal Society for the Protection of Birds
Sandy, Bedfordshire
United Kingdom

Peter Andrew Hosner
Cornell University
Ithaca, New York

Brian Douglas Hoyle PhD
Bedford, Nova Scotia
Canada

Julian Hughes
Royal Society for the Protection of Birds
Sandy, Bedfordshire
United Kingdom

Robert Arthur Hume, BA
Royal Society for the Protection of Birds
Sandy, Bedfordshire
United Kingdom

Gavin Raymond Hunt, PhD
University of Auckland
Auckland, New Zealand

Jerome A. Jackson, PhD
Florida Gulf Coast University
Ft. Myers, Florida

Bette J. S. Jackson, PhD
Florida Gulf Coast University
Ft. Myers, Florida

Darryl N. Jones, PhD
Griffith University
Queensland, Australia

Alan C. Kemp, PhD
Naturalists & Nomads
Pretoria, South Africa

Angela Kay Kepler, PhD
Pan-Pacific Ecological Consulting
Maui, Hawaii

Jiro Kikkawa, DSc
Professor Emeritus
University of Queensland,
Brisbane, Queensland
Australia

Margaret Field Kinnaird, PhD
Wildlife Conservation Society
Bronx, New York

Guy M. Kirwan, BA
Ornithological Society of the Middle East
Sandy, Bedfordshire
United Kingdom

Melissa Knopper, MS
Denver Colorado

Niels K. Krabbe, PhD
University of Copenhagen
Copenhagen, Denmark

James A. Kushlan, PhD
U.S. Geological Survey
Smithsonian Environmental Research Center
Edgewater, Maryland

Norbert Lefranc, PhD
Ministère de l'Environnement,
Direction Régionale
Metz, France

P. D. Lewis, BS
Jacksonville Zoological Gardens
Jacksonville, Florida

Josef H. Lindholm III, BA
Cameron Park Zoo
Waco, Texas

Peter E. Lowther, PhD
Field Museum
Chicago, Illinois

Gordon Lindsay Maclean, PhD, DSc
Rosetta, South Africa

Steve Madge
Downderry, Torpoint
Cornwall
United Kingdom

Albrecht Manegold
Institut für Biologie/Zoologie
Berlin, Germany

Jeffrey S. Marks, PhD
University of Montana
Missoula, Montana

Juan Gabriel Martínez, PhD
Universidad de Granada
Departamento de Biologia
Animal y Ecologia
Granada, Spain

Barbara Jean Maynard, PhD
Laporte, Colorado

Cherie A. McCollough, MS
PhD candidate, University of Texas
Austin, Texas

Leslie Ann Mertz, PhD
Fish Lake Biological Program
Wayne State University
Biological Station
Lapeer, Michigan

Derek William Niemann, BA
Royal Society for the Protection of Birds
Sandy, Bedfordshire
United Kingdom

Malcolm Ogilvie, PhD
Glencairn, Bruichladdich
Isle of Islay
United Kingdom

Penny Olsen, PhD
Australian National University
Canberra, A.C.T.
Australia

Jemima Parry-Jones, MBE
National Birds of Prey Centre
Newent, Gloucestershire
United Kingdom

Colin Pennycuick, PhD, FRS
University of Bristol
Bristol, United Kingdom

James David Rising, PhD
University of Toronto
Department of Zoology
Toronto, Ontario
Canada

Christopher John Rutherford Robertson
Wellington, New Zealand

Peter Martin Sanzenbacher, MS
USGS Forest & Rangeland Ecosystem Science Center
Corvallis, Oregon

Matthew J. Sarver, BS
Ithaca, New York

Herbert K. Schifter, PhD
Naturhistorisches Museum
Vienna, Austria

Richard Schodde PhD, CFAOU
Australian National Wildlife Collection, CSIRO
Canberra, A.C.T.
Australia

Karl-L. Schuchmann, PhD
Alexander Koenig Zoological Research Institute and Zoological Museum
Bonn, Germany

Tamara Schuyler, MA
Santa Cruz, California

Nathaniel E. Seavy, MS
Department of Zoology
University of Florida
Gainesville, Florida

Charles E. Siegel, MS
Dallas Zoo
Dallas, Texas

Julian Smith, MS
Katonah, New York

Joseph Allen Smith
Baton Rouge, Louisiana

Walter Sudhaus, PhD
Institut für Zoologie
Berlin, Germany

J. Denis Summers-Smith, PhD
Cleveland, North England
United Kingdom

Barry Taylor, PhD
University of Natal
Pietermaritzburg, South Africa

Markus Patricio Tellkamp, MS
University of Florida
Gainesville, Florida

Joseph Andrew Tobias, PhD
BirdLife International
Cambridge
United Kingdom

Susan L. Tomlinson, PhD
Texas Tech University
Lubbock, Texas

Donald Arthur Turner, PhD
East African Natural History Society
Nairobi, Kenya

Michael Phillip Wallace, PhD
Zoological Society of San Diego
San Diego, California

John Warham, PhD, DSc
University of Canterbury
Christchurch, New Zealand

Tony Whitehead, BSc
Ipplepen, Devon
United Kingdom

Peter H. Wrege, PhD
Cornell University
Ithaca, New York

Contributing illustrators

Drawings by Michigan Science Art

Joseph E. Trumpey, Director, AB, MFA
Science Illustration, School of Art and Design, University of Michigan

Wendy Baker, ADN, BFA

Brian Cressman, BFA, MFA

Emily S. Damstra, BFA, MFA

Maggie Dongvillo, BFA

Barbara Duperron, BFA, MFA

Dan Erickson, BA, MS

Patricia Ferrer, AB, BFA, MFA

Gillian Harris, BA

Jonathan Higgins, BFA, MFA

Amanda Humphrey, BFA

Jacqueline Mahannah, BFA, MFA

John Megahan, BA, BS, MS

Michelle L. Meneghini, BFA, MFA

Bruce D. Worden, BFA

Thanks are due to the University of Michigan, Museum of Zoology, which provided specimens that served as models for the images.

Maps by XNR Productions

Paul Exner, Chief cartographer
XNR Productions, Madison, WI

Tanya Buckingham

Jon Daugherity

Laura Exner

Andy Grosvold

Cory Johnson

Paula Robbins

Topic overviews

What is a bird?

Birds and humans

Avian migration and navigation

Avian song

Avian flight

What is a bird?

Birds

Everyone recognizes birds. They have feathers, wings, two legs, and a bill. Less uniquely, they have a backbone, are warm-blooded, and lay eggs. All but a few birds can fly. Birds have much in common with reptiles, from which they have evolved. They share several skeletal characteristics, nucleated red blood cells, and their young develop in cleidoic eggs. The main difference is feathers, which are modified scales. Not only do feathers allow flight, they are insulated, more so than mammalian hair, enabling birds to maintain steady internal temperatures and stay active even in extreme climates. The acquisition of flight and homeothermia has influenced the evolution of other anatomical and physiological changes in birds and led to increased cerebral and sensory development. It has freed them to travel the globe, colonizing most environments and diversifying to fill many ecological niches. Consequently, it is not surprising that birds are the most successful of the vertebrates, outnumbering the number of mammal species twofold.

Evolution and systematics

The fossil record of birds is patchy and their evolutionary history is poorly known. The first feathered animal, *Archaeopteryx*, has been identified in Upper Jurassic deposits, from 150 million years ago (mya). However, while it does appear intermediate between early reptiles and birds, there is some disagreement over whether it is a direct ancestor of present day birds. Fossils unequivocally of birds do not appear until the Cretaceous period, 80–120 mya, although the number of species suggests that they radiated earlier. The earliest remains are of large flightless diving birds, *Hesperornis* spp., with primitive teeth. Other toothed sea birds also lived during the Cretaceous, including the flighted ichthyosaurs. Also appearing in the Early Cretaceous were the *Enantiornithes*, a little understood group of seemingly primitive birds. At the end of the period, the toothed birds disappeared with the dinosaurs. Since then, only toothless birds have been found in the record and it is not clear how or when they arose, though it is thought that it was during the Cretaceous. By the Eocene (c. 50 mya), many modern forms were recognizable. These are non-passerines, including ostriches, penguins, storks, ducks, hawks, cuckoos, and kingfishers. The passerines (small songbirds) appear to have diversified 36–45 mya, along with flowering plants and insects. Several other forms, mostly large birds, were also present in the Eocene but died out. Other giant birds such as the larger moas of New Zealand and the elephant birds of Africa and Madagascar survived until about 10,000 years ago when they were exterminated by humans.

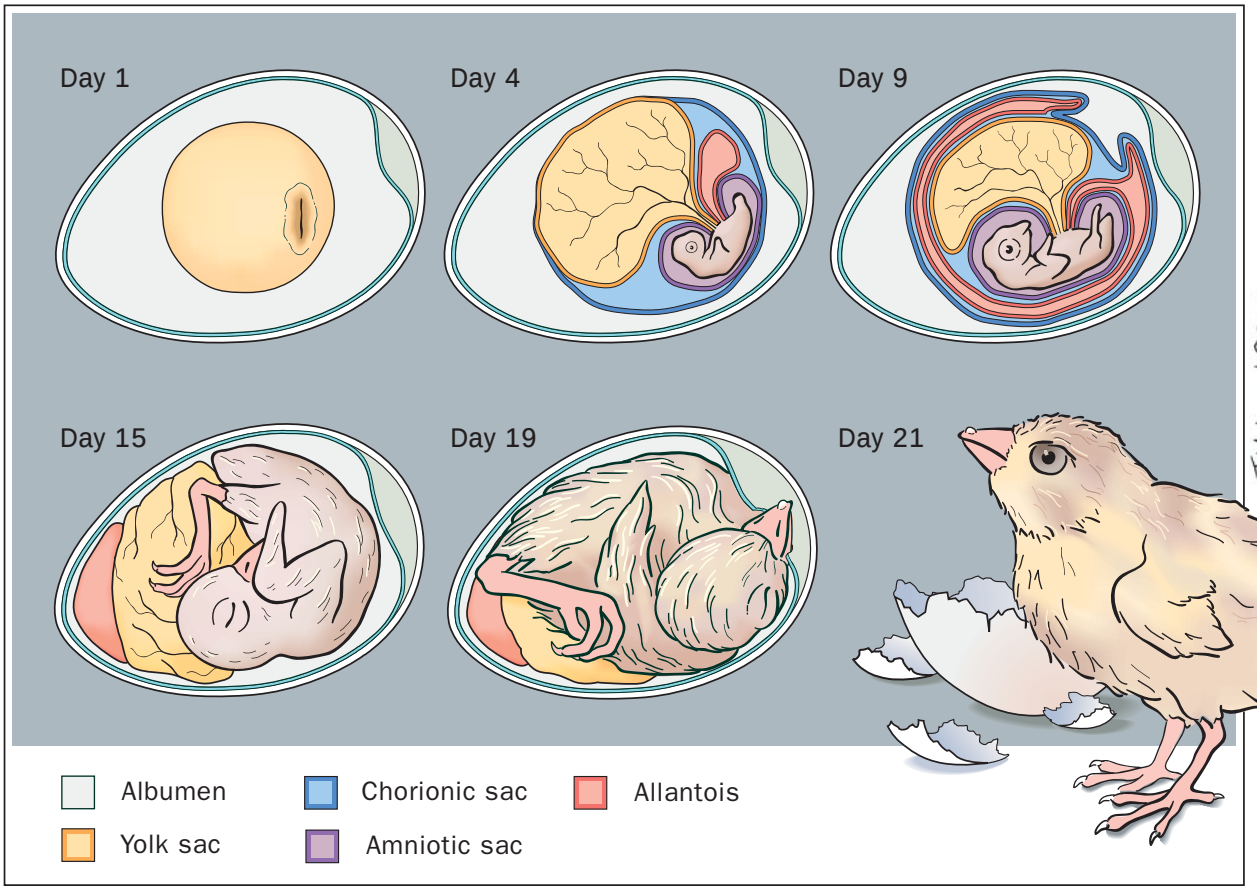
The evolutionary success of birds is evidenced by the wide variety of present-day forms. They have long been popular subjects of study for taxonomists. Traditional classifications are based mainly on morphological and anatomical differences in structure, plumage, and so forth. More recently, behavioral traits, song, and biochemical techniques (including DNA) have been employed. Yet, while there is general agreement as to the families to which the 9,000 or so extant bird species belong, a variety of opinions exists on the relationships within and between families.

Structure and function

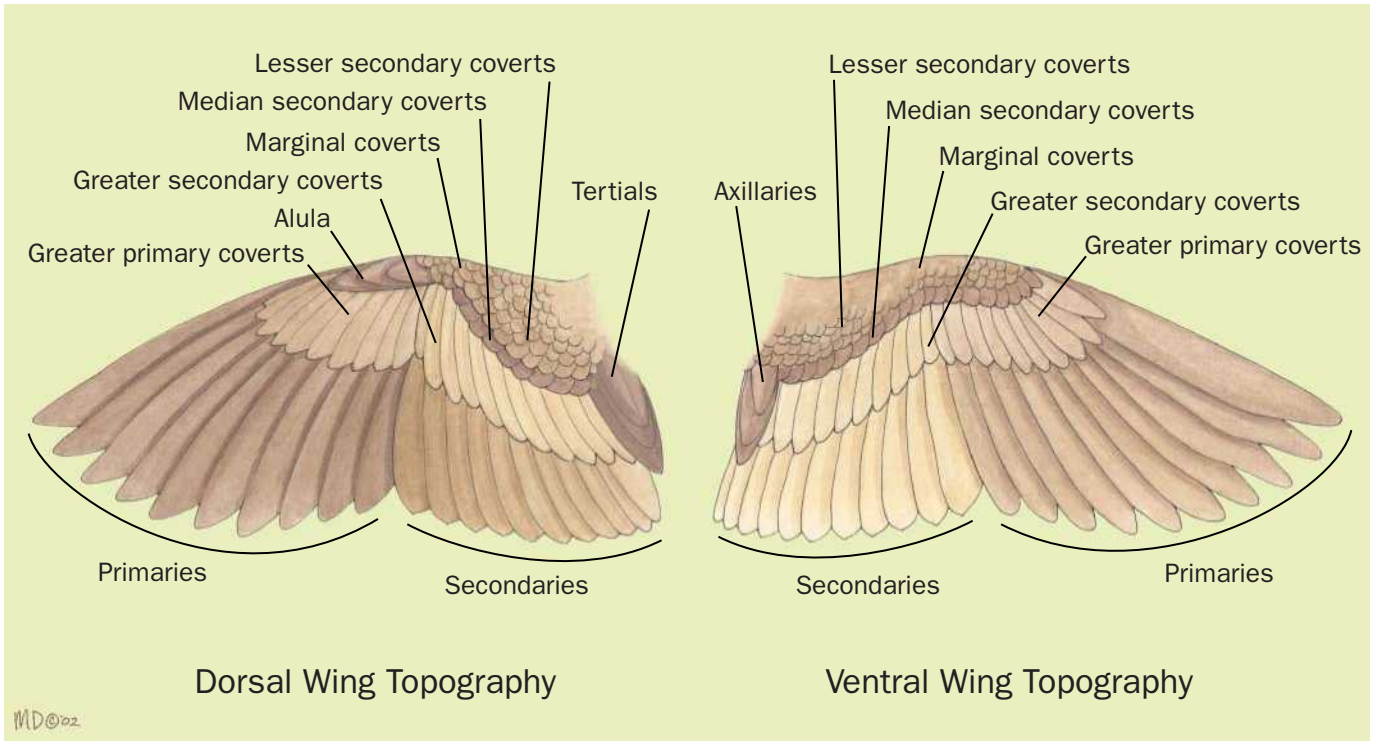
General structure

Birds have adapted to a multitude of situations. For this reason, they occur in a wide diversity of shapes, sizes, and colors. Weighing up to 285 lbs (130 kg), and reaching 9 ft (2.75 m), the flightless ostrich is the largest of the living birds. At a mere 0.7 oz (2 g) and around 2.4 in (6 cm), the tiny bee hummingbird is the smallest. Even closely related forms can look very different (adaptive radiation). A famous example is the enormous range of bill shapes and sizes in Charles Darwin's Galápagos finches; a single over-water colonizing species is thought to have undergone repeated evolutionary divergence to produce the 14 or so contemporary species on the different islands. Conversely, unrelated species can closely resemble each other (convergent evolution) because they have evolved for the same lifestyle. Examples of this are the Old World and New World vultures, which belong to the diurnal birds of prey and storks, respectively.

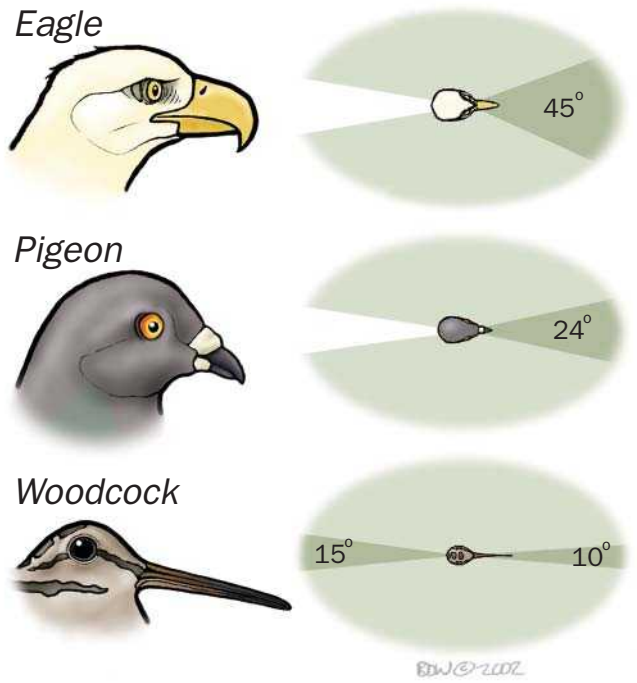
Body shapes vary enormously, from the flexible, long-necked form of the cranes and ibises to short-necked, stiff-backed falcons and penguins. These latter species, the speedy, predatory hunters of the air and the seas, have torpedo-shaped bodies to minimize drag. Bills and beaks take a variety of forms that generally reflect their major function in feeding: from the sturdy, seed-cracking bills of finches to the long, soil-probing



Embryonic development in birds. (Illustration by Jacqueline Mahannah)



Dorsal and ventral views of a birds wing, showing the different feather groups. (Illustration by Marguette Dongvillo)



Fields of view: an eagle has about 45° of frontal binocular vision, with 147.5° of monocular vision on both sides and 20° behind out of its visual range. A pigeon has about 24° of frontal binocular, 158° of monocular on each side, and 20° behind out of its visual range. The woodcock has 10° of frontal binocular vision, 15° of binocular behind it, and 167.5° of monocular vision to either side. (Illustration by Bruce Worden)

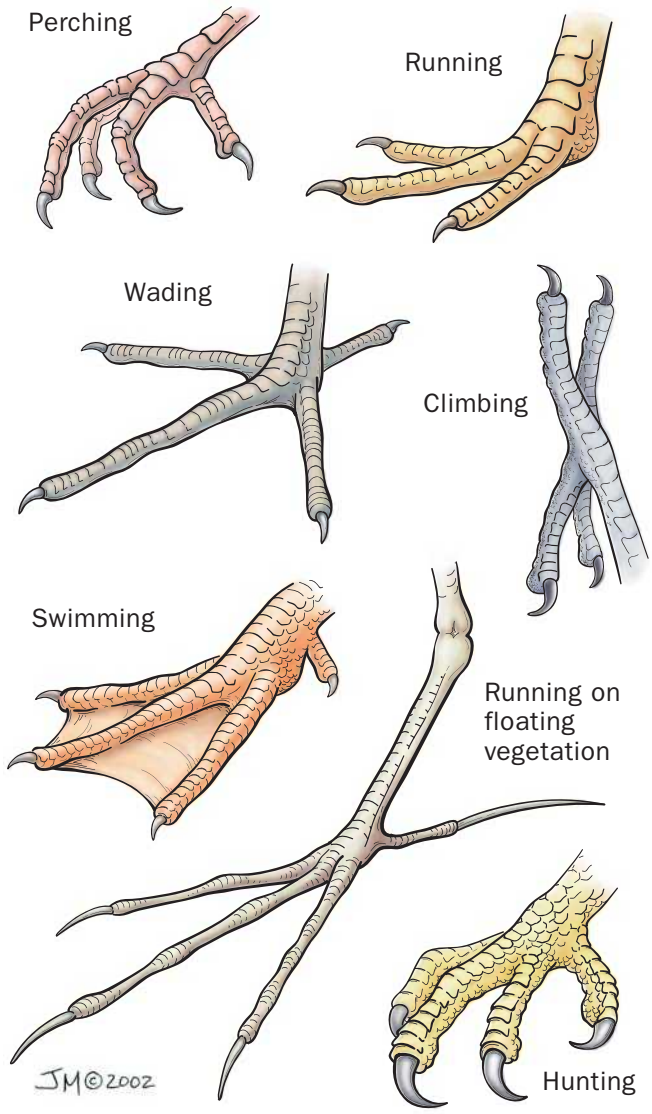
bill of a kiwi, the delicate curve of a nectar feeder's bill and the massive bone-shearing beak of a large vulture. In a few species, bills also serve as signals of breeding condition and sexual ornaments to attract the opposite sex. For example, the bills of cattle egrets turn from yellow to orange-yellow in the breeding season and the huge gorgeously rainbow-hued bills of the sulphur-breasted toucans may separate species. Similarly, birds' feet and legs suit their lifestyle: webbed for swimming; short and flat for ground dwellers; longer and grasping for perching species; powerful and heavily taloned for raptorial species. Stilt-like legs and spider-like toes with a span the length of the bird's body are a feature of the lily-pad walking jacanas. The legs are almost nonexistent in swifts and other birds that spend much of their lives on the wing, and long and muscular in ostriches and emus that stride and run across the plains. The ostrich has two toes, and a few species such as those that run on hard surfaces have lost the first (hind) toe or it is very small. Most species have four toes but their arrangement differs: in most perching birds, toes two, three, and four point forward and the hind toe opposes them; some species have two toes pointing forward, two back; others can move a toe to have either arrangement; swifts have all four toes pointing forward.

Wings are less variable than lower limbs, although their different forms can be extreme: much reduced in the flightless ratites, put to good use as fins in penguins, and at their most extended in gliding species that spend much of their lives riding air currents. Not only are there differences between species, variation can be quite marked within species, either geographically or between the sexes.

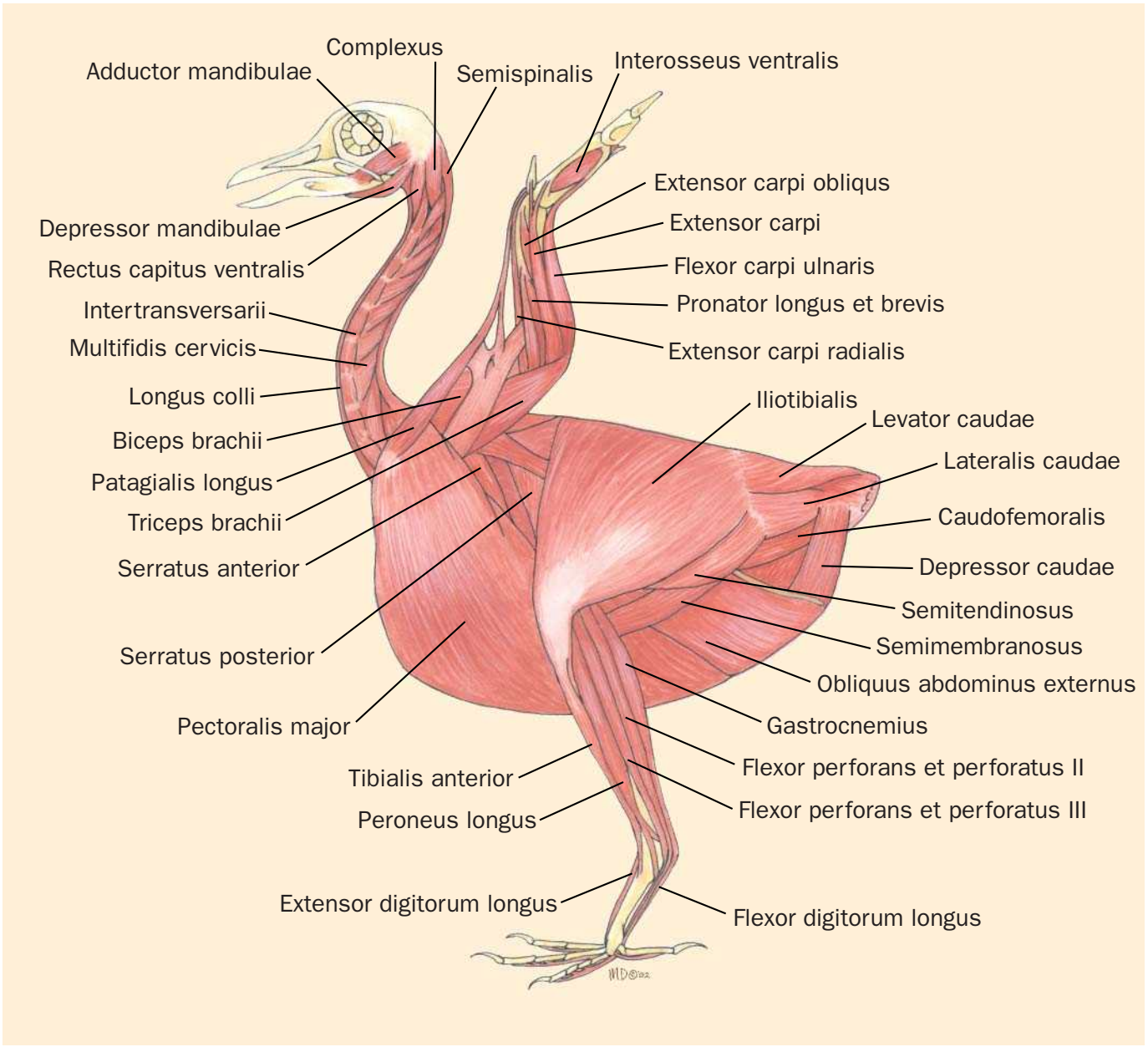
Species often vary in size clinally (with environmental or geographic change), usually increasing in size between from hotter to cooler parts of their range (Bergman's rule); races at either end of the cline can be remarkably different. A few species even have different forms, for example, the large- and small-beaked snail kites. Males are often larger (sexual dimorphism), but in some species, including birds of prey, some seabirds, and game birds, the female is larger.

The senses

Birds' active lifestyles require highly developed senses. For the vast majority of species, sight is the dominant sense and the eyes are relatively large. The eyes are generally set to the sides of the head, allowing a wide field of view, (about 300°), presumably useful for detecting approaching predators. For predatory birds (insectivores and raptors), the eyes are set



Birds' feet have different shapes and uses. (Illustration by Jacqueline Mahannah)



Bird musculature. (Illustration by Marguette Dongvillo)

more forward to give a greater overlap in the field of vision of the two eyes. This increase in binocular vision is important for depth perception. Compared with mammals' eyes, birds' eyes are relatively immobile. They compensate by being able to rotate the head by as much as 270° in species such as owls, which have the most forward facing eyes. Their eyes are protected by a nictitating membrane, which closes from the inside to the outside corner, and a top and bottom eyelid. Birds can focus their eyes rapidly, which is important in flight and when diving underwater. In general, they may not have exceptional visual acuity compared with humans. However, birds have a larger field of sharp vision, good color perception, and can also discriminate in the ultraviolet part of spectrum and in polarized light. Nocturnal species have more rods than cones in their retinas to enhance their vision in dim light.

The ear of birds is simpler than that of mammals, but their sense of hearing appears to be at least as sensitive. Some species, such as some of the owls, have a disc of stiff feathers around the face that directs sound to the ears, and asymmetrically placed ear openings and enlarged inner ears to enhance discrimination of direction and distance of the source of the sound. Oilbirds and some swiftlets that live in caves use echolocation. They emit audible clicks to help them navigate and locate prey in the dark.

The great number of sensory receptors and nerve endings distributed about the body indicate that birds' sense of touch,

A collection of eggs from British birds. (Photo by E. & D. Hosking. Photo Researchers, Inc. Reproduced by permission.)

A bird cares for its feathers by grooming and preening. (Illustration by Jonathan Higgins)

What *Archaeopteryx* may have looked like. (Illustration by Brian Cressman)

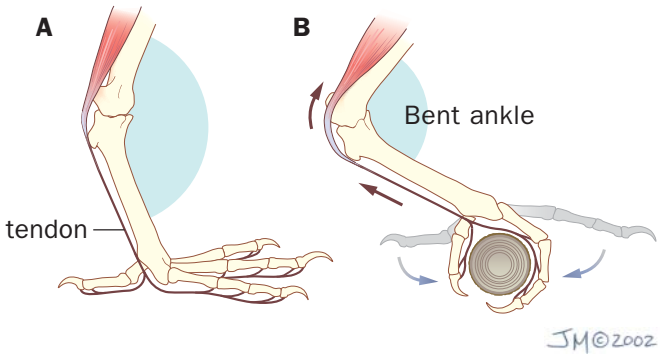
pain, and temperature is keen. By contrast, the olfactory system is poorly developed and few birds seem to make great use of smell. Exceptions include the New World vultures and the kiwi, which can detect prey by its scent.

Plumage

Feathers distinguish birds from all other living animals (there is recent evidence that some dinosaurs were feathered but this remains controversial). Light, strong, and colorful, feathers are extraordinarily multifunctional. They provide warmth, protection from the elements, decoration and camouflage, and are specialized for aerodynamics and flight (most birds), hydrodynamics and diving (e.g., penguins), or to cope with both elements (e.g., cormorants). A few species use them to make sound (e.g., snipe) or carry water to their young (e.g., sandgrouse). Not least, they identify species and subspecies, may vary with age, sex and breeding condition, and signal emotion.

Feathers are made of keratin and, once grown, are entirely dead tissue. They are of six main types. The most obvious are the long, stiff feathers of the wings and tail that provide the flight surfaces; more flexible, contour feathers make the sculpted outer covering for the body; and down makes a soft insulative underlayer. Semi-plumes, which are between down and contour feathers in form, help to provide insulation and fill out body contours so that air (or water) flows easily over the body. Two types of feathers are mainly sensory in function: stiff bristles that are usually found around the face (around the feet in the *Tyto* owls) like the whiskers of a cat or a net around the gape of some insect-eating species, and filoplumes, which are fine, hair-like feathers with a tuft of barbs at the tip that lie beside contour feathers and monitor whether the plumage is in place. In some species, modified feathers form features such as crests, ornamental bristles, cheek tufts, plumes, and tail flags and trains.

The contour, flight feathers, and semi-plumes have a central shaft, and a vane made up of barbs and barbules that interlock with each other and sometimes with neighboring feathers. The bird carefully maintains these links by nibbling and pulling the feathers through its bill. Many birds bathe regularly, most in water, but a few in dust. Some such as herons and elanine kites have powder down that grows continuously and crumbles into a fine powder that is spread through the feathers for cleaning and water resistance. Other



When a bird perches, its ankle bends and contracts the tendons in its foot, forcing its foot to close around the perch (B). (Illustration by Jacqueline Mahannah)

birds have oil glands at the base of the tail for the same purpose. Sunbathing also helps to maintain the health and curvature of feathers. Some birds, including many passerines, appear to use biting ants in feather maintenance, perhaps to control ectoparasites, either by wallowing among the swarm or by wiping individual ants through their plumage.

Over time, feathers become worn and bleached, and damaged by parasites. They are completely replaced annually in most except very large birds such as eagles and albatrosses, which spread the molt over two or so years. Some species, notably those that change from dull winter plumage into bright breeding colors (e.g., American goldfinch), have two molts a year: a full molt after breeding, and a partial body molt into breeding plumage. Most species shed their feathers sequentially to maintain their powers of flight. However, a few, particularly waterbirds that can find food in the relative safety of open water, replace all their flight feathers at once and are grounded for about five weeks.

Spectacular colors are a feature of birds, from the soft, mottled leaf patterns of nightjars (cryptic) to the gaudy, ornate plumes of a peacock (conspicuous). Cryptic colors conceal the bird from predators or rivals; conspicuous colors are used in courtship or threat. The colors themselves are produced by pigments in the feathers themselves or by structural features that interact with the pigment and the light to produce iridescent color, which can only be seen from certain angles, or non-iridescent color, that can be seen from any angle. In many species, the sexes are similar in color. In others, the sexes differ, and usually the male is showier and the female resembles a juvenile bird. In these species, sexual selection is thought to have favored dichromatism (and dimorphism) through female preference for partners with bright colors (and extravagant ornamentation). In the few polyandrous species, the reverse is that case and the females are more vibrant. Plumage may also vary geographically, with races from warm, humid climates tending to be more heavily pigmented than those from cool, dry regions (Gloger's rule).

Anatomy and physiology

The skeleto-muscular system of birds combines light weight with high power for flight. Muscle mass is concentrated near the center of gravity—around the breast and bases of the wings and legs—which gives a compact, aerodynamic form. Long tendons control movements at the ends of the limbs. Flighted birds have more massive breasts and wing muscles; in terrestrial birds, much of the muscle mass is in the upper legs. In perching birds, the tendon from the flexor muscle loops behind the ankle; when the ankle bends on landing, the toes automatically close around the perch and maintain the grip without effort, anchoring the bird even in sleep. In many species, the toe tendons have ridges, which also help to lock the feet around the perch.

In contrast to the mammalian skeleton, birds' bones are hollow and less massive and several have fused to form a strong, light frame. A bird's skeleton constitutes only about 5% of its mass. Another distinctive feature is that the bones, including the skull, are pneumatized: their core is filled with air via a system of interconnecting passages that connect with the air sacs of the respiratory system and nasal/tympanic cavities. Flighted species tend to have extensive pneumatization but it is reduced or lacking in diving birds, which would be hindered by such buoyancy. Even birds' bills are light—the horny equivalent of the heavy, toothed muzzle of mammals.

Respiration, circulation, and body temperature

Unlike mammals, birds lack a diaphragm. Instead, air is drawn into the rigid lungs by bellow-like expansion and contraction of the air sacs surrounding the lungs and another group in the head, which is driven by muscles that move the ribs and sternum up and out and back again. Features of birds' circulatory and respiratory systems make their respiration more efficient than that of most mammals, allowing them to use 25% more oxygen from each breath. This enables them to sustain a high metabolic rate and, among other benefits, as-

An ostrich (*Struthio camelus*) shades its chicks in Etosha National Park, Namibia. (Photo by Nigel Dennis. Photo Researchers, Inc. Reproduced by permission.)

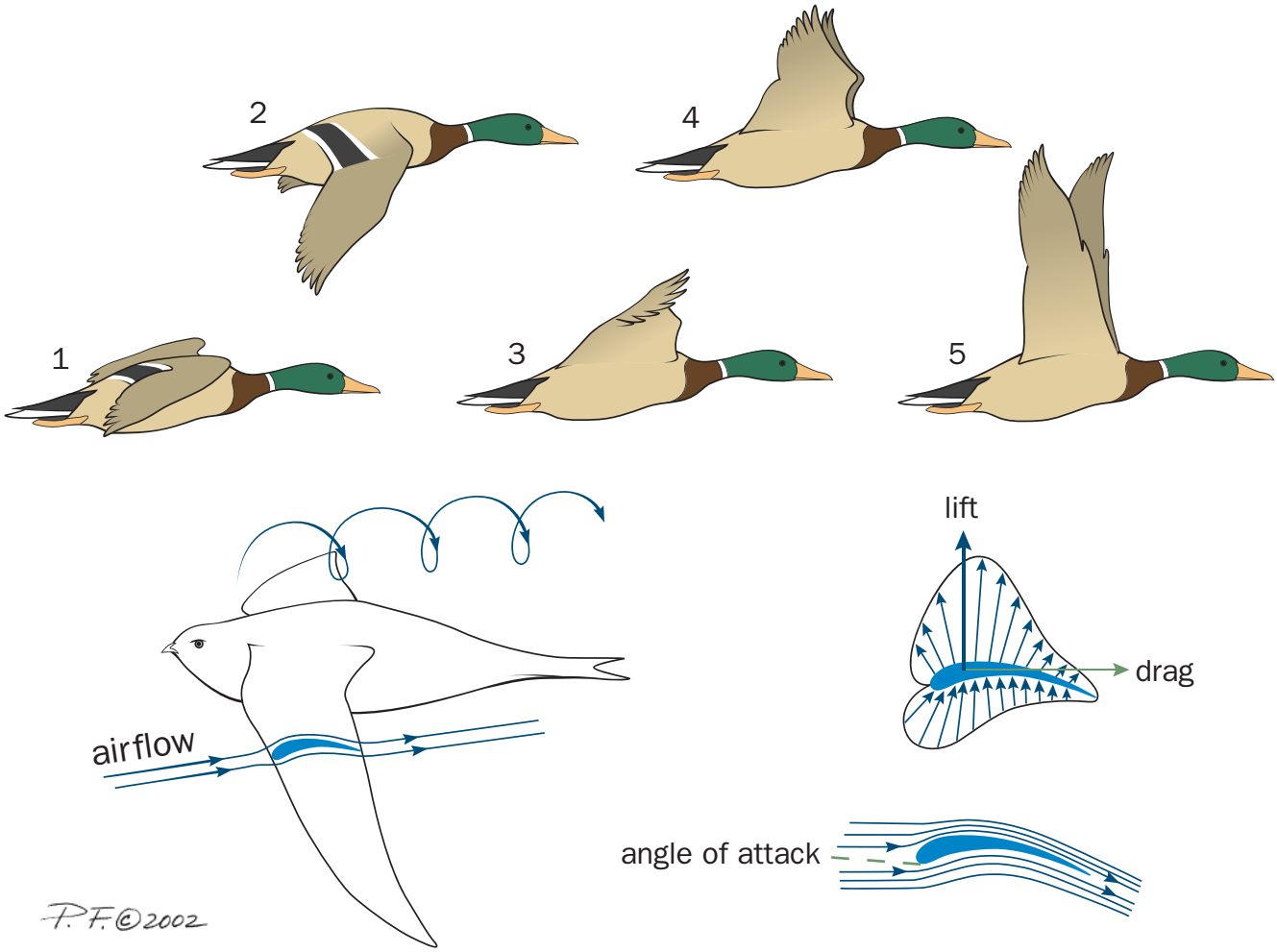
Bill morphology differs with use: 1. Greater flamingo filters microorganisms from water; 2. Peregrine falcon tears prey; 3. Roseate spoonbill sifts water for fish; 4. Dalmation pelican scoops fish in pouch; 5. Anna's hummingbird sips nectar; 6. Brown kiwi probes soil for invertebrates; 7. Green woodhoopoe probes bark crevices for insects; 8. Rufous flycatcher captures insects in flight; 9. Java sparrow eats seeds; 10. Papuan frogmouth trawls for insects; 11. Bicornis hornbill eats fruit; 12. American anhinga spears fish; 13. Rainbow lorikeet cracks nuts. (Illustration by Jacqueline Mahannah)

sists those high-flying migrants that cross the world's tallest mountains and reach altitudes up to 29,500 ft (9,000 m), where the oxygen content of the air is low.

Birds and mammals both generate their own body heat, but birds' high metabolic rate helps to maintain theirs at around 100°F (38–42°C), depending on species; 5–7°F (3–4°C) hotter than most mammals. When it becomes difficult to obtain enough energy to stay warm and active, a few species become torpid (lower their body temperature and become inactive) on the coldest days or during bad weather, usually for a few days or overnight. Other birds cope with cold by increasing their metabolic rate slightly, growing denser feathers, having a layer of fat, or by behavioral means such as huddling with others, tucking up a leg to decrease the heat loss surface, and fluffing out the feathers to trap more air. Lacking sweat glands to shed body heat, they may pant, lower their metabolic rate, seek shade, or raise their feathers to catch the breeze in hot weather.

Digestion and excretion

To provide the energy needed for flight, and so that they are not weighed down for a long time by the food they have



1. Downstroke; 2. Wings sweep forward at the end of the downstroke; 3. Feathers fan open on the upstroke; 4. Each primary becomes a small propeller in the upstroke; 5. Primaries swoop back, ready for a new downstroke. (Illustration by Patricia Ferrer)

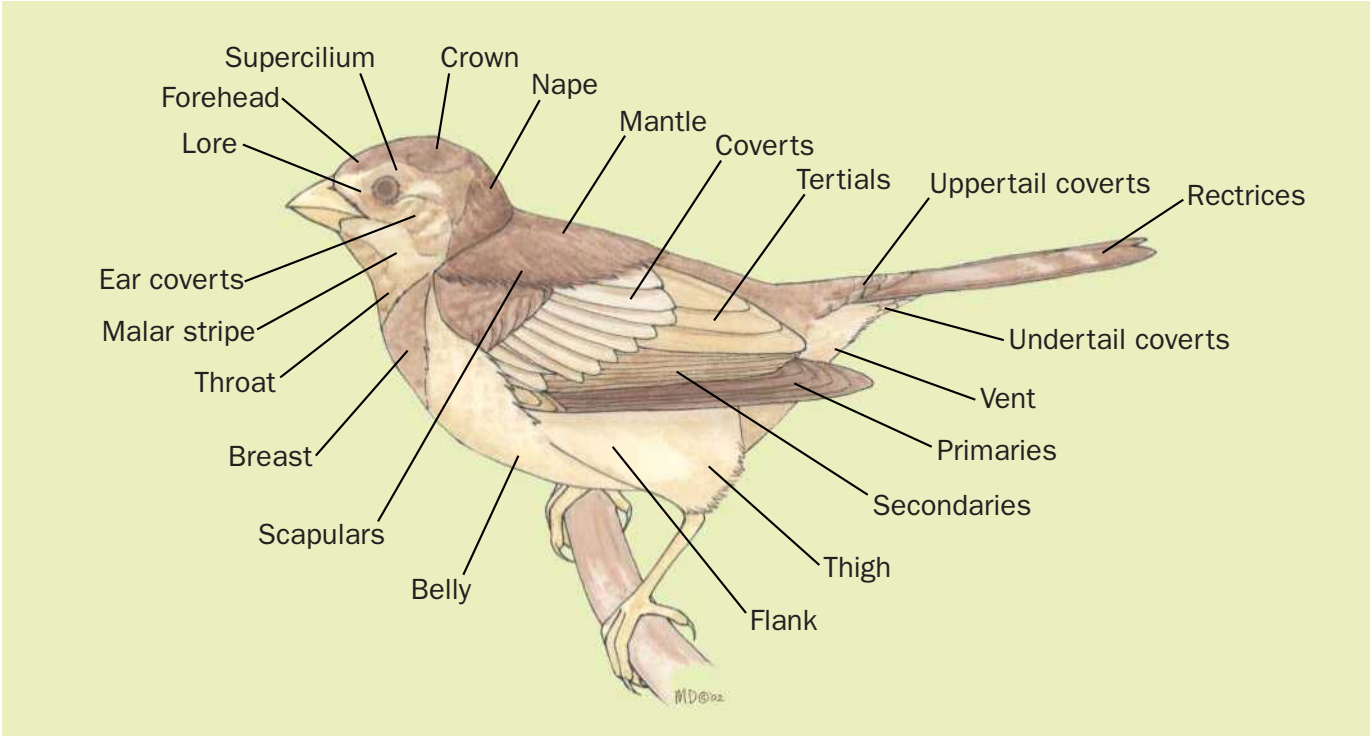
consumed, birds have a high metabolic rate and digest food rapidly and efficiently. Their digestive tract is modified accordingly, and many species have the second part of their two-part stomach modified into a muscular gizzard where hard food is physically ground down so that gastric juices can penetrate easily. Some species swallow pebbles to assist with this breakdown. The digestive tract tends to be long in grazers, fish-eaters, and seed-eaters, and short in meat- and insect-eaters.

Birds have three ways to rid themselves of excess water, salts, and waste products: through breathing and the skin; the renal system; and salt glands. The salt glands are located in the orbit of each eye. They secrete sodium chloride and, therefore, are well developed in seabirds that have a salty diet, and non-functional in some other groups. Birds' kidneys are more complex than those of mammals: they produce concentrated urine with nitrogen waste in the form of insoluble uric acid, rather than urea. Such a water-efficient system does not require a (heavy) bladder, with obvious advantages for flight. It also enables many species, especially those with a moist diet (carnivores, insectivores, and frugivores), to drink seldom or not at all. Both the white urine and dark fecal matter are voided through the anus, and bird droppings often contain both.

Life history and reproduction

Life history features

To a large extent, body size determines life history. Compared with smaller species, larger species tend to live longer, breed at a later age, have a longer breeding cycle, and, at each breeding attempt, produce fewer young with a greater chance of survival. There are always exceptions, and climate and risk of predation and other factors impinge on this overlying pattern. For example, some small temperate zone Australian passerines live up to 18 years and have small clutches, whereas ground-nesting grouse may live a few years and have large clutches. For convenience, species may be classed as fast-breeders (*r*-selected), which have many large clutches and short periods of nestling care, and slow-breeders (*K*-selected) that have a few small clutches and extended periods of offspring care. In reality, there is a continuum between the two extremes.



Birds' feather tracts—types of feathers on a bird's body have different functions. (Illustration by Marguette Dongvillo)

Mating systems

The majority of bird species are at least socially monogamous, that is, a pair of birds cooperates to raise young. They may stay together for the breeding attempt or mate for life. However, many other arrangements exist. Some birds have a polygynous mating system, particularly species that use rich resources that are clumped, so that a male can support more than one female (e.g., New World blackbirds, some harriers). Successive polygyny is less common, mainly practiced by species in which the female alone raises the chicks and visits a lek where males display. The female may mate with several (e.g., black grouse and some birds of paradise) males. Less frequent again is polyandry, where the females mate with various males and leave them to care for the eggs and chicks (e.g., emus, buttonquail, and jacanas). Within these systems, there is also scope for cheating, and the advent of DNA fingerprinting has revealed that in many monogamous species, there are broods of mixed paternity. At its extreme are species such as the superb fairy-wren in which about three-quarters of the chicks are raised by males that are not the biological father.

Most birds nest as solitary pairs, but some 13% of species are colonial, particularly seabirds. Colonies may be a few pairs (e.g., king penguin) or millions (e.g., queleas). In between are species that nest in loose colonies, either regularly or when conditions are favorable. Nest spacing varies enormously from a few inches/centimeters in some colonies to several miles/kilometers in species that have large territories. Spacing is linked to food and nest sites; nests are closer together where resources are plentiful.

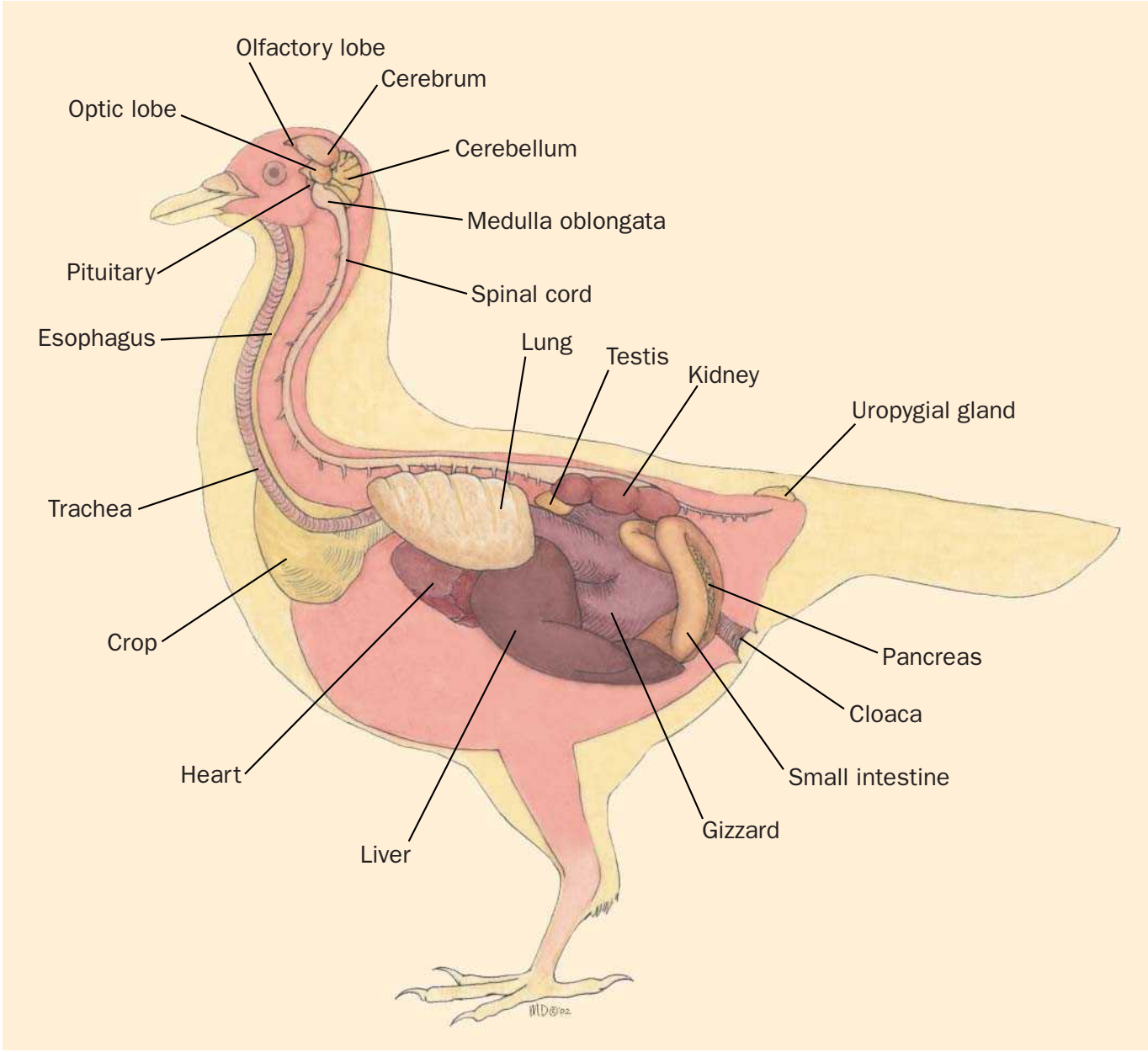
Breeding seasons and nests

Most birds have a regular breeding season, timed to coincide with the most abundant season of the year, but some, particularly those adapted to unpredictable climates, are opportunistic, only breeding when conditions allow. The largest species may breed every two years, but most attempt to breed at least annually, some raising several broods over the breeding season.

Birds build their nests of several substrates; the most important issues are protection from predators and the elements. Therefore, species that nest on predator-free islands often build close to the ground but, on the mainland, species build in higher locations. The nest itself must hold and shelter the eggs; in form, they vary enormously from simple scrapes in the dirt to large complex stick nests and hanging structures, woven together or glued with cobwebs or mud, and lined with soft material. Tree holes and holes in banks or cliffs also make good nests but competition for them may be fierce. The megapodes construct a mound in which they bury their eggs and maintain the temperature at about 90–95°F (32–35°C) by scratching soil on or off. Many species use the same nest area, nest site, or actual nest year after year.

Eggs and incubation

Birds' eggs are beautiful in their variety. They may be plain or colored, marked or unmarked, oval or round. All are slightly more pointed at one end so that the egg tends to roll in a circle. Species that lay in the open where eggs may roll tend to have long-oval, cryptically colored eggs, and those that lay in holes tend to have rounder, unmarked eggs. Egg laying can be energetically costly, especially for small birds: for a hum-

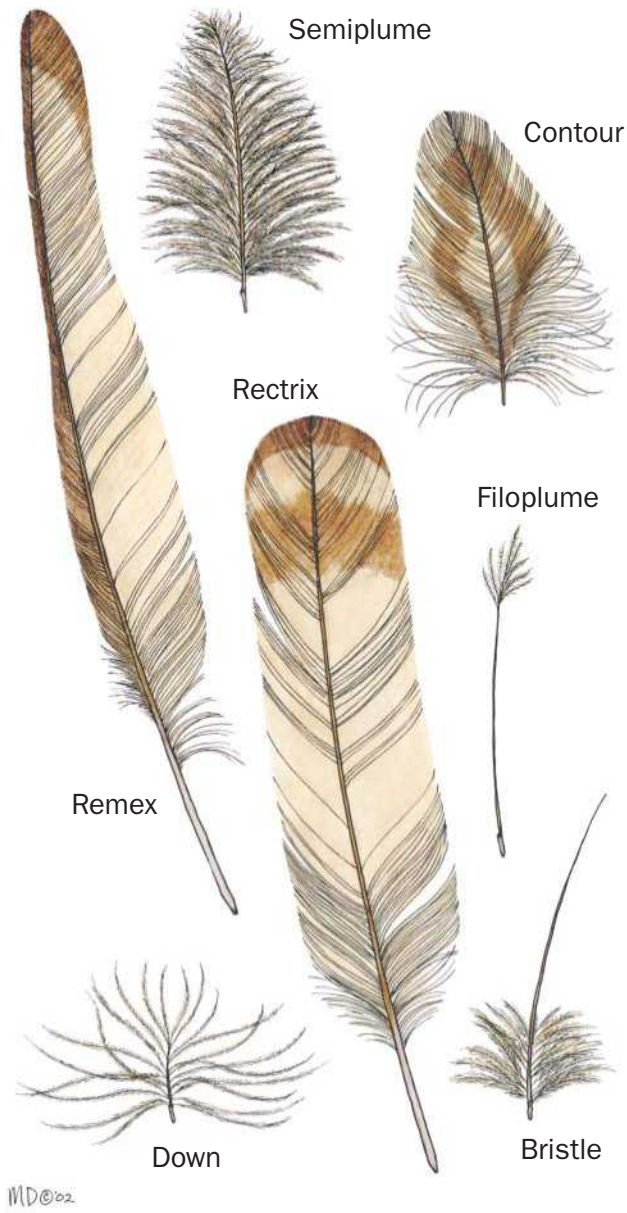


Bird internal organs. (Illustration by Marguette Dongvillo)

mingbird, each egg (0.01 oz/0.3g) represents 25% of the bird's mass; for an ostrich, the 50 oz (1,500 g) egg is 1% of the hen's weight. Birds that have precocial chicks tend to have large eggs (about 35% yolk compared with 20% in altricial [more helpless] species) because the chick must be advanced and well-developed when it hatches. Clutch size varies enormously both within and between species. Nevertheless, most species have a typical number of eggs; one in the kiwi, perhaps 20 in some ducks. Larger species tend to have fewer eggs. In some species, two are laid but only one ever hatches. Across species, there tends to be a trade-off between egg-size and clutch-size, some species lay a few large eggs, others many smaller eggs. In some species, the clutch size is fixed (determinate layers), in others, if the eggs are lost or removed within the breeding season, the bird will go on laying eggs (indeterminate layers). The majority of species lay every second day until the clutch is complete; in a few of the largest species, the interval is four days. In the vast majority of species incubation is carried out by one or both of the parents, but a few species, such as some ducks, nest-dump (lay some of their eggs in a neighbor's nest), and some such as the cuckoos are parasites and lay their eggs in the nest of another species. Incubation varies little within species. Among species, it ranges in length from 10 days for some woodpeckers to about 80 days for albatross and the very large-egged kiwi.

Egg formation and embryo development

To most people, eggs and birds go together. Certainly all bird species lay shelled eggs, but so too do some reptiles. In



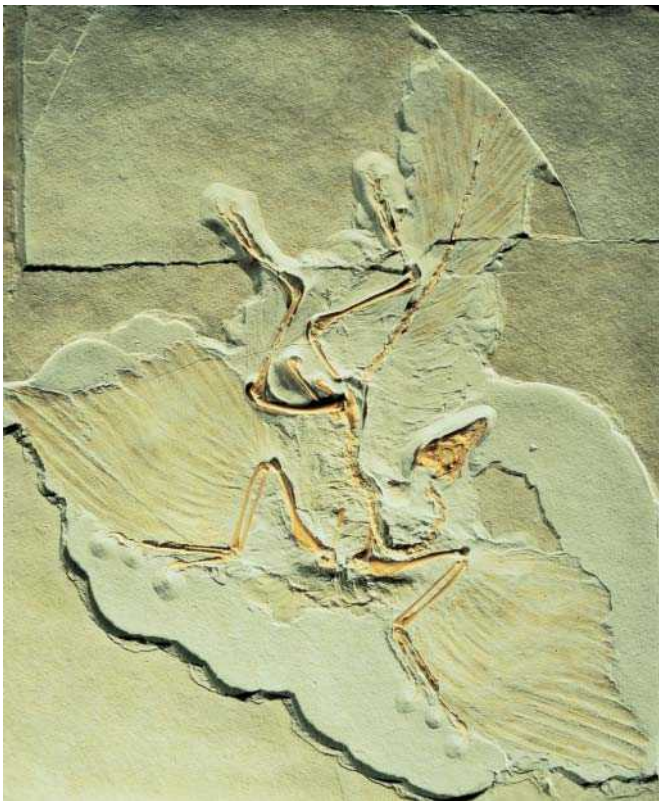
Types of bird feathers. (Illustration by Marguette Dongvillo)

most bird species, only the left ovary develops. The ovary holds a large number of oocytes. During the breeding season, a few oocytes (immature eggs) start to develop. They are covered in a follicle that lays down yolk, which is manufactured in the liver and carried in the blood. The one with the most yolk is shed first; the follicle ruptures and the oocyte moves into the first part of the oviduct where it may be fertilized from sperm stored in the sperm storage glands. During about 20 hours it passes down the oviduct where it is covered in albumin and, towards the end, the outer layer calcifies to form the shell and any markings are laid down from blood (red-brown) or bile (blue-green) pigments. About this time, if another egg is to be laid, another oocyte is released. In a few large species, the process may take longer.

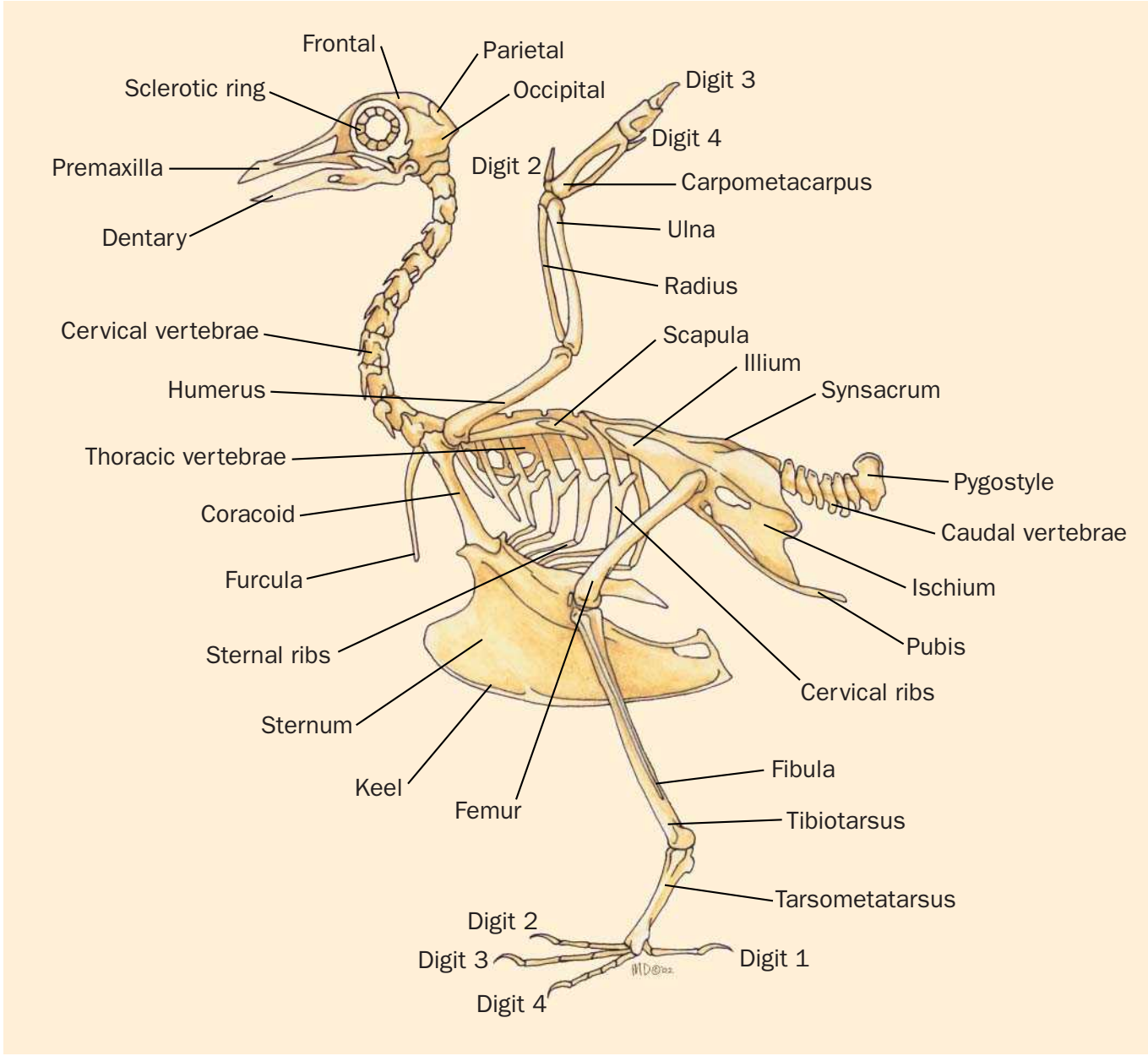
The egg contains nutrients for the developing embryo. There is some exchange of gases and water across the shell, and waste from the embryo is stored in a sac that develops outside of the embryo, but within the shell (the allantois). Another sac develops into an air sac for ventilation. Once incubation begins, development is rapid, triggered by heat either from a brooding parent, as in most birds, or the environment, as in mound builders, which bury their eggs to capture heat from the sun. Within days, the embryo has large eyes and rudimentary organs. As it develops, the yolk sac is absorbed and the embryo fills more of the shell. By hatching, the yolk is fully absorbed and the embryo has moved its bill into the air sac and begins to breathe air. By this time, mainly through water loss, the egg is about 12–15% lighter than at the start of incubation. The embryo uses an egg tooth on the tip of its bill to chip away a ring around one end of the shell (already thinned by loss of calcium to the embryo) and hatch. If it is altricial (e.g., songbirds and seabirds), the chick will be naked or downy, and helpless; the chick of a precocial species (e.g., ostriches, ducks, and game birds) will be feathered, able to regulate its own body temperature, and can follow its parent and feed itself almost immediately. The chicks of precocial species hatch synchronously (at the same time), those of other species are sometimes asynchronous, resulting in a mixed-age brood.

Growth and care of young

Most birds grow remarkably fast and, in many altricial species, are more or less fully grown by the time they leave the nest. At the extremes, chicks stay in the nest about 10–20 days



Archaeopteryx (*Archaeopteryx lithographica*) fossil from the late Jurassic period, found in Bavaria, Germany limestone in 1860. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)



Bird skeleton. (Illustration by Marguette Dongvillo)

in passerines and 150–250 days in albatrosses. Precocial species, which are free of the nest, are slower growing—their rate of growth is approximately one-third that of altricial species.

The amount and type of care given is diverse. Nidicolous species, in which the chicks stay in the nest, put in considerable effort bringing food to the nest, either bringing many small items (e.g., insectivores) or a few large ones (raptors). Some species regurgitate food for the chicks (e.g., seabirds). These species must also keep the chicks warm and dry and protect them from predators, and may also keep the nest free of droppings. Nudifugous species, in which the chicks follow adult(s), are either fed by the adult (some seabirds) or, more commonly, feed themselves on plant material (e.g., many waterfowl and game birds). Parental care varies accordingly. As protection against predators, some waterfowl carry their young on their backs and, in colonial species, several neighbors unite to try to drive off an intruder. In some species, the breeding pair is accompanied by "helpers," which may be offspring from earlier breeding attempts or unrelated individuals, males or females or both sexes, juveniles or adults. Helpers help particularly in those species in which prey is difficult to find or catch.

Ecology

All species have a niche—the range of environmental conditions under which they can survive and reproduce. The

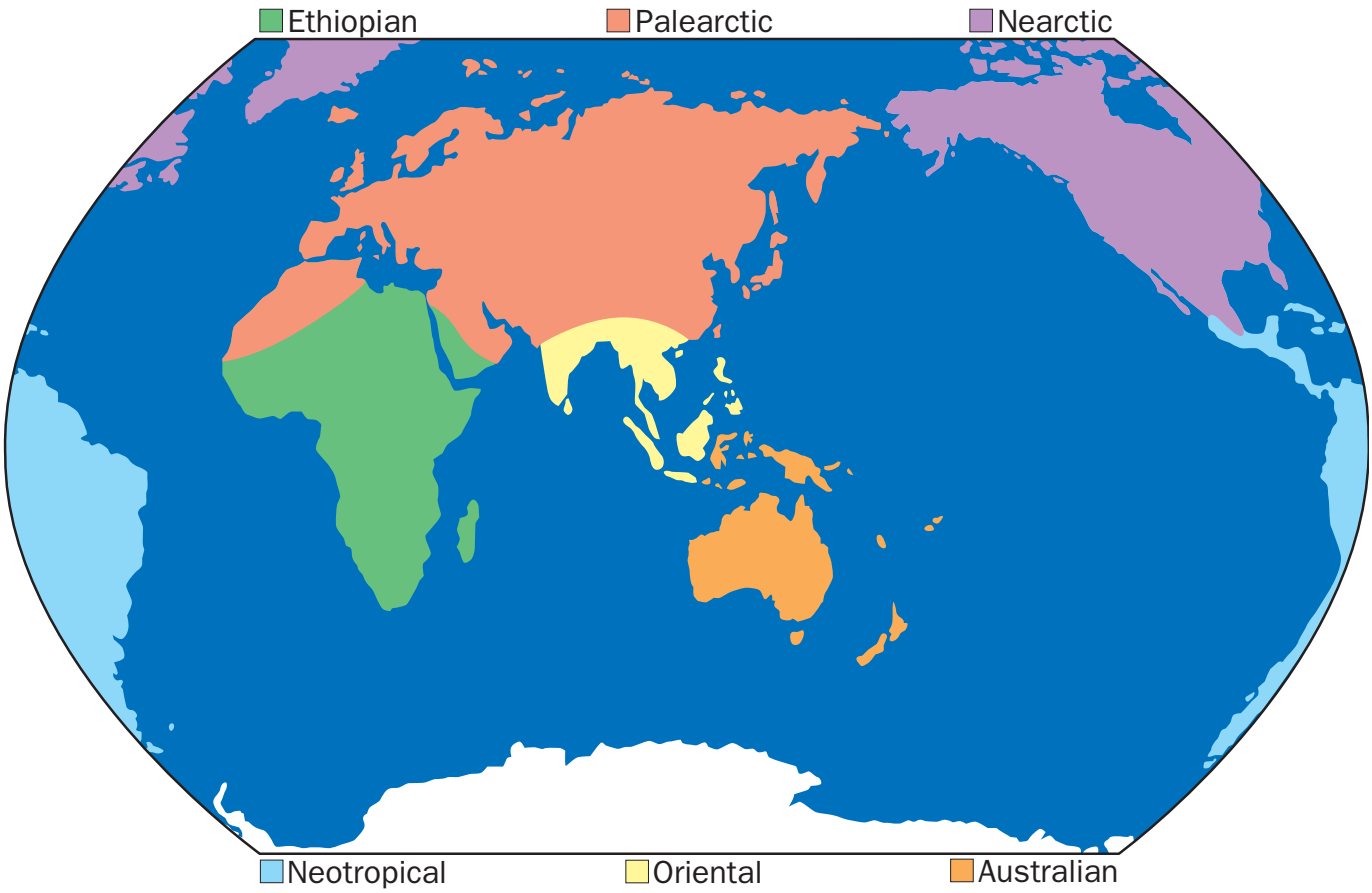
Emperor penguin (*Aptenodytes forsteri*) adult and chick, Antarctica. (Photo by Art Wolfe. Photo Researchers, Inc. Reproduced by permission.)

niche may be broad and unspecialized or narrow and highly specialized. Coexisting species tend not to overlap much in their niche requirements. This is particularly obvious with food: the type and where, when, and how it is collected. For example, three hawks coexist in some Australian woodlands and they roughly segregate by species and sex: the small male sparrow hawk takes passerines in the canopy; the medium-sized brown goshawk hunts birds and small mammals in the air and on the ground in more open spaces; and the largest, the female gray goshawk, captures medium-sized birds and mammals on or near the ground.

To provide energy for flight, birds need highly nutritive food. For this reason, most birds eat at least some arthropods, especially insects. They may do this incidentally, for example, mixed in with nectar, but mostly they are actively captured. In addition to this, there are four basic diet groups: the carnivores (those that eat other vertebrates, including the fish-eaters); berry- and seedeaters; eaters of non-flowering plants (fungi, mosses, algae, and so forth); eaters of flowering plants (roots, tubers, leaves, nectar). Grasses and herbage are low in nutritive value and must be consumed in too-large quantities to be of major importance to many species, and few birds have the ability to digest cellulose. Not surprisingly, birds are pollinators and seed dispersers for a great variety of plants. Some species specialize, others are more varied in their diet. Methods of collecting food are numerous, but most involve sight.

Birds are infected by a variety of diseases, both internal and external, caused by bacteria, viruses, and parasites. Some of these can also affect humans and their livestock. In general, healthy birds can carry both internal and external parasites without obvious harm. Nevertheless, disease outbreaks occur; for example, following floods, outbreaks of insect-borne pox can occur in wild birds. Birds can also suffer from exposure to toxic substances of both natural (e.g., toxic algal blooms) and human-made origin (e.g., oil spills, pesticides, lead-shot, and other pollutants). Predation is a fact of life for the majority of bird species, particularly for their eggs and young. Their life history has evolved to allow for losses, which are naturally high. For example, in passerines, perhaps 5% of eggs result in adult birds and annual mortality of adults may be as high as 60%. For larger species, the rate of mortality tends to be lower. Provided that they are not too prolonged or severe, starvation, predation, disease, and other causes of

Down feathers form part of a bird's insulating underplumage. The central axis, or rachis, bears the flat vane of the feather made up of many slender barbs. Feathers allow a bird to fly, and provide waterproofing, camouflage, and color and shape to attract mates. (Photo by Gusto Productions/Science Photo Library. Photo Researchers, Inc. Reproduced by permission.)



Regions of bird distribution. (Illustration by Emily Damstra)

mortality are compensatory and, in general, bird populations recover quickly.

Distribution and biogeography

Birds are distributed across all continents and on most islands, and in all major habitats from caves to mountaintops, deserts to rainforests. Many factors limit the distribution of species, all relating to their ecology: climate, habitat availability, and the presence of predators, competitors, and food. There may also be physical barriers such as mountain ranges, oceans, and impassable expanses of unsuitable habitat. The breeding range often differs from the nonbreeding range because of seasonal or other movements to remain in the most favorable conditions. There are broad patterns to general distribution; for example, woodpeckers are found in many regions of the world but are absent from Australia, New Zealand, and Madagascar. The ratites are southern in distribution, pointing to their early evolution in Gondwana (the huge southern super-continent that split into the southern continents). These patterns reveal six major biogeographical realms: Neotropical, Nearctic, Ethiopian, Palearctic, Oriental, and Australian. The greatest number of species is found in the Neotropics (South and Central America, the West Indies, and southern Mexico) with roughly 3,000 species, and 31 endemic families. The Nearctic (North America, Greenland, Iceland), with about 1,000 breeding species and no endemic bird families, is among those areas with the fewest species.

Bird populations vary enormously in their abundance and density. Some species are widely scattered across the landscape (e.g., the solitary eagles), others live in crowded colonies of millions (queleas). There are several general patterns: population density is related to body size (smaller species tend to be more numerous); the number of species and of individuals tends to be greatest in complex habitats (e.g., forest compared with grassland) and where several habitats meet (ecotones); the number of species increases with the size of the habitat patch; and, the number of species and overall densities tend to increase from the poles to the equator.

Behavior

Bird species can be social or solitary; they may nest, roost, and feed in small or large groups for part of their lives (e.g., when young or in the nonbreeding season) or their entire lives. Some form feeding flocks with other bird species or nest near more powerful species for protection. Some associate loosely with other vertebrates, such as following monkey troops to catch the insects they flush. A few live more or less

commensally, for example, by feeding on ticks from ungulates. Some species spend much of their lives on the ground (terrestrial species), others in the air, in water, or in various combinations. The majority of species are active by day (diurnal), but many are crepuscular (active in twilight) or truly nocturnal. During inactive periods, most retire to a safe roost where they socialize, preen, relax, or sleep. They appear to need to sleep several hours a day.

Birds have developed complex communication systems, including various calls and song and visual signals involving posture, movements, facial expressions, display of certain characteristics of plumage, and, in some species, flushing of the skin (e.g., vultures) or popping of the eyes (Australian choughs). Some behaviors, like the dance of brolgas and synchronized swimming of swans, is ritualized, others appear more spontaneous. Courtship is a highly ritualized sequence of displays, on the ground or in the air, and can involve courtship feeding, which may be a way for females to judge the quality of their partner.

As a group, birds are cerebrally advanced. Much of their behavior is innate but they also learn by experience throughout life. They have good memories, such as retrieving cached food items from several stores several weeks after they were hidden. Some species appear to be particularly adaptable if not intelligent. Certainly, their behavior can be complex and interesting. Individual rooks wait to cache nuts if a non-hoarding rook is passing by, yet are unconcerned by rooks that are also hoarding. Jays that steal food are more likely to move their caches to prevent theft than are jays that are not thieves. Parrots have a complex social system and enjoy playing with each other and with found objects. Black kites and green-backed herons have learned to place bread on water to attract fish. One of the Galápagos finches uses a cactus thorn to probe bark crevices for insects that it cannot reach with its short tongue.

Resources

Books

Brooke, M., and T. Birkhead. *The Cambridge Encyclopedia of Ornithology.* Cambridge: Cambridge University Press, 1991.

Campbell, B., and E. Lack, eds. *A Dictionary of Birds.* Calton: Poyser, 1985.

de Juana, E. *Handbook of the Birds of the World.* Vol. 1. *Ostrich to Ducks,* edited by J. A. del Hoyo, A. Elliot, and J. Sargatal. Barcelona: Lynx Edicions, 1992.

Farner, D. S., J. R. King, and K. C. Parkes, eds. *Avian Biology.* Vols. 6, 7, and 8. London: Academic Press, 1982 through 1985.

Farner, D. S., and J. R. King, eds. *Avian Biology.* Vols. 1, 2, 3, 4, and 5. London: Academic Press, 1971 through 1975.

Perrins, C. M. *The Illustrated Encyclopedia of Birds.* London: Headline, 1990.

Perrins, C. M., and T. R. Birkhead. *Avian Ecology.* Glasgow: Blackie, 1983.

Welty, J. C., and L. Baptista. *The Life of Birds.* 4th ed. London: Poyser, 1988.

Organizations

American Ornithologists' Union. Suite 402, 1313 Dolley Madison Blvd, McLean, VA 22101 USA. E-mail: AOU@BurkInc.com Web site: <www.aou.org>

BirdLife International. Wellbrook Court, Girton Road, Cambridge, Cambridgeshire CB3 ONA United Kingdom. Phone: +44 1 223 277 318. Fax: +44-1-223-277-200. E-mail: birdlife@birdlife.org.uk Web site: <http://www.birdlife.net>

Birds Australia. 415 Riversdale Road, Hawthorn East, Victoria 3123 Australia. Phone: +61 3 9882 2622. Fax: +61 3 9882 2677. E-mail: mail@birdsaustralia.com.au Web site: <http://www.birdsaustralia.com.au>

British Trust for Ornithology. The Nunnery, Thetford, Norfolk IP24 2PU United Kingdom. Phone: +44 0 1842 750050. Fax: +44 0 1842 750030. E-mail: info@bto.org Web site: <www.bto.org>

National Audubon Society. 700 Broadway, New York, NY 10003 USA. Phone: (212) 979-3000. Fax: (212) 978-3188. Web site: <www.Audubon.org>

Royal Society for the Protection of Birds. Admail 975 Freepost ANG 6335, The Lodge, Sandy, Bedfordshire SG19 2TN United Kingdom. Web site: <www.rspb.org.uk>

Penny Olsen, PhD

Birds and humans

Introduction

Why are we so fascinated with birds? From the earliest cave paintings and ceramic effigies of prehistoric humans to the present, we find close links between birds and ourselves. Those links are related to several things that draw us together: (1) our fascination with and envy of the ability of birds to fly; (2) the meat and eggs they provide us; (3) their colorful plumage that we admire and often use to decorate our own attire; (4) their down feathers that we use for insulation, and other feathers that we've used as writing instruments, to fletch arrows, to fan royalty, and to dust our homes; (5) their beautiful voices; (6) their hollow bones which we have at times used to produce tools and even flutes with which to emulate their songs; (7) their ritualistic courtship behavior; (8) their attentive parental care; (9) the vigor of their territorial defense; (10) their seasonal migrations; and (11) their diversity.

Certainly the utilitarian aspects of our association with birds would remain even if birds were less conspicuous. Our fascination with birds might be found in many seemingly simple things we share with them: perception of color, song, concern for the decor of our homes, parental care, the awkwardness of adolescence, territorial defense—the list could go on. Our fascination with birds might also be found in things deeper within our psyche—things we don't really share with birds, but that we can imagine as sharing: emotional things such as love, hate, fear, pride, sadness, and hope. Yes, as one recent book title has it, "Hope is the thing with feathers."

Cultural significance of birds

We, like most birds, are most active in the light of day—a time when the light-sensitive cone cells of our respective eyes allow our brains to interpret the world in color. Color has a common basic value to primitive humans and to birds. It allows both to identify ripe fruit from that which is not ripe, poisonous fruits from those that are edible. With the ability to see color come a number of gifts—lagniappe—something a little extra. From the human perspective we might think of them as aesthetic, but from the birds' perspective they seem utilitarian as well. The diversity of patterns and colors in the plumages of birds facilitate recognition of members of their own species, just as colors of uniforms allow us to recognize players for the home team. We use color we find pleasing as decoration for ourselves and our surroundings—to please ourselves and those we wish to please. Birds do the same thing. The bowerbirds of Australia have drab plumage, but decorate their courtship bowers with objects of specific hues. Natural selection has favored the development of colors and patterns that help fulfill needs among birds for the attraction of a mate and defense of a territory, and camouflage for protection from enemies. In many ways we share such needs and such benefits of color. We differ from most mammals in being able to see color, a trait we share with most birds. The beauty we recognize in the colors of birds might be looked upon as a celebration of our uniqueness.

Birds and music

The purity of tones, diversity of melody, and the predictability of the rhythms of bird songs and mechanical sounds are music to our ears. For birds the sounds are messages: "This territory is occupied," "I'm an available and desirable suitor." We have intercepted—no, merely eavesdropped—on their conversations. We have borrowed them for our own uses and embellishment. For us the songs are messages as well, reflections of our well-being and desires. Bird songs have influenced the works of great composers. The common cuckoo (*Cuculus canorus*), nightingale (*Luscinia megarhynchus*), and common quail (*Coturnix coturnix*) can all be heard in Beethoven's Sixth Symphony, the "Pastoral Symphony." Béla Bartók recorded bird songs in musical notation and included them in his compositions. His final work, "Piano Concerto no. 3" includes bird songs he heard during his stay in North Carolina. Antonín Dvořák also used bird songs and the red-winged blackbird's (*Agelaius phoeniceus*) territorial "oak and leo" call can be heard in his Opus 96 from his days in Spillville, Iowa.

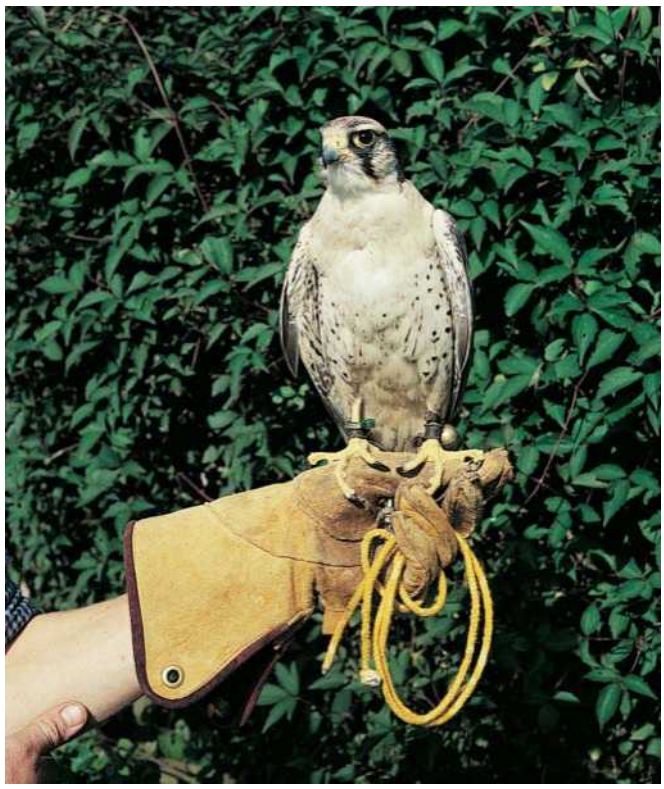
Birds imitate us as we imitate them; they have borrowed sounds from our musical repertoire. My African gray parrot (*Psittacus erithacus*), whose name is "Smoky" dutifully sings "On Top of Old Smoky"—but his rendition is no better than mine. In a possible turn about of truly musical influence, Mozart was passing a pet store near his home in May of 1784 when he heard the strains of the allegretto theme from his G major concerto which he had written just five weeks earlier. He immediately went into the store and purchased the European starling (*Sturnus vulgaris*) that was singing it!

Hundreds of turkeys are raised for food at the Givat Hayim kibbutz near Natanya, Israel. (Photo by Rick Browne. Photo Researchers, Inc. Reproduced by permission.)

We have not only borrowed from the music of birds, but around the world various cultures have also incorporated elements of bird courtship displays in their own dances. The Blackfoot Indians of the northwestern United States mimicked the foot-stomping and strutting of displaying male sage grouse (*Centrocercus urophasianus*) and even wore feathered costumes that mimicked the birds' plumage. The Jivaros of Amazonia, perhaps best known for shrinking human heads, mimic the courtship displays of the brilliant orange cock-of-the-rock (*Rupicola rupicola*). The people of Monumbo of Papua New Guinea mimic the courtship of the cassowary (*Casuarius* sp.).

The behavior of birds has always provided the basis for metaphors, symbolism, mythology, and lessons to be learned. The courtship cooing of doves has long been symbolic of human love and courtship, the powerful beak and talons of eagles have similarly served as a metaphor for strength and a symbol of our armies. The silence, stillness, attentiveness to our presence, and human-like expression created by the forward-facing eyes and facial disc of feathers on an owl have led to owls becoming symbolic of wisdom. Yet owls are not wise, but highly instinctive in their behavior, the symbolism resulting from the accident of their diurnal inactivity and the convergence of their binocular vision with our own—an adaptation that gives both of us the ability to judge distance and size—critical abilities for an animal to possess if leaping from limb to limb as our ancestors did or if diving suddenly to pounce on a mouse in near darkness, as an owl does.

Many expressions in human languages draw symbolism from the language and actions of birds. At times visual metaphors are obvious, such as our association of the peacock (*Pavo cristatus*) with vanity—or with the kaleidoscope of colors on a television network. At other times the links are fanciful, such as the notion that white storks (*Ciconia ciconia*) bring babies or that ravens (*Corvus corax*) foretell death. The link between magpies (*Pica pica*) and talkative humans is a clear reference to the chatter of the birds, as is the use of the word "parrot" to refer to an individual who repeats what has been said. "Eagle-eye" is a reasonable descriptor for a human who picks up on details. To have one's "ducks in a row" is a verbal expression of the visual impression of organization provided by a view of a duck being followed by a brood of ducklings in single file behind her. The impact of "bird words" on our language and culture is immense, though at times the link to birds has been lost and only the expression remains. Have you ever been "goosed?" Really? If you've walked across a pasture that was patrolled by a vigilant gander you might understand. Yes, they do come up from behind in a surprise attack with a sharp "goose."



Saker falcon (*Falco cherrug*), a bird used in falconry. (Photo by Eric & David Hosking. Photo Researchers, Inc. Reproduced by permission.)

Birds used to hunt and fish

Falconry, using a falcon or other bird of prey to hunt, was the sport of kings in the Middle Ages. It was practiced from the steppes of Asia to the sands of the Middle East and the British Isles. Social position not only allowed time for the sport, but also dictated which species of bird could be used. The techniques and vocabulary of falconry were ritualized. Falconry persisted through the centuries and in the twentieth century experienced a popularity that, without regulation, contributed to the decline of such prized species as the peregrine (*Falco peregrinus*) and gyrfalcon (*F. rusticolus*). By the mid-twentieth century laws were in place to protect falcons, but raiding of traditional nest sites continued. Then came the pesticide years when birds of prey suffered as a result of biomagnification of organochlorines in their tissues and populations of birds like the peregrine plummeted. In the last decades of the twentieth century, following bans on the pesticides, the tools of falconry were used to save the birds.

Other birds have also played the role of hunter for humans. For more than 1,000 years, Japanese and Chinese fishermen have used trained cormorants to capture fish for them. A ring is often placed around a cormorant's neck to prevent it from swallowing large fish, but well-trained birds need no such ring.

Domestication of birds/artificial selection

Domestication of birds has occurred in several human cultures, typically involving species kept for meat or eggs, but at times birds were domesticated for other reasons first. Chickens were likely the earliest domesticated birds; archaeological evidence suggests domestication in the Indus Valley more than 5,000 years ago. There is no historic record of the domestication of the red jungle fowl (*Gallus gallus*), a bird native to Southeast Asia, but by the early days of the Roman Empire it was already a commonly kept bird throughout the civilized world. No bird has been so important to humans as the chicken—nor so selectively bred. Varieties have been developed not only for meat and egg production and for fighting, but also for eggs of specific shell color, ability to tolerate crowding, and for a diversity of fancy plumages.

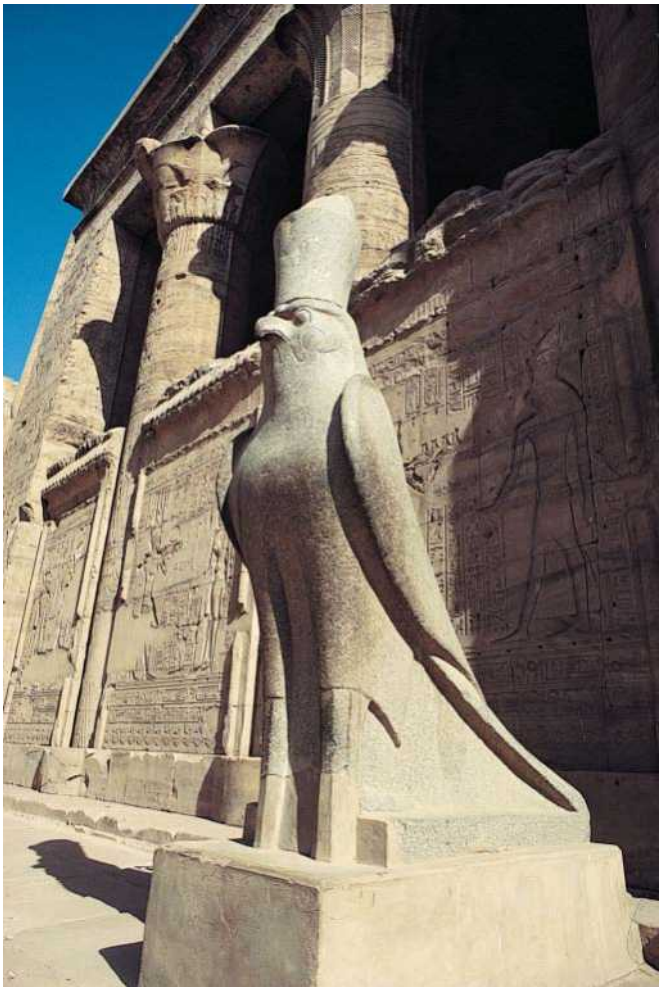
As urban human populations have grown, so have needs for mass production of foods. Factory farming of poultry now provides considerable protein to populations around the world. During the last two decades of the 20th century the production of chicken meat increased by an average of 6% per year and by the year 2000, factory farming of chickens was producing more than 20 billion broiler chickens per year.

While we have developed chickens that produce more meat and eggs, there are consequences to such efforts. Animal rights advocates question conditions under which the chickens are kept, charging that we maximize production in minimal space, processing chickens as if they were widgets at a manufacturing plant. Confinement of birds in high-density populations makes them more susceptible to disease, a problem we have addressed by dosing industrial flocks with antibiotics. These are often the same or similar antibiotics used by humans, and widespread use for poultry production has led to development of bacterial resistance to antibiotics. Now these resistant strains of bacteria are making humans sick and treatment difficult. Industrial poultry farming involving millions of chickens produced per farm has also resulted in high nitrogen runoff into rivers and streams, contaminating water supplies and contributing to other environmental problems.

Turkeys (*Meleagris gallopavo*) were domesticated in Mexico about 2,000 years ago and were first taken to Europe in the sixteenth century. They spread rapidly through Europe as a domesticated bird and were taken back to the New World early in the seventeenth century. The turkeys served by the Pilgrims on that first Thanksgiving were likely descendants of the Mexican birds rather than the native wild turkeys. Modern commercial turkeys are the result of hybridization of the domesticated Mexican form with the wild turkey of the eastern United States.

Ducks (the mallard, *Anas platyrhynchos*) and the greylag goose (*Anser anser*) were domesticated centuries ago in temperate Eurasia for meat, eggs, and down. Mute swans (*Cygnus olor*) were domesticated in Britain for their meat and, had they not been domesticated, might have become extinct as a result of overhunting. Two species of guineafowl (*Numida* spp.) were domesticated in Africa for meat and eggs.

The only South American bird to be truly domesticated is the muscovy duck (*Cairina moschata*). The ostrich (*Struthio camelus*), emu (*Dromaius novaehollandiae*), and rhea (*Rhea*



Temple of Horus, a god represented by a falcon, in Egypt. (Photo by C.J. Collins. Photo Researchers, Inc. Reproduced by permission.)

americana) are kept for meat, feathers, skins, and eggs. Ostrich eggs were made into elaborately carved and decorated cups by Egyptians centuries ago, and in the late twentieth century as ostrich farming grew in popularity, there has been a rebirth of artistic uses of ostrich eggs.

Birds as companions

Although the first association of birds and humans almost certainly included birds in the role of lunch, they have also been kept as messengers, for the sport of racing, for fighting, hunting, and as pets. The origins of these associations are lost in prehistory. The early Greeks and Romans kept birds for meat and for mail service. Early armies—and even armies of the twentieth century—used homing pigeons to send word of the tide of battle home from the front lines.

One 2002 estimate suggests that there are over 31 million pet birds in the United States alone. Companion animals such as birds long have been recognized as making us "feel good" and as helping to relieve our stress. Medical specialists now recognize the therapeutic role that pet birds can have.

Birds in entertainment

Our recognition of the behaviors and voices of birds have become so much a part of our culture that some have become stylized as icons of entertainment and sports that have been enjoyed now by several generations of humans. Donald Duck's waddle may not quite be that of a real bird, but the caricature fits, as does Donald's human-duck hybrid voice. Woody Woodpecker's appearance and voice are movie icons borrowed in stylized form from the North American pileated woodpecker. Big Bird is much more generic, but a lovable character recognized by young and old. The role of birds as mascots for athletic teams is really big business—and sometimes contentious. When the University of Central Florida opened its doors in the 1970s, the student body twice voted for "Vincent the Vulture" as their mascot, conjuring up images of a trained turkey vulture (*Cathartes aura*) circling the opponents' bench. But the administration overruled the choice, settling instead for Pegasus, a mythical winged horse.

Real birds have had roles in human entertainment as well, ranging from both staged and real cock fights, to the many birds in Alfred Hitchcock's "The Birds," to pets that have helped define a star's screen persona, such as the television private investigator, Beretta, who had a cockatoo named Fred, and the African gray parrot in the movie *Being John Malkovich*.

Modern birding

The interest that humans have shown in birds has evolved from seeing them as a source of food, feathers, or other products and as a source of awe, to keeping birds for sport or as pets, to collecting the skins and eggs of birds, to attracting wild birds to feeders, to observing birds as a pastime, to tallying observations of birds as a sport—sometimes even under competitive circumstances. Like the collectors of old, birders today find thrill in seeking birds. Unlike them, the culmination of the hunt is not measured in skins and eggs, but in lists of species seen or heard. Among the earliest of organized birding efforts are Christmas Bird Counts, initiated by the National Association of Audubon Societies in 1900 to replace the traditional "after Christmas dinner" shooting of birds. Birders keep life lists, year lists, state lists, and yard lists. Many birders do "Big Days" in which they strive to see as many species as possible within a 24-hour period. A "World Series of Birding" in New Jersey pits teams against one another in a grand 24-hour hunt through the state.

Some modern birders pursue their sport from an easy chair in front of a television set, carefully listing those caught, sometimes deliberately, sometimes by accident, on film or sound tracks in the background of movie sets. As an ornithologist, I have often smiled at old westerns that always seem to include a view of a turkey vulture circling high over a dead or dying desperado. Directors of those films always seemed compelled to include the "skreee" cry of a red-tailed hawk dubbed in as if produced by the naturally mute vulture. Equally amusing are the Star Trek episodes with scenes on far off planets that have Carolina wrens (*Thryothorus ludovicianus*) calling in the background. Identifying those televsion

Aborigine emu dancers in Northern Territory, Australia. (Photo by Gordon Gaman. Photo Researchers, Inc. Reproduced by permission.)

and movie birds is often a challenge and can reveal just how intimately some birders come to know birds. The challenge contributes to learning more, and it's all part of the lure of the list.

Old Tarzan movies with the story set in Africa often had the loud call of a pileated woodpecker in the background. These were not all chance recordings. Some were likely the result of deliberate dubbing in of a call that had been recorded in the 1930s by Arthur A. Allen, an ornithologist at Cornell University. Allen collaborated with Hollywood filmmakers in developing techniques for recording natural sounds. The results of those efforts not only added "realism" to movies, but also contributed much to the scientific study of bird sounds.

The contributions of birders to the science of ornithology

Amateurs have often made important contributions to science through their avocations, but there are few sciences where amateurs have made as many contributions as in ornithology. The bird-finding and bird-identification expertise of modern birders has contributed greatly to our knowledge and understanding of birds through both independent research and through organized research programs that enlist the aid of amateurs. The Christmas Bird Count was not initiated as a research program, but over the years data from it have been used in efforts to monitor bird populations. The Breeding Bird Survey of the United States Fish and Wildlife Service makes use of this large cadre of skilled amateurs. So too does Project Feeder Watch and other programs through the Cornell Laboratory of Ornithology. While watching birds has grown from a simple pastime to a competitive sport for some, we are now seeing an emphasis on "birding with a purpose"—furthering our knowledge and abilities to conserve birds and their habitats through collaborative scientific studies.

Feeding wild birds

Feeding backyard birds became popular at the close of the nineteenth century and at the close of the twentieth century it was enjoying further resurgence, especially in temperate areas of developed nations, developing into a multi-billion-dollar a year industry. In 1980–81, about 20% of North American adults purchased seed to feed wild birds; by 1997, about 30% of North Americans over age 16 were involved in feeding wild birds. Bird feeding was long ignored by scientists, viewed with apathy, or even viewed as harmful to bird populations, but in the late twentieth century it became the subject of several scientific studies. Clearly, feeding backyard birds has tremendous educational potential, bringing birds to within easy

A fancy domestic pigeon—Old Dutch Capuchine breed. (Photo by Kenneth W. Fink. Photo Researchers, Inc. Reproduced by permission.)

viewing distance for young and old. Range expansion of many North American bird species has likely been facilitated by bird feeding. Such expansions may include the northward movements of the tufted titmouse (*Parus bicolor*) and red-bellied woodpecker (*Melanerpes carolinus*), the southward expansion of the evening grosbeak, and the eastward expansion of wintering rufous hummingbirds (*Selasphorus rufus*). The extent to which such range expansions can be attributed to bird feeding, versus the extent to which it is simply easier to document the expansions as a result of bird feeding, is not clear. Many factors are usually involved in range expansions, including such things as habitat modifications, changing climate, and elimination or reduction of predators or competitors, as well as increased or more dependable food supplies.

Introduced species

North America has been the "melting pot" not only for immigrant humans from many nations, but also for more than 120 bird species that have been deliberately or accidentally released in sufficient numbers to establish breeding populations. About 40 of those have been successful; some, such as the European starling, rock dove (*Columba livia*), and house sparrow (*Passer domesticus*), have been incredibly successful. Each has its own story. Rock doves were brought with early immigrants as semi-domesticated birds that were kept for food and sport. House sparrows were brought to control insect pests in the gardens of immigrants, and though not prone to long distance dispersal, succeeded in conquering North America and many other areas as a result of deliberate introductions. For example, many wagon trains heading west from St. Louis took along a cage of house sparrows to assure pest control in gardens at the end of the journey. Early attempts to introduce the European starling apparently failed, but an attempt in 1890 succeeded beyond all expectations. That effort was for the sole purpose of introducing a bird that had been mentioned in Shakespeare's Henry IV! Today the European starling is touted as the most abundant bird in North America.

The greatest diversity of successfully introduced exotic birds can be found in warmer areas. Florida, southern California, and Hawaii all have significant exotic bird populations. The most successful of these birds are ones that can live in association with humans. Indeed, many have been inadvertent introductions as a result of escape of pet birds and birds destined for the pet trade. Some, such as the Eurasian tree sparrow (*Passer montanus*) and crested myna (*Acridotheres cristatellus*) in North America have established small, relatively stable breeding populations and such small populations are rarely linked to problems. As numbers increase, however, competition with native species and other problems have often become evident. Many of the introduced exotics are secondary cavity nesters that compete with native cavity nesters—birds that nest in cavities such as a hole in a tree. Populations of many native North American birds have suffered as a result of competition with house sparrows and European starlings. The budgerigar (*Melopsittacus undulatus*) has been reported competing with purple martins (*Progne subis*) for nest sites in Florida. Aside from competition with native species, European starlings, house sparrows, and rock doves are often a nuisance in making messy nests on buildings, have the potential for dispersing diseases and parasites to poultry, other birds, and humans. Their droppings have damaged buildings and monuments and have created health hazards for humans. While the monk parakeet (*Myiopsitta monachus*) is considered a serious agricultural pest in Argentina, it has for many years been imported into the United States for the pet trade. In 1972, a crate of monk parakeets destined for the pet trade was dropped as it was being unloaded during a snowstorm in New York. The birds survived and began nesting in the area. Other escaped monk parakeets have likely augmented their population and the species now nests along the Atlantic coast from New York to Florida and west to Louisiana. In Florida the species has become a serious problem as a result of building its large stick nests on electric transformers.

In the last years of the twentieth century the Eurasian collared dove (*Streptopelia decaocto*) made it to south Florida after escaping captivity in the Bahamas. It succeeded in establishing breeding populations there and by 2002 was nesting in much of eastern North America. Other exotic doves have become locally established, such as the ringed turtle doves (*Streptopelia risoria*) in several North American cities, but have shown no tendency for wide dispersal.

Some introduced birds have been moved about the world not only with government approval, but also by various governments. Exotic game bird programs of the United States Fish and Wildlife Service and various state and provincial governments have resulted in the introduction of many species, few of which have been successful and most of which have left us with continuing questions. Even for the ring-necked pheasant (*Phasianus colchicus*), often touted as a highly successful introduction, questions have been raised about competition with native species. In at least some areas, populations have not been sustained and more pheasants are released from game farms than are shot by hunters each year. These programs have fallen out of favor because of the recognition of problems with such introductions, but the "potential" for new

game birds is continually discussed and there have been past subsidence and resurgence in interest in introducing exotic game birds. Memory of the problems and failures often seems short-lived.

Among the famous failures were repeated introductions to North America of the European common quail (*Coturnix coturnix*), a migratory species that simply disappeared following introductions. Some apparently followed migration pathways long incorporated into their genetic make-up. Instinct seems to have programmed them to head a certain direction, and fly a certain distance or length of time to reach wintering areas. But when moved from Europe to North America, following that genetic roadmap at least sometimes dumped them in the Gulf of Mexico.

Totem poles in Vancouver, Canada, carved by Native Americans of that area. (Photo by Porterfield/Chickering. Photo Researchers, Inc. Reproduced by permission.)

Birds as vectors of human disease

In the summer of 1997, a particularly lethal form of influenza appeared in Hong Kong and chickens were identified as an intermediate link in its transmission to humans. Thousands of chickens were killed and a human catastrophe was averted. One of the consequences of maintaining high numbers of birds near human population centers is the hazard posed by their role as intermediate hosts for human diseases.

In August 1999, Americans were shaken by the news of a new disease in North America—one that was killing humans, horses, and birds. West Nile virus, originally discovered in Africa, had spread to Europe, then to North America, and wild birds were part of the transmission cycle. This mosquito-borne virus in its most serious form causes encephalitis, an often fatal inflammation of the brain. As of July 2001, more than 70 species of North American birds have tested positive for the disease, though most were crows (*Corvus* spp.). Birds don't "cause" the disease, but their role as an intermediate host, and the potential for rapid spread of the disease through bird migrations, have generated some negative attitudes towards birds. As of 2002 the disease has been found along the Atlantic coast from New York to Florida and as far west as Louisiana. The threat to humans is important, and the threat to wild birds is very serious. Since members of the crow and jay family (Corvidae) seem particularly vulnerable, an increased incidence of the disease in Florida could seriously threaten the endangered Florida scrub-jay (*Aphelocoma coerulescens*). Thus far there is no evidence that West Nile virus can be transmitted directly from birds to humans, though those handling dead birds are urged to take appropriate cautions. In this case, chickens serve us in the fight to prevent the disease. Penned chickens have been placed in many areas and their blood is regularly checked for evidence of the virus, thus these sentinel chickens serve as an early warning system.

Other bird-human disease links have generated concern in the past, although most of the diseases involved are not commonly found in humans. Psittacosis also known as parrot fever, is a rare human disease caused by a chlamydia, a parasite closely related to bacteria. Humans usually get the disease by inhaling spores in dust from dried bird droppings or from handling infected birds. In humans the disease causes flu-like or pneumonia-like symptoms and it is usually not fatal. We know now that birds other than parrots can transmit the disease and the disease is increasingly referred to by the more appropriate names "chamydiosis" or "ornithosis."

Aside from publicity associated with the discovery of West Nile virus in North America, one of the most frequently reported "disease links" between birds and humans in the United States is with the fungal disease histoplasmosis. In this case, birds do not deserve the negative association made: they neither harbor nor carry the disease. The disease-causing organism, *Histoplasma capsulatum*, is a fungus that grows in nitrogen-rich soils in the southeastern United States. It is spread to humans when such soil is disturbed and generally when spores or bits of the fungus are blown by the wind and inhaled by humans. The link with birds is related to the millions of blackbirds that are sometimes found in individual winter roosts in the Southeast. Excrement from the roosting birds enriches the soil and provides optimum conditions for the growth of the fungus. But many other sources of soil enrichment also occur: including cattle feed lots, poultry farms, heavily fertilized agricultural fields, and roosting concentration of bats (which also get blamed for the disease). The problem comes when such enriched soil is disturbed, dries out, and the fungus becomes airborne.

Problems between birds and humans have always included bird consumption of foods we might otherwise eat or feed to livestock. Flocking birds such as crows, starlings (Sturnidae), doves (Columbidae), blackbirds (Icteridae), gulls (Laridae), and parrots (Psittacidae) are among the primary offenders. The same and other flocking birds also create problems in urban centers, around airports, and other areas. Whole industries have built up around the development, sale, and deployment of devices and chemicals to thwart depredation of crops by birds. Yet in some areas the problem remains very serious. In parts of Argentina, for example, the monk parakeet is said to consume about 50% of the annual grain crop. Such figures, however, must be viewed with a skeptical eye. There is no doubt that the birds take grain, some of which would otherwise make it to human tables. But how much of the grain taken is spilled grain coming from the ground? And

Metal bands are often used to track endangered birds, such as this Victoria crowned-pigeon (*Goura victoria*), found on the island of New Guinea. (Photo by Robert J. Huffman. Field Mark Publications. Reproduced by permission.)

how many weed seeds and harmful insect pests do these same birds take? The charges against birds are rarely presented in the form of a "cost-benefit" analysis, but they should be. Here is a challenge for economists and where greater understanding is needed.

Ornamental uses of bird feathers and bills

Native cultures around the world have employed bird feathers in art and decorative efforts. Some of these efforts have contributed to the extinction of species. For example, the first humans to reach the Hawaiian Islands made cloaks for their royalty of the yellow-feathered skins of the Kauai oo (*Moho braccatus*). It took feathers from thousands of birds to make a single cloak. Similarly, the Maoris of New Zealand made use of the skins and feathers of the huia (*Heteralocha acutirostris*), contributing to their extinction.

In the late 1800s feathers—and even whole birds—became popular ornamentation for ladies' hats in Western cultures. At one point the aigrette feathers of egret species sold for as much as 32 dollars an ounce; they were literally worth their weight in gold. The decline in populations of species such as the snowy egret (*Egretta thula*) was recognized before it was too late and became a cause that led to the Audubon movement in North America and a new era of conservation activity around the world.

Birds as religious symbols

In most cultures, birds have always played major roles as symbols. A few of these include the sacred ibis (*Threskiornis aethiopicus*) of Egypt symbolized the moon god, Thoth, a deity of wisdom, apparently because its curved bill resembled the crescent moon. Cranes were symbolic of Apollo, the Greek god of the sun. The hoopoe (*Upupa epops*) plays a major role in the "The Conference of the Birds" in Islamic mysticism. Doves are well recognized as symbols of love and peace, and the Holy Spirit in Judeo-Christian cultures is often symbolized as a dove.

Birds in myths, literature, and art

The legend of the Roc brought back from Marco Polo's travels may well have a basis in fact in the elephant birds (Aepyornithidae) that appear to have survived into historic times on Madagascar. These birds were flightless, stood 11 feet tall (335 cm) and laid an egg that was large enough to hold the contents of seven ostrich eggs—or as one author suggested, 10,000 hummingbird eggs! Elephant bird eggs are still occasionally found buried on Madagascar and have at times been salvaged by native peoples for use as buckets. A more profitable use has been their sale to eclectic collectors.

The causes of endangerment

Certainly the single most important cause of endangerment of modern birds is habitat destruction. Deforestation and conversion of natural habitats to landscaped, irrigated, and fertilized areas dominated by exotic species not only replace native habitats, but also fragment remaining natural environments, thus limiting movement of habitat-limited birds among populations. Exotic animals often compete with or prey on native birds. Particularly on islands, the impacts of exotics can be devastating. On the island of Guam, for example, the brown tree snake was accidentally introduced in the 1950s. Without natural controls, it has increased in abundance and has decimated native forest birds. At least twelve species of birds have disappeared from the island. For a brief time from the 1940s into the early 1970s, organochlorine pesticides were an incredibly serious threat to birds high on the food chain such as herons, egrets, hawks, falcons, eagles, pelicans, and their relatives. These pesticides were entirely human-made and had been developed to be persistent—to stay around and continue to control insect pests without frequent spraying. The developers succeeded in their efforts only to learn that vertebrates could not break down the chemicals and they were stored in fatty tissue, becoming more concentrated, "biomagnified," with every meal.

Studies of the accumulation of toxins in bird tissues taught us that humans too were vulnerable to these chemicals and birds became recognized as "environmental barometers" capable of providing us an early warning of serious environmental problems. In the mid-twentieth century, we learned that heavy metals such as lead and mercury were biomagnified in living tissues. So too was another class of human-made compounds, the polychlorinated biphenyls—known as PCBs. PCBs had been developed for use in electrical transformers, but are now recognized as posing serious threats to both birds and humans.

Hope for a feathered future

By the early twenty-first century, nearly every state in the United States had a state Ornithological Society or state Audubon Society that published a journal including results of original observations and research with birds. Most developed nations of the world have at least one national ornithological journal—some have several. In North America *The Auk*, *The Wilson Bulletin*, *The Condor*, and *The Journal of Field Ornithology* are international journals focusing primarily on the results of original research with birds. The list merely begins with these because they encompass the whole field of ornithology. We could continue with specialty journals such as *Waterbirds*, *Birding*, and *The Journal of Raptor Research*. In the United Kingdom, *The Ibis*, and in Germany, the *Journal für Ornithologie*, stand among the oldest of continuously published scientific journals. In short, our knowledge and understanding of birds is increasing at a geometric rate. This knowledge is no longer remaining within the realm of science, but is now quickly passed on to a growing birding public through the pages of such popular magazines as *Birder's World*, *Bird Watcher's Digest*, and *WildBird* in North America, and literally scores of popular bird magazines published around the world.

In the first half of the twentieth century motion pictures brought birds to audiences around the world, often through organized programs such as the Audubon Screen Tours in North America. Then television brought such programming into our homes. Then satellites sent such programming around the world. In the early twenty-first century, the Internet has further revolutionized the way we disseminate knowledge about birds. This information age has, of course, also brought growth of human populations and accelerated destruction of habitats. But with new understanding of birds and their needs, and the ability for individuals around the world to band together on behalf of troubled species, conservation efforts have reached new levels and provide us with great hope. Efforts to conserve birds and their habitats and to reduce the rate of human-induced extinction of species grew immensely in the closing decades of the twentieth century. These endeavors are intimately linked not only to research and dissemination of information, but to the approval and implementation of laws such as the Endangered Species Act of 1973 in the United States. This monumental piece of legislation has a primary focus on North America's endangered species, but ramifications that are global. In concert with the Convention on International Trade in Endangered Species (CITES), and endangered species laws in other countries around the world, a framework for global protection of the diversity of birds and other living creatures has been put in place. The key is to keep the momentum going, but for many species and in many areas of the world, it is a close race with extinction.

There are many successes and signs of hope in this race. Following the banning of many organochlorine pesticides in the 1970s, there have been major increases in populations of species such as the double-crested cormorant (*Phalacrocorax auritus*) and other fish-eating birds whose numbers had declined precipitously. It was a sad day when the last free-living California condors (*Gymnogyps californicus*) were taken into captivity in a partnership involving zoos, federal and state agencies, and conservation organizations. It was a last ditch effort to save the species through captive breeding, but the effort paid off. Condor numbers grew through careful stewardship and, though still critically endangered, the species once again flies free. Along the way a great deal was learned that has been applied to conservation efforts for other species.

Other captive breeding and release programs have brought nesting peregrine falcons back to North American cities, and increased bald eagle (*Haliaeetus leucocephalus*) populations dramatically. Combinations of captive-breeding, habitat-restoration, nest-box, and educational programs in the early twenty-first century are assisting many species on the brink of extinction. In Hawaii, captive rearing of the 'alala, or Hawaiian crow (*Corvus hawaiiensis*) is underway. In Puerto Rico the Puerto Rican parrot (*Amazona vittata*) teeters on the edge of extinction, aided by captive breeding and nest boxes, but so low in numbers that hurricanes, predators, and poachers continually threaten it. In Mauritius, captive breeding and nest boxes saved the Mauritius kestrel (*Falco punctatus*) from imminent extinction, bringing a low of only six known individuals in 1974 to nearly 300 birds by 1994.

Other unique, often high-technology, tools have contributed to conservation efforts at the beginning of the twenty-first century. These include biochemical tools such as DNA-DNA hybridization to look at relationships among birds and examination of trace minerals in feathers to determine site of origin of individuals. Miniature transmitters and satellite radio-tracking have been used to monitor movements of some species. Ultralight aircraft have been used to teach whooping cranes (*Grus americana*) a new migratory pathway.

The ultimate keys to conservation of biodiversity rest neither with laws and their enforcement, nor with captive breeding and other costly and labor-intensive manipulations of the creatures. All of these are good, and at times critically necessary. But they are not inherently sustainable. The keys to conservation of biodiversity are to be found in providing the habitats needed for naturally reproducing populations and in understanding the values of biodiversity. What does each species contribute to that diversity? How does each interact with its world and with us? Sound research and education are the ultimate keys, because to know is to love—and we protect what we love. If we know the wonders of these feathered beings we share our world with, we will want to protect them.

Resources

Books

Dunn, E. H., and D. L. Tessaglia-Hymes. *Birds at your Feeder.* New York: W.W. Norton and Company. 1999.

Gibbons, F., and D. Strom. *Neighbors to the Birds.* New York: W.W. Norton and Co. 1988.

Hyams, E. 1972. *Animals in the Service of Man.* Philadelphia, PA: Lippincott. 1972.

Jackson, J. A. *Bird Watch.* Washington, D.C.: Starwood Publishing Co. 1994.

Jackson, J. A., and B. J. S. Jackson. "Avian Ecology." In *The Birds Around Us.* San Francisco: Ortho Publishing Co, 1987.

Zeuner, F. E. *A History of Domesticated Animals.* New York: Harper and Row. 1963.

Periodicals

Crawford, R. D. "Introduction to Europe and diffusion of domesticated Turkeys from the Americas." *Archivos de Zootechnia* 41 (154, extra): 307–314.

Jackson, J. A. "Century of birdwatching." *Birder's World* 13 (6): 58–63.

Other

Geiss, A. D. *Relative attractiveness of different foods at wild bird feeders.*Washington, D.C.: United States Fish and Wildlife Service, Special Scientific Report, Wildlife No. 233: 1–11.

Jerome A. Jackson, PhD

Avian migration and navigation

What is migration?

Ornithologists typically think of migration in terms of the dramatic round-trip journeys undertaken by species that move between high and low latitudes. Even in birds, however, migrations of many types occur that vary in regularity of occurrence, duration, and distance covered. The theme that ties the various types of migration together is that they are all evolved adaptations to fluctuating environmental conditions that render some areas uninhabitable during some portion of the year.

The adaptations to fluctuating environmental conditions that render some areas uninhabitable range from irruptive movements to true migration. Irruptive movements involve irregular dispersal from an unfavorable area to a more favorable area. In contrast, true migration characteristically involves return to the place of origin when conditions improve.

Bird migration includes a broad spectrum of movements by individuals that range from irregular eruptions of individuals to the long-distance round-trip flights that we typically think of when migration is mentioned. There are between 9,000 and 10,000 species of birds and more than half of these migrate regularly. Billions of individual birds are involved in these migrations. Depending upon species, the migration might comprise a journey on foot up and down a mountain (as in some grouse), or it might involve a flight that literally spans the globe. Some species fly by day, others almost exclusively at night; some migrate alone, others in flocks that may reach immense size; many migrations involve a return, often with uncanny precision, to localities previously occupied.

In terms of sheer magnitude, the migrations of many seabirds are the most impressive. The famous Arctic tern (*Sterna paradisea*) nests as far north as open ground exists and migrates the length of the oceans to spend the winter in Antarctic waters, a round-trip of some 25,000 mi (40,000 km) performed every year of the bird's life. Some of the great albatrosses, such as the wandering albatross (*Diomedia exulans*), circumnavigate the globe by moving west to east over the turbulent oceans within the "roaring forties" latitudes south of the tips of the southern continents. Sooty shearwaters (*Puffinus griseus*) are extremely abundant seabirds that breed on islands deep in the Southern Hemisphere, mostly around New Zealand and the southern tip of South America. In late spring and throughout the northern summer, sooty shearwaters migrate northward and circle the basins of the northern Pacific and northern Atlantic Oceans. Flocks of many thousands of individuals may be seen along the Pacific coast of North America. By late summer they are headed back across the ocean to their distant nesting islands, having circled the ocean in the process.

Many shorebirds nest at high latitudes in the Arctic and spend the winter far into the Southern Hemisphere. Their chicks are precocial and thus require relatively little parental care. Adult birds often depart on autumn migration before juveniles, leaving the inexperienced youngsters to make their way to the wintering grounds on their own. Typically, shorebirds migrate in flocks, often at night, but also during the day when crossing large ecological barriers such as oceans, gulfs, or deserts requires extremely long flights. American golden-plovers (*Pluvialis dominica*) make a non-stop flight from the Maritime Provinces of Canada across the western Atlantic Ocean to South America, often flying at altitudes that exceed 20,000 ft (6,000 m). In spring, the species follows a different route northward, crossing the Caribbean and Gulf of Mexico and then heading north through the interior of North America. Its western cousin, the Pacific golden-plover (*P. fulva*), departs its Alaskan nesting areas and flies over the Pacific to Hawaii and beyond, performing single flights of 25,000 mi (7,500 km) or more.

Most waterfowl (swans, geese, and ducks) are shorter-distance migrants, typically nesting and overwintering on the same continent. They tend to migrate in cohesive flocks that often contain family groups and repeatedly use traditional stop-over locations to rest and refuel. Often flying both day and night, migrating waterfowl are strongly influenced by weather conditions. When the conditions are right, they can cover many hundreds of miles in a single, high-altitude flight.

Soaring birds can take advantage of a free energy-subsidy from the atmosphere. Warming of the earth's surface induces columns of rising warmer air (thermals). Hawks, eagles, vultures, storks, and cranes use this atmospheric structure by finding a thermal and then circling within the column of rising air, gaining altitude with almost no expenditure of energy. Once a substantial altitude has been reached, the birds glide

Migration route of the blackpoll warbler (*Dendroica striata*). (Illustration by Emily Damstra)

off, covering ground as their path slowly descends. After covering a considerable distance, often without the need to flap their wings, the birds need to locate another thermal and repeat the process. Under the right weather conditions, large distances over the ground can be covered with very little energetic cost. Because thermals are present only during the warmer portions of the day, soaring migrants are almost exclusively diurnal and selective in terms of the weather conditions under which they migrate.

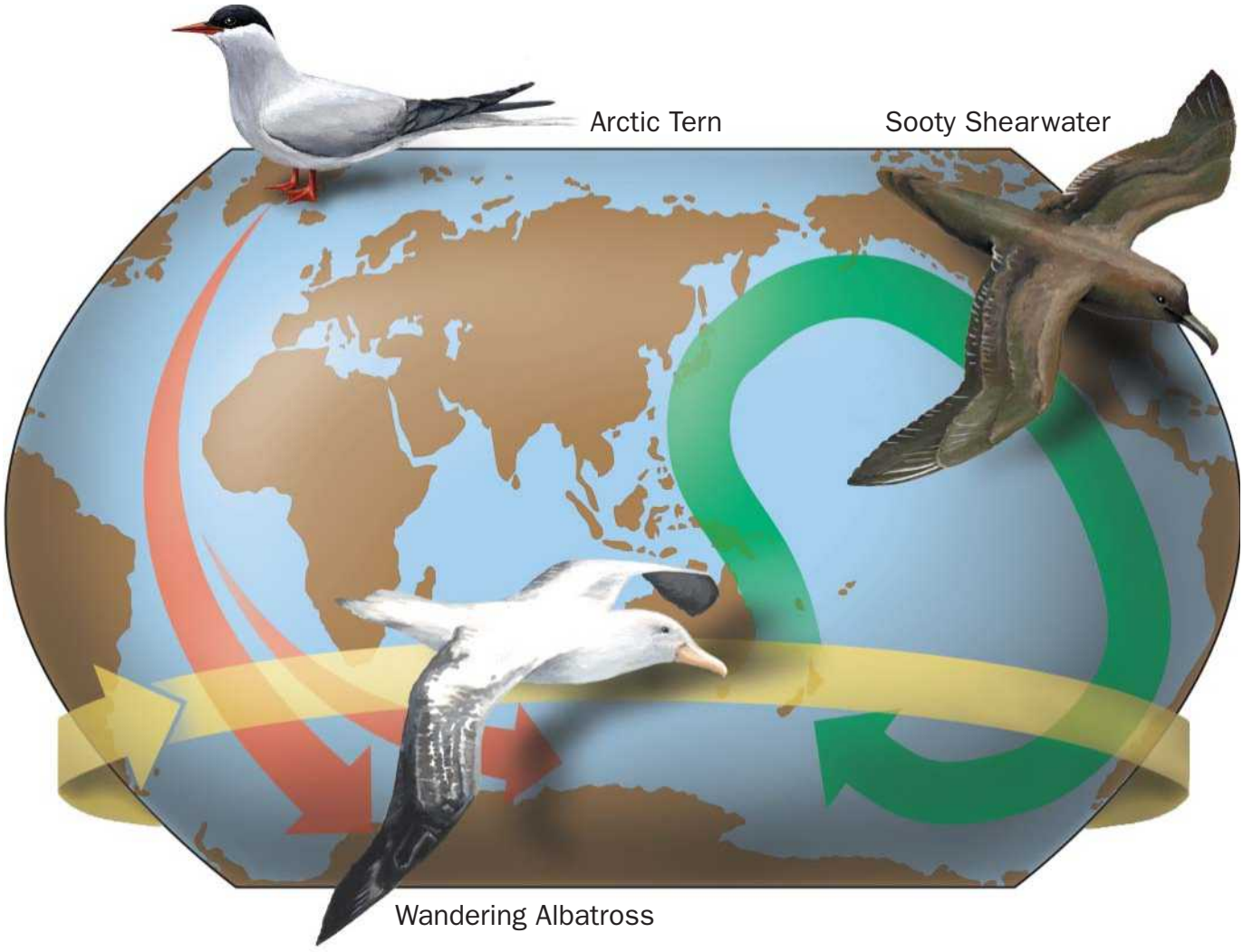
Some common landbirds (including the passerines) migrate during daylight hours. These include swifts, some woodpeckers, swallows, some New World flycatchers, jays, crows, bluebirds, American robin (*Turdus migratorius*), New World blackbirds, European starling (*Sturnus vulgaris*), larks, pipits, some buntings, cardueline finches, and others. Most songbirds, however, migrate almost exclusively at night. Nocturnal migrants include many thrushes, flycatchers, sylviid and parulid warblers, vireos, orioles, tanagers, and many buntings and New World sparrows. Night migrants typically fly alone or in only very loosely organized flocks and because of their lesser powers of flight, most make shorter individual flights and overall migrations than larger, stronger fliers. A typical night migration under good flying conditions might encompass 200 mi (320 km) and be followed by two or three days on the ground during which the birds rest, feed, and deposit fat supplies that will fuel the next leg of the migration. Some small songbirds regularly cross the Gulf of Mexico and the Mediterranean Sea-Sahara Desert. Such flights, initiated at dusk, often require more than the night to complete, thus the birds continue to fly into the following day until a suitable landing place is reached. If bad weather is encountered, especially over water, many birds may become exhausted and perish.

The blackpoll warbler (*Dendroica striata*) of North America is exceptional. Weighing about 0.4 oz (11 g) at the end of its breeding season, blackpolls may accumulate enough subcutaneous fat in autumn to increase its body weight to approximately 0.7 oz (21 g) before departing from northeastern North America on a non-stop flight over the western Atlantic Ocean. The trip takes from three to four days to complete, and with an in-flight fat consumption rate of 0.6% of its body weight per hour, the blackpoll has enough added fuel for approximately 90 hours of flight. There is essentially no place to stop enroute and most individuals overfly the Antilles and make first landfall on the continent of South America. Their autumn journey is surely among the greatest feats of endurance in the bird world.

Why migrate?

Despite the obvious diversity in migration strategies among birds, they all represent adaptations to variability in resources and the predictability of that variability. These two variables determine to a large extent what kind of migratory behavior will evolve. Resources are the necessities of life: food, water, shelter, etc. Many animals respond to the seasonal disappearance of some essential resource by entering an inactive or dormant state (e.g., hibernation). Most birds, however, preadapted by the ability to fly long distances, have responded to variable resources by moving to more hospitable areas.

The more variable the resources on which a bird depends, the stronger will be the selection pressure favoring the evolution of migration. Another important consideration is the predictability with which the resources fluctuate. There is no option for an insectivorous bird such as the blackpoll warbler to spend the winter in its breeding range. Selection favoring obligatory migratory behavior will be strong because any individual that fails to migrate will not survive the winter. In more temperate areas, differences in the severity of winter from year to year might make it possible for a bird to overwinter in some years, but not in others. Selection in these less predictable environments should favor the evolution of more flexible strategies such as partial migration in which some individuals of a population migrate whereas others remain year round in the breeding area. Some fluctuations in resources do not always follow regular seasonal changes in climate. The coniferous seeds and buds eaten by various cardueline finches, such as crossbills, fluctuate not only seasonally, but also from year to year and region to region. These fluctuations may be



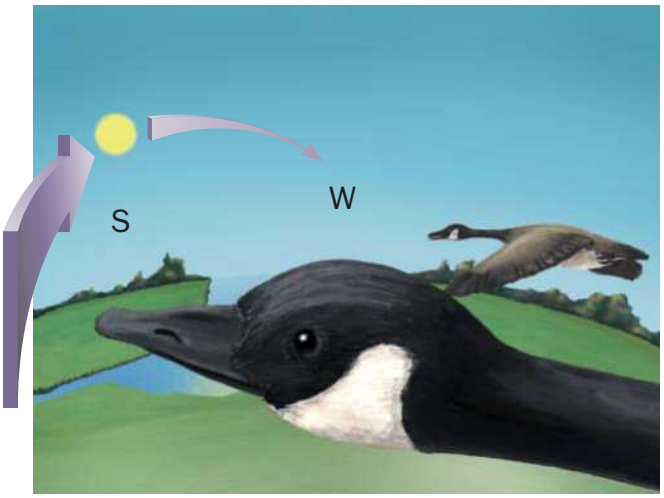
Migration routes of the arctic tern (*Sterna paradisaea*), sooty shearwater (*Puffinus griseus*), and the wandering albatross (*Diomedea exulans*). (Illustration by Emily Damstra)

quite unpredictable, so migration in these species must be facultative, responding directly to local conditions. These movements are termed irruptive because large numbers of birds emigrate from the boreal forests in some years, but remain there in others. Nomadism implies that individuals are perpetually on the move. It is not clear that any bird species are truly nomadic, although birds of the desert interior of Australia are often cited as examples.

Origin and evolution of migration

Seasonal migration is found on all the continents and among species as diverse as penguins, owls, parrots, and hummingbirds. Evidence of the first origins of migration are probably lost forever, but recent phylogenetic reconstructions suggest that migratory behavior has appeared and disappeared repeatedly in avian lineages. Its first appearance may well have coincided with the acquisition of efficient long-distance flight capability. Although present patterns of migration may have been influenced by global climatic events such as glaciation, migration on a large scale probably predated these events.

There is considerable evidence that migratory behavior can appear and disappear quite rapidly in populations. House finches (*Carpodacus mexicanus*) introduced into the more seasonal climate of the northeastern United States from a sedentary population in southern California have evolved full-scale partial migration in fewer than 50 years. Experiments with a sylviid warbler, the blackcap (*Sylvia atricapilla*), have demonstrated strong genetic control over several aspects of migratory behavior. The blackcap is widespread in western Europe from Scandinavia south to areas around the Mediterranean, and island populations live on the Canary and Cape Verde Islands. This single species exhibits a wide range of migratory behavior from obligate long distance migrants in the north to non-migratory populations on the Cape Verdes. Cross-breeding of Canary Island birds with northern obligate migrants produced individuals that showed almost exactly intermediate levels of migratory activity in captivity. This activity, known as *Zugunruhe* or migratory restlessness, is exhibited twice a year in captive migratory birds. It is characterized by a daily rhythm in which these birds rest for a short



During daylight, birds can tell direction as the sun moves through the sky from east to west. (Illustration by Emily Damstra)

period in the evening and then awaken and flutter vigorously on their perches throughout much of the night.

Control of the annual cycle

Migratory behavior is an integral part of the annual cycle of those species that are obligate migrants. Like other events that occur during each year of a bird's life (e.g., molt, breeding), migration is under the control of an endogenous clock called a circannual rhythm, a clock that runs with a periodicity of approximately one year. In birds held under constant environmental conditions (constant temperature, constant dim light), the events of the annual cycle, including migratory behavior, continue to recur in the proper sequence for years. Thus, although migration in the real world is certainly influenced by ambient environmental conditions (climate, weather, food supply, changes in photoperiod), the underlying stimulus comes from within. In nature, circannual rhythms are synchronized with the real world changes in seasons through the associated systematic changes in day-length (photoperiod).

Energetics of migration

Birds are remarkably adapted to flight by virtue of a lung and air-sac system that permits maximal oxygen uptake, hollow bones and other weight-reduction adaptations, and extraordinarily efficient hemoglobin. Nonetheless, long migratory flights are extremely strenuous and energy-demanding. Gram for gram, fat is the most calorie-rich substance that animals can sequester in their bodies. It provides about twice the calories per gram as a carbohydrate or protein, and oxidation of fat is a more efficient metabolic process. Fat deposition prior to migration results from changes in diet, increases in food intake, and changes in metabolism. Migratory fat is deposited throughout a bird's body, including within internal organs such as the heart and liver, but most is laid down in subcutaneous "fat bodies." The amount of fat deposited varies greatly among migratory species. Long-distance migrants and those that must cross large ecological barriers (e.g., the blackpoll warbler) deposit larger amounts of fat prior to initiating flight. Typical nonmigratory birds carry 3–5% of fat-free mass as fat; in passerine migrants this figure may reach 60–100% at the beginning of a long flight.

Once in flight, the migrant's fat deposits are depleted. Fuel stores must be replenished during a migratory stop-over before the bird will be able to execute another flight segment. The rate of fuel recovery will depend upon the quality of the habitat in which the bird lands and lays over. Typically, songbirds are able to deposit fat at rates of 2–3% per day and under optimal conditions the rate may reach 10% of fat-free body mass. Given the obvious importance of stored fat to the success of a continuing migration, finding stop-over habitat in which fuel supplies can be quickly replenished is critical to a migrant's success.

Altitude of migration and flight speed

Most bird migration proceeds at rather low altitudes, as has been revealed by radar studies. Larger, faster-flying species such as shorebirds and waterfowl tend to fly at the highest altitudes. It is usual to find them up to 15,000 ft (4,500 m) or higher when migrating over land. Shorebirds on a trans-oceanic flight have been detected passing over Puerto Rico at 23,000 ft (7,000 m). Bar-headed geese (*Anser indicus*), regularly migrate over the tops of the highest Himalayas. Songbirds migrate at substantially lower altitudes. At night, most typically fly below 2,000 ft (600 m) and nearly all will be below 6,500 ft (2,000 m).

The speed at which a migrating bird makes progress over the ground depends upon how fast it flies (its air speed) and the wind direction and speed where it is flying. Most passerine migrants fly at relatively slow air speeds of 20–30 mph (32–48 km/hr). Flying in a tail wind could easily double their speed over the ground; likewise a head wind could substantially retard progress and a cross-wind could cause the bird to drift from its preferred heading direction. Waterfowl and shorebirds fly faster, with air speeds in the 30–50 mph (48–80 km/hr) range. Given the potential influence of winds on the progress and success of migration, it is not surprising that migrating birds show quite refined selectivity in terms of the weather conditions under which they initiate flight.

Orientation and navigation

One of the most remarkable things about birds, and migrating birds in particular, is their ability to return to specific spots on the earth with amazing precision. This phenomenon is termed homing. Many different kinds of animals exhibit homing ability, but the behavior reaches its pinnacle in birds where the scale of homing flights may reach thousands of miles in a long-distance migrant. Not all migratory species show strong fidelity to previously occupied places, but many do, returning year after year to exactly the same place to nest and to exactly the same place to spend the winter. How they are able to navigate with such precision over great distances is a question that we still cannot answer completely.

Many young birds on their first migration travel alone, without the potential aid of more experienced parents or other older birds. Having never been to the winter range of their

population before, they are not navigating toward a precise locality, but rather toward the general region in which their relatives spend the winter. But, how do they know in which direction the wintering place lies and how far it is from their birthplace? At least some of this information is genetically coded and controlled by the endogenous circannual rhythms discussed above. This migratory program provides the young bird with information about the direction it should fly on its first migration. This can be demonstrated readily by captive nocturnal migrants during the seasons of migration when the birds become restless and active at night. Displaying a behavior known as *Zugunruhe*, birds placed in a circular orientation cage will exhibit hopping that indicates the direction in which they would migrate if free-flying. Cross-breeding experiments with European blackcaps from populations with quite different migration directions have shown that the bearing taken up by inexperienced first-time migrants is strongly heritable and controlled by a small number of genes. Some species have complicated migration routes involving large changes in direction. The garden warbler (*Sylvia borin*) and blackcap are examples that have been studied. Western European populations initially migrate southwestward toward the Iberian Peninsula and then change direction to a more southward heading that takes them into Africa. Hand-raised warblers kept in Germany for the entire season and tested repeatedly in orientation cages showed this change in direction at approximately the right time during the migration season.

It is less clear how the distance of the first migration might be coded. It is known that the amount and duration of migratory restlessness exhibited by different species and populations is correlated with the distances that they migrate and the lengths of their migration seasons, suggesting that some component of the endogenous time-based program also controls the distance migrated. However, migrants are often stopped and held up by bad weather and it is not clear how the endogenous program might adjust for these changes.

Once having bred or spent the winter in a specific place, many birds will show strong site fidelity to those places. To home to a specific site requires more than a simple direction and distance program. The animal must be able to navigate to a particular goal, compensating for errors made along the way or for departures from course caused by wind. This has been demonstrated with individuals of many species that have homed after being artificially transported to places where they have never been before. In the case of various seabirds, homing distances were thousands of miles. Animals employ a variety of different mechanisms in order to home. For short distances, a number of relatively simple strategies will work: laying down a trail that is retraced; maintaining sensory contact with the goal by sight, sound, or smell; inertial navigation; referring to learned landmarks; or even random or systematic search. But for the very large distances involved in some cases of goal navigation in birds, including long-distance homing by pigeons, some other explanation is required. The best evidence suggests that birds employ a navigational mechanism based on possessing an extensive map that provides the individual with information about its spatial location relative to its goal (home), and a compass that is used to identify the course direction indicated by the map. Obviously, neither component will work by itself. A compass will be useless without information about the direction toward home from the map. Likewise, the map, telling the bird that home lies to the north of its present location, will also be ineffective in the absence of a compass to indicate the direction "north."

Birds tell direction at night by using the stars as a guide. (Illustration by Emily Damstra)

Homing pigeons, and probably other birds as well, employ a number of strategies when attempting to return to a specific goal. There is good evidence that they use information perceived during the displacement journey to the release site to determine the direction of displacement (route-based navigation). They probably also use familiar landmarks when navigating close to home. These means will be of limited effectiveness at great distances, yet even when released at unfamiliar sites hundreds of miles from their home loft, pigeons with some homing experience return directly and rapidly. Therefore, whereas pigeons may make use of various strategies when homing, it appears that a map based solely on stimuli perceived at a distant and unfamiliar location are sufficient to provide the requisite homing information.

During the last half of the twentieth century, a great deal of experimental effort was devoted to discovering the physical basis of the compass and map employed in homing navigation by birds. Interestingly, compasses have been studied primarily in migratory birds, especially those species that migrate at night, whereas the map component of navigation has been studied almost exclusively in nonmigratory homing pigeons.

Bird compasses

A compass is involved not only in map and compass navigation such as occurs when a homing pigeon is taken away from its loft; it is also a fundamental component of orientation by migrating birds. Two main experimental approaches have been used to study bird compasses. First, various manipulations have been performed on homing pigeons and their effects monitored by observing the initial flight direction taken by pigeons when they were released at distant sites. Second,

orientation in migratory birds has been studied by observing captive birds in a migratory condition. These birds will hop and flutter in the intended migratory direction when placed in a circular orientation cage (a behavior known as *Zugunruhe*). The studies on pigeons and captive migrants revealed that birds possess several different compass capabilities.

Magnetic compass

The ability to detect the earth's magnetic field is widespread among animals and microbes. The magnetic compass in birds has been demonstrated by predictably altering the migratory orientation of birds through manipulating the magnetic field within their cages, and by altering the initial homing bearings of pigeons by changing the magnetic field around a bird's head with miniature magnetic coils. By independently manipulating the horizontal and vertical components of an earth-strength magnetic field, it has been shown that the magnetic compass of birds is not based on the polarity of the field as is our technical compass. Rather, the bird compass relies on the inclination or dip angle of magnetic field lines to determine the direction toward the pole or toward the equator. Within both the Northern and Southern Hemispheres, magnetic lines of force dip downward toward the poles, so the same magnetic compass mechanism is effective for species living within either hemisphere. Birds that cross the magnetic equator will face a problem and in two species of trans-equatorial migrants it has been shown that the birds' directional response, with respect to magnetic inclination, reverses after they experience a period in a magnetic field without inclination, simulating an equatorial field.

A magnetic orientation capability develops spontaneously in young birds. The mechanism by which birds perceive the magnetic field remains uncertain. There is experimental evidence to support a receptor based on tiny particles of magnetite located in the anterior region of the head and evidence suggesting that photoreceptive pigments in the eye provide the sensor.

Sun compass

The sun compass is found in many animals. To use the sun as a compass, of course, one must take time of day into account. Animals accomplish this because the sun compass is linked to the internal circadian clock possessed by all animals. With this time-compensation mechanism in place, a bird can orient in a given compass direction at any time of day. The link between the circadian clock and sun-compass orientation can be demonstrated by changing the bird's internal clock by confining it in a room with a light:dark cycle that differs by several hours from that outside. If this is done with a homing pigeon that is then released on a sunny day, it will make a predictable error in identifying the direction in which to fly. It will take the time indicated by its internal clock to be correct and thus misinterpret the direction of the sun. With this sort of experiment it can be shown, for example, that a pigeon will mistake a midday sun, high in the sky, for a rising or setting sun that would be near the horizon. This is because only the azimuth direction of the sun is used in sun compass orientation; the sun's elevation is ignored. Birds apparently have to learn the sun's path across the sky and that path varies considerably with latitude and with season. Once the path is learned, compass directions must be assigned to it, i.e., the pigeon must learn that the sun rises in the east, etc. There is evidence that the magnetic compass provides the compass directions that are then associated with the azimuths of the sun's path. The sun compass is the primary compass employed by homing pigeons to identify the direction that its map indicates is homeward. Its role in migratory birds is less clear, but it may be important for species that migrate at very high latitudes in the Arctic where daylight is nearly continuous and magnetic directions often unreliable.

Star-pattern compass

Night-migrating birds are the only animals known to use the stars as a compass. Once learned, orientation is based on the fixed spatial relationships among stars and groups of stars: birds can orient even under the fixed sky of a planetarium. Young birds learn the relationships among star patterns by observing the rotation of the night sky that results from the earth's rotation on its axis. In this way they are able to localize the center of rotation (Polaris) and thus true north. The innate migratory direction is coded with respect to stellar rotation in young birds.

Polarized-light compass

Most nocturnal migrants initiate flights shortly after sunset and diurnal migrants often take flight around sunrise. At these times of day, patterns of polarized skylight, resulting from the sun's light passing through the earth's atmosphere are very conspicuous across the vault of the sky. Because it is sunlight that is being polarized, the patterns of polarized light in the sky change in parallel with the movement of the sun and rotate around the celestial pole similar to stars at night. Thus observation of celestial rotation via polarized light in the sky can also reveal true north. Experiments with migrants in orientation cages in which polarized light has been manipulated and skylight polarization patterns have been eliminated show that the birds employ a polarized light compass.

Multiple compasses and interactions

It is impossible to know why evolution has endowed birds with so many compasses, but presumably it is advantageous to have back-up systems available when navigational problems such as overcast skies or magnetic anomalies are encountered enroute. The compasses appear to be related to one another hierarchically. In homing pigeons, for example, the sun compass is used preferentially whenever the sun is visible; the magnetic compass seems to provide an overcast sky back-up. In adult migrants, the relationship among compasses is somewhat less clear and there may be differences among species. Based on the information available as of 2001, the magnetic compass appears to be central to migratory orientation, providing the primary directional information. When an immediate choice of direction needs to be made, visual compasses may be used, but ultimately the birds seem to rely on their magnetic compass.

In many areas, especially at high latitudes, magnetic and geographic compass directions may differ substantially (magnetic declination). In these situations, the true or geographic compass directions will be the more reliable indicators of the directions that birds need to travel. During the development

of compass capabilities in young songbirds, true compass directions identified by observing celestial rotation of stars at night and skylight polarization patterns during the day are used to calibrate the preferred magnetic migratory direction. In this way, the visual and non-visual compasses are brought into conformity.

Navigational maps

The search for the physical basis of the navigational map sense has been one of the more controversial issues in the study of animal behavior. There are currently two hypotheses to explain the map sense of birds. They may not be mutually exclusive and as is the case with the compass, birds may have more than one map to consult when faced with a navigational problem. Experimental studies of the navigational map have been confined almost exclusively to homing pigeons.

The olfactory map hypothesis is based almost entirely on work done with homing pigeons. It states that pigeons learn an odor map of the region by associating different odors with the different directions from which winds carry them past the loft. A large body of experimental evidence involving both manipulations of the pigeon's olfactory system and manipulations of the odor environment supports the odor map. Experienced pigeons seem to be able to use an odor-based map over surprisingly large distances (up to 250 mi [400 km]). How odorous substances could provide reliable spatial information while being transported in an often turbulent atmosphere has been a contentious issue. Very recently, analysis of trace gases in the atmosphere has shown that spatially stable patterns of odorants sufficient to account for the known levels of precision exhibited by homing pigeons do exist, although the odors actually used by the pigeons remain unknown.

The other hypothesis is that birds might use the earth's magnetic field as a map. Components of the magnetic field vary systematically over the earth, particularly as a function of latitude. There is good evidence that homing pigeons can detect very small differences in magnetic fields that would be required to use the information as a map (a much more challenging task than using the magnetic field as a compass). The best evidence supporting the idea of a magnetic map is indirect. Homing pigeons are often disoriented when released at magnetic anomalies—places where the earth's field is disturbed, usually as a result of large iron deposits underground. The effect occurs only when the pigeons are forced to make their navigational decisions right at the anomaly: if released outside the anomaly, they are not disturbed by flying across it on the way home. That the pigeons are disturbed even under sunny skies when their sun compass is readily available further suggests that the magnetic anomalies are somehow affecting the map step of navigation rather than the compass.

We know that migratory birds exhibit striking site accuracy and therefore must possess sophisticated homing abilities. However, very little is known about navigational maps in these species. Although many migrants return with precision to previously occupied places, we do not know whether they are really goal-orienting throughout the migratory journey or only when they get closer to the destination.

Resources

Books

Able, Kenneth P., and Mary A. Able. "Migratory Orientation: Learning Rules for a Complex Behaviour." In *Proceedings of the 22nd International Ornithological Congress, Durban*, edited by Nigel J. Adams and Robert H. Slotow. Johannesburg: Birdlife South Africa, 1999.

Berthold, Peter. *Bird Migration.* 2nd ed. New York: Oxford University Press, 2001.

Berthold, Peter. *Control of Bird Migration.* New York: Chapman and Hall, 1996.

Wiltschko, Roswitha, and Wolfgang Wiltschko. "Compass Orientation as a Basic Element in Avian Orientation and Navigation." In *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes*, ed. R. G. Golledge. Baltimore: Johns Hopkins University Press, 1999.

Wiltschko, Roswitha, and Wolfgang Wiltschko. *Magnetic Orientation in Animals.* Berlin: Springer-Verlag, 1995.

Periodicals

Able, Kenneth P. "The Concepts and Terminology of Bird Navigation." *Journal of Avian Biology* 32 (2000): 174–183.

Able, Kenneth P. "The Debate Over Olfactory Navigation by Homing Pigeons." *Journal of Experimental Biology* 199 (1999): 121–124.

Phillips, John B. "Magnetic Navigation." *Journal of Theoretical Biology* 180 (1996): 309–319.

Wallraff, Hans G. "Navigation by Homing Pigeons: Updated Perspective." *Ethology, Ecology and Evolution* 13 (2001): 1–48.

Wallraff, Hans G., and M. O. Andreae. "Spatial Gradients in Ratios of Atmospheric Trace Gases: A Study Stimulated by Experiments on Bird Navigation." *Tellus* 52B (2000): 1138–1157.

Wiltschko, Wolfgang, et al. "Interaction of Magnetic and Celestial Cues in the Migratory Orientation of Passerines." *Journal of Avian Biology* 29 (1998): 606–617.

Other

Have Wings, Will Travel: Avian Adaptations to Migration. 25 July 1997. <http://www.umd/umich.edu/dept/rouge_river/migration.html>

Bird, David M. "Migration: Your Questions Answered." *Bird Watcher's Digest* <http://www.petersononline.com/birds/bwd/backyard/watching.shtml>

Kenneth Paul Able, PhD

Avian song

Introduction

Many people have been captivated by the soaring melodies of a singing bird, or have been amazed by the diversity of sounds and the sheer noisiness of a dawn chorus in the rainforest. Keen birdwatchers soon realize that listening more closely leads to an appreciation not only of the aesthetic beauty of song, but also of differences between songs: the whistles, warbles, trills, chirrups, squeaks, and buzzes that distinguish species. Following a single bird reveals even more; it may sing different songs when it interacts with its mate compared to to those it uses when it interacts with a neighbor, or give shrieking alarm calls when danger threatens. Detailed scientific studies of bird song have revealed the intricate complexity of communication in birds, and contributed to diverse fields such as ethology (study of animal behavior), neurobiology, evolutionary biology, and bioacoustics (study of sound and living systems).

There is tremendous variation in the sounds that birds produce. Some species produce non-vocal sounds in addition to vocalizations. Woodpeckers use their bills to drum loudly and rhythmically on tree trunks. Snipes have modified tail feathers that vibrate to produce a bleating sound as the bird plummets downward. The oscines, or songbirds, which comprise nearly half of all the species of birds in the world, are known for their well-developed singing abilities. Songs vary considerably, not only between species, but also at a finer level between different populations of the same species, between different individuals in the same population, and even within a single individual that sings a repertoire of different song types. Songs are sometimes distinguished from calls, a difference that is obvious in some species but not in others. Generally, calls are short, simple, stereotyped, and innate, while songs are longer, more complex and varied, and have to be learned. However, in some species, calls are also learned; two non-oscine groups, the parrots and hummingbirds, learn their vocalizations.

Bird species vary in who does the singing. In some species, only male birds sing. This is the case in many of the long-studied birds of the north temperate regions like Europe and North America, but it is not true of many tropical and south temperate species where it is quite common for females to sing as well. In some of the species where both sexes sing, breeding partners may coordinate their songs to produce duets that can be so precisely coordinated that it sounds as if only one bird is singing. Duetting is particularly common among the *Thryothorus* wrens of South America and the shrikes of Africa. Differences in the singing behavior of males and females are reflected in their brain structure. In species where only males sing, the song control regions in the brain are much larger in males than females, but in duetting species, females also have well-developed song control regions.

There are some patterns in when and where birds sing that are common to many species, and that hint at the function of song. Many species have what is known as a dawn chorus, where they start the day with high song rates, and some also have a smaller chorus at dusk. As well as this daily variation in song rates, there are also seasonal fluctuations. Spring is heralded in many parts of the world by a profusion of birdsong. This peak in song rates coincides with the time that many birds are establishing territories and finding mates, suggesting that song has a role in these activities. Birds often sing from a song post, where they have a clear view and may be near the border of their territory. When one bird sings, its neighbor often sings immediately afterwards, also suggesting that song is used in maintaining territory boundaries.

Methods of studying bird song

Looking and listening

Much can be learned about bird song using nothing more than a keen pair of eyes and ears, and a notebook. Many different vocalizations can be distinguished from one another by careful listening, though specialized sound analysis equipment may be necessary to detect some of the more subtle variation in form. Counting the number of songs given in different contexts allows variation in song rates associated with time of day, season, and stage of the breeding season to be identified. Observing the social context of singing can indicate whether song is directed at a partner, a neighbor, or an intruder, and what kind of response it elicits.

Recording song

Tape recorders and microphones are used to record birdsong so that it can be analyzed or used for playback in more detailed studies. Anyone can record the songs of a bird,

Marsh wren (*Cistothorus palustris*) singing in Alpena County, Michigan. (Photo by Rod Planck. Photo Researchers, Inc. Reproduced by permission.)

though getting a high quality recording can be challenging. Getting as close as possible to the bird without disturbing it is a good start. It is also important to choose a time when song rates are high and there is little other noise around; dawn is often best. Parabolic reflectors or highly directional microphones focused on the singing bird help to reduce background noise. Advanced recording techniques such as microphone arrays involve recording the songs of several birds simultaneously onto a series of microphones, and using differences in the time it takes a sound to reach each microphone to map the position and movements of the birds as they interact.

Analyzing song

Analyzing birdsong requires an understanding of some of the properties of sound. Sound consists of alternating waves of high and low pressure generated by a vibrating object, and the length of one complete cycle of high and low pressure is known as the wavelength of a sound. The number of cycles reaching an observation point per second depends on the wavelength and is called the frequency, measured in hertz (Hz). Frequency differences are heard as differences in pitch; for example, middle C has a frequency of 261 cycles per second while the C an octave higher has a frequency of 783 Hz. The amplitude, or intensity, of the pressure in the sound waves determines how loud the sound is. Georgia State University's Hyperphysics Web site (<hyperphysics .phy-astr.gsu.edu/hbase/hframe.html>) has more about the properties of sound.

For sound analysis, sound spectrograph machines and sound analysis computer software measure the physical properties of sound and convert them into pictures. These images allow different song types to be categorized by visual inspection of patterns, or by measuring particular features of the song such as length, frequency range, or maximum amplitude. Sonograms are images that show changes in frequency over time, while "waveforms" graph amplitude against time. Looking at a sonogram can give an idea of what a song sounds like, remembering that the vertical axis shows the pitch of the sound. A whistle at a single pitch appears as a horizontal line on a sonogram, while a descending whistle appears as a descending line. A very short sound spanning a wide frequency range appears as a vertical line, and sounds like a click, while buzzing sounds consist of a series of these clicks given in rapid succession.

Experimenting

Experiments are an important component of the scientific study of birdsong. One of the techniques used most commonly is playback, in which recorded songs are broadcast through a speaker and the response of birds to the song is monitored. Playback experiments allow responses to the song itself to be measured without any influence of other effects, like the behavior of the singing bird. Many birds respond dramatically to playback, flying toward the speaker and singing as if there were an intruder. Differences in the intensity of response to different playback suggest different levels of threat. The closer the speaker is to the center of their territory, the more aggressive the response. Even on the territory boundary, if an unfamiliar song is broadcast, it will elicit a more aggressive response than songs of a familiar neighbor. Also, if a neighbor's songs are not played from the appropriate territory boundary but from the opposite boundary, then they too will elicit a more aggressive response. Playback experiments have thus been used to show that birds can recognize different neighbors solely on the basis of their songs.

Innovative technology allows more advanced, interactive playback experiments to be conducted. Experimenters link a computer to the speaker and choose which songs to broadcast, depending on the behavior of the bird being tested. For example, the experimenter might choose to play a song that is the same length or the same type as the song the bird itself has just sung, to see how that influences its response.

The approach

Niko Tinbergen, a pioneer in the study of animal behavior, highlighted four approaches to answering questions about animal behavior. First, there are causal factors that can be studied, including both internal mechanisms and external fac-

tors such as the environment. Second, there is the developmental perspective, for example how birds learn to sing and who they learn from. Third, the survival value, or function, of a behavior can be studied, such as the role of birdsong in territorial defense and mate attraction. Fourth, the evolution of the behavior over time can be investigated.

Causes and mechanisms

Song production

Birds sing using an organ called the syrinx, which operates in much the same way as the mammalian larynx. Both are associated with the windpipe, or trachea; the larynx is at the top of the trachea, while the syrinx is at the bottom where it splits into two bronchi before entering the lungs. When they sing, birds push thin tympaniform membranes into the flow of air passing through the syrinx, causing the membranes to vibrate and generate sound waves. Because of the location of the syrinx at the junction of the bronchi, birds have two voices and can produce two harmonically unrelated sounds at once. Suthers implanted tiny devices for measuring air oscillations in each side of the syrinx to show that gray catbirds (*Dumetella carolinensis*) and brown thrashers (*Toxostoma rufum*) use both sides of the syrinx in producing their songs, while some birds, like the canary (*Serinus canaria*), use predominantly one side or the other.

Sounds generated in the syrinx are modified as they pass through the trachea and bill higher up in the vocal tract. The vocal tract selectively filters overtones produced by the syrinx, emphasizing some frequencies and filtering out others. Nowicki found that birds in helium-enriched air, which is less dense and allows sound to travel faster, produce songs with more harmonic overtones. So, like humans, higher pitched components of the sound that are normally filtered out by the vocal tract become audible in helium. Postural changes also affect song. When birds sing, they move their bills, puff out their throats, and stretch their necks, modifying the effective length of the trachea and influencing the resonance properties of their vocal tract and the frequencies of the sounds they produce. Trumpet manucodes (*Manucodia keraudrenii*) have greatly elongated trachea coiled in their breasts that give resonance to their loud, deep, trumpet-like vocalizations.

The production of diverse and complex sounds by the syrinx is achieved by an integrated system involving muscles, nerves, and hormones. The muscles of the syrinx control the tympaniform membranes to finely modify the physical properties of the sound. Syringeal muscles, in turn, are controlled by nerve impulses from specialized areas of the brain including the higher vocal center (HVC). Individual nerve cells in these areas are specialized and active only when particular songs are sung. Seasonal changes in song production are associated with seasonal changes in the size of the HVC, and also with changes in testosterone levels. Implanting males with testosterone in the nonbreeding season causes them to sing more, and females in species that do not normally sing can be induced to sing by injections of testosterone. The relationship between birdsong and hormones goes both ways; as well as hormones inducing song, hearing the song of male birds causes hormonal changes in females that induce them to start building nests.

Transmission of birdsong

The farther away the singer is, the fainter its song sounds. This attenuation (weakening) of sound is partly just because of a physical principle, the inverse square law. This states that sound radiates out in all directions from a source, so doubling the distance from the source causes a four-fold decrease in sound intensity, while trebling the distance decreases intensity nine-fold, and so on. The air itself also absorbs sound, thus windy, hot, or humid weather conditions cause sound to be attenuated more rapidly. Obstacles in the environment, such as vegetation, reflect and scatter sound waves, causing further attenuation. This attenuation by air and obstacles in the environment is frequency dependent; longer wavelengths do not attenuate as quickly, so lower frequency sounds travel farther than high frequency sounds. As well as becoming attenuated as it passes through the environment, sound is also degraded and the different elements of a song start to blur as sound is reflected off the ground, canopy, and tree trunks. Songs that have rapidly changing amplitudes or frequencies are especially susceptible to this degradation, known as reverberation.

These various constraints on sound transmission affect how, when, and where birds sing. Birds seem to have songs that are structured to transmit most effectively in their environment; for example, forest-dwelling birds have songs with acoustic properties that minimize the effects of reverberation due to vegetation. Song structure is also related to function, so species with larger territories have territorial songs that are louder and will travel farther. Many birds do a lot of their singing from special song posts in their territories, choosing a perch well above the ground with not much vegetation around, so that interference from these obstacles is minimized and the song will carry farther. Birds tend to sing less on windy days when their songs are less likely to be heard. They also avoid singing at the same time as other birds, and interactions between neighboring birds often take the form of countersinging where the song of one bird is followed almost immediately by a song from its neighbor, and then the first bird may sing again as soon as its neighbor finishes. In some species, overlapping a neighbor's song is a sign of aggression that can escalate into conflict.

Hearing songs

Bird ears are not very obvious because there is no outer ear funneling sound waves into the inner ear, and feathers cover the opening of the ear. Some birds have special feather structures that serve a similar purpose to an outer ear; the dish-shaped faces of owls concentrate sound waves on their ear openings. Internally, bird ears are similar to other vertebrates, with a thin tympanic membrane that detects sound waves. Vibrations of the tympanic membrane are transferred via a small bone, the columella, to the fluid-filled cochlea of the inner ear. Movements of fluid in the cochlea stimulate underlying hair cells that are sensitive to different sound frequencies. Generally, birds are most sensitive to frequencies in the range of 1–5 kHz, but there is variation between species that influences the design of signals. Prey species can produce

vocalizations that take advantage of subtle differences in the hearing abilities of their predators, enabling them to communicate with members of their own species using frequencies that predators are less sensitive to, and reducing the risk of eavesdropping.

Signals from the inner ear are transferred by the nervous system to specialized areas of the brain that extract all sorts of information about the sound. Different frequencies activate different nerve cells so that certain song types only activate particular cells. The location of the sound is worked out by integrating the signals from each ear; comparing differences in arrival time and intensity of sound at each ear tells what direction it came from. Relative intensity, reverberation, and degree of attenuation of different frequencies provide information about the distance of a sound. Barn owls (*Tyto alba*) hunt in the dark, pinpointing prey by listening. A special arrangement of their ears, with one slightly higher than the other, and one pointing downward while the other points upward, increases the detectability of the differences between ears that the brain uses to locate the source of the sound with extreme precision in three dimensions. Again, mechanisms of sound perception have implications for signal design because aspects of the structure of a song, like timing and frequency range, influence how easily listeners can locate it. Song structure, whether its acoustic properties reveal or hide the location of the singer, can therefore reveal something about song function.

Learning to sing

Nature and nurture

Like human speech, birdsong in the songbirds (Oscines) is something that has to be learned. The way in which song develops is one of the most well studied processes in animal behavior, and illustrates the complex interactions between nature and nurture, or instinct and learning, that are involved in the development of behavior. Young songbirds make only simple begging noises at first to solicit food from their parents, but later they begin trying to produce adult-sounding songs that initially are wobbly and not very precise. This "subsong" gradually improves with practice to become "plastic song," which sounds more like adult song but is still quite variable, before crystallizing to the stereotyped adult song.

Experiments have been used to identify various components of the normal song-learning process. Young birds raised in isolation in captivity develop songs that are crude approximations of normal adult song. Only if they hear adult song do they develop normal adult song. Some species copy songs heard from tapes, while others only copy songs heard from live tutors. Some species will copy adult songs of other species, but only if it is similar to that of their own. It seems that young birds hatch with a genetically determined template of song that enables them to recognize species-specific songs. The innate template allows them to produce something resembling a species-specific song even if they have never heard one, but memorizing songs they hear refines the template and enables them to produce normal songs. The second component in the process of song development is lots of practice, known as the sensorimotor phase because it involves both sound production and perception. Young birds deafened before they begin singing are unable to produce anything resembling a normal adult song. Auditory feedback is essential at this stage; in other words, they have to hear themselves sing to be able to match the sounds they produce to the songs they are copying.

When do they learn?

The timing of song learning varies considerably among species. Some have only a very short sensitive period, and if they do not hear adult songs during this period, they never develop normal songs. Other species, open-ended learners, continue learning new songs throughout their lives. Social influences are very important for facilitating learning. White-crowned sparrows (*Zonotrichia leucophrys*) exposed to taped song are sensitive only during the period from 10 to 50 days old, and do not copy songs of other species. However, when housed with live tutors, they learn songs after 50 days of age, and copy songs of other species. Changes in social circumstances at later stages in life can also lead to learning; captive budgerigars (*Melopsittacus undulatus*) moved to a new flock modify the structure of their calls to more closely match those of their new flock mates.

What do they learn?

Most birds copy the songs of their fathers or neighbors. Who birds learn from depends partly on when they learn. If they learn only after leaving the territory where they were born, then they may learn from other males in the neighborhood where they settle. Sharing song types with neighbors is important for communication in song sparrows (*Melospiza melodia*), and Beecher and his colleagues found that young males learn the songs of three or four neighboring males, selecting song types that are shared by the neighbors. In another population, where song sharing is less important, Hughes and her colleagues found that young birds copy parts of songs and recombine song segments, rather than copying whole songs.

The number of songs that each individual learns varies considerably among species, with some learning only a single song type, while others sing hundreds or even thousands of different songs. The number of song types that birds can learn seems to be related to brain space. Individuals with large repertoire sizes have larger song-control areas in the brain. Brenowitz argues that, rather than the size of song control areas being determined by the number of songs learned, it is likely that other factors such as genetic differences or early development may cause differences in the size of song-control areas that determine how many song types can be learned.

Some species are virtuosos when it comes to learning; they sing not only species-specific songs, but also the songs of other species. A survey by Baylis showed that a diverse range of birds engage in vocal mimicry. The function of vocal mimicry is not well understood, and may vary between species. Some mimicry is associated with brood parasitism, where females of one species lay their eggs in nests of another species, the host that then provides parental care. Male indigo birds (*Vidua* spp.) learn the songs of their host species. Single

nestling cuckoos (*Cuculus canorus*) mimic nestling begging calls of a whole brood of host chicks to stimulate their host parents to feed at high rates, though this deceptive mimicry is innate rather than learned. Many accomplished mimics are not brood parasites. Lyrebirds (*Menura novaehollandiae*) sing the songs of many different species, and even incorporate other sounds into their repertoires. Once these sounds have been incorporated into a repertoire, they are learned along with species-specific songs by young birds. Male lyrebirds have display areas where they try to attract females with spectacular visual as well as vocal displays. It is possible that mimicry increases their repertoire sizes and makes them more attractive to females.

Functions of song

Signaling

Song is one of the most obvious and important ways that birds communicate with one another. Although birds also use visual signals like bright colors and displays, acoustic signals can often be heard from farther away than visual signals can be seen, and can be used to either avoid or mediate closer contact. Signals, of whatever variety, are used to convey information to others, and induce a change in behavior that benefits the signaler. Birds use song to convey information about themselves, such as identity or location. Birds may also convey information about the environment, for example, by using alarm calls to warn of approaching danger. Because song facilitates recognition, it plays an important role in mediating social interactions, hence what is known as the dual function of song in territorial defense and mate attraction.

Recognition

The immense variation in the structure of songs allows birds to recognize others as belonging to the same species, to identify their sex, and even to recognize particular individuals, be it a neighbor, mate, or offspring. Recognition at all these levels is vital for survival and successful reproduction. Sound analysis and playback experiments have been used to identify the features of song that permit recognition, and to show that recognition occurs. For example, in some species, males and females sing different song types, or there may be subtle differences in male and female renditions of the same song types. Birds respond differently to playback of their neighbors, their mate, and unfamiliar birds, indicating that they can distinguish between them on the basis of song alone. Vocal recognition is particularly important for parent-offspring recognition in species that breed in large colonies.

Defending a territory

Song is vital as a first line of defense for birds that hold territories. Many species defend a territory during their breeding season, and some species defend a territory throughout the year. Song serves as a long-distance proclamation of territory ownership, and as a threat to intruders that, if unheeded, may be followed up by physical aggression. The fact that birds respond to playback by singing suggests that song has a role in territorial defense. More direct evidence comes from experiments where birds have been removed from their territories and replaced by a speaker. Far fewer intruders are seen in territories where the speaker is playing their songs than where the speaker is playing control songs of a different species. Clearly, song alone, even without the physical presence of the bird, serves to deter intruders. A different type of experiment, involving temporarily muting birds, also shows that birds that are unable to sing are slower to establish territories and suffer more intrusions by other birds. Most studies on song have focused on male song, but research on song by female birds, reviewed by Langmore, indicates that their song also has a territorial function. It seems therefore that song is used to repel birds of the same sex.

Studies on interactions between birds occupying territories adjacent to one another have revealed some interesting details about the way songs are used in territorial defense. Birds save time and energy in defense by recognizing the songs of individuals living around them. In playback experiments, birds respond less aggressively to playback of their neighbors' songs than strangers' songs. Nevertheless, birds may direct song at neighbors, approaching the common boundary and singing in reply to their neighbor's songs, or countersinging. Birds also use their repertoires to communicate with neighbors; when individuals share song types with neighbors, they can direct songs to specific birds by matching song types. Burt and his colleagues used interactive playback experiments with song sparrows to show that song-type matching (replying with the same song type) elicits a more aggressive response than repertoire matching (replying with a shared song type other than the one just sung), and can escalate conflict between neighbors.

Although birds have ways of indicating that a song is intended for a particular recipient, McGregor and Dabelsteen argue that, because sound is transmitted in all directions, communication networks are set up where individuals can eavesdrop on signals between others. By eavesdropping on neighbors and listening to their vocal interactions with intruders, birds obtain an early warning if the intruder comes their way. They may also learn something about the competitive ability of the intruder by listening to how it fares in an interaction with a neighbor whose competitive ability is known. Females may also eavesdrop on singing interactions between males to assess their relative competitive abilities.

Attracting a mate

Male song rates are highest in spring, suggesting that song has a mate-attracting function. Consistent with this, males of some species stop singing once they have a partner, and experiments removing the female of a mated pair cause an increase in male song rates until the female is returned. More direct evidence that song attracts females comes from experiments on birds that breed in nestboxes. Nestboxes fitted with a trap to catch prospecting females and with speakers broadcasting male song catch more females than nestboxes from which no song is broadcast.

Male song can be quite elaborate, and it appears that females are not only attracted by song, but may choose between males on the basis of the amount or variety of song they produce. Males that have the time and energy to sing at high rates often have a good territory with a plentiful supply of food. Females also seem to prefer males with larger repertoires of song

types. Female great reed warblers (*Acrocephalus arundinaceus*) pair with males that have better territories and bigger repertoires. They also sometimes mate with a male other than their social partner, and these males have larger repertoires. Hasselquist and his colleagues found that the offspring of males with larger repertoires of song types generally have higher survival rates, so it seems as if females are getting better quality males when they choose males that sing more song types.

As well as attracting females, male song also stimulates females to reproduce. Kroodsma played male song to captive female canaries, stimulating them to build nests and lay eggs. Again, larger repertoires seem to be better, because when he played large song repertoires to some females and small song repertoires to others, those hearing the larger repertoires built nests faster and laid more eggs than those hearing small repertoires.

Evolution of song

Regional variation

Fine-scale geographic variation is most obvious in species where each individual sings only one or two song types and neighbors share song types. Boundaries between song types are often sharp, creating dialect areas where males all sing the same song. Differences between areas are less obvious in species where each individual has large repertoires. Nevertheless, because birds generally learn their songs from parents or neighbors, songs tend to differ more between populations than within populations. Differences between populations can also be due partly to adaptations for sound transmission in different environments. Social influences might also contribute to differences between areas if individuals modify their songs to be more similar to their neighbors because there are benefits from sharing songs with neighbors.

Cultural change

Because there are slight changes every time birds learn songs, the songs in a population undergo a process of cultural evolution over time that is similar to genetic evolution. Also, because copying errors occur more frequently in the song-learning process than mutations occur in genetic evolution, birdsong provides an excellent system for studying evolutionary processes. Movement of birds between populations introduces new songs to a population and increases diversity within populations. Selection can act on song if habitats limit transmission of some songs, or if females prefer some songs.

Song and speciation

Because song is important in mate choice, it can be a powerful isolating mechanism leading to the formation of new species. Gradual changes in the form of songs could accumulate to the point where individuals no longer recognize one another as being from the same species, and therefore do not reproduce. In Darwin's finches of the Galápagos Islands, natural selection caused changes in bill size and shape, which in turn influenced the acoustics of song production. Podos suggested that these changes in the temporal and frequency structure of songs may have caused reproductive isolation and facilitated the rapid speciation that occurred.

Resources

Books

Baylis, Jeffrey R. "Avian Vocal Mimicry: Its Function and Evolution." In vol. 2 of *Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller, 51–83. New York: Academic Press, 1982.

Bradbury, J. W., and S. L. Vehrencamp. *Principles of Animal Communication.* Sunderland, MA: Sinauer Associates Inc., 1998.

Catchpole, C. K., and P. J. B. Slater. *Bird Song: Biological Themes and Variations.* Cambridge: Cambridge University Press, 1995.

McGregor, P. K., and T. Dabelsteen. "Communication Networks." In *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller. Ithaca: Cornell University Press, 1996.

Periodicals

Beecher, M. D., S. E. Campbell, and P. K. Stoddard. "Correlation of Song Learning and Territory Establishment Strategies in the Song Sparrow." *Proceedings of the National Academy of Sciences of the United States of America* 91 (1994): 1450–1454.

Brenowitz, E. A. "Comparative Approaches to the Avian Song System." *Journal of Neurobiology* 33 (1997): 517–531.

Burt, J. M., S. E. Campbell, and M. D. Beecher. "Song Type Matching as Threat: A Test Using Interactive Playback." *Animal Behavior* 62 (2001): 1163–1170.

Kroodsma, D. E. "Reproductive Development in a Female Songbird: Differential Stimulation by Quality of Male Song." *Science* 192 (1976): 574–575.

Hasselquist, D., S. Bensch, and T. Vonschantz. "Correlation between Male Song Repertoire, Extra-Pair Paternity and Offspring Survival in the Great Reed Warbler." *Nature* 381 (1996): 229–232.

Hughes, M., S. Nowicki, W. A. Searcy, and S. Peters. "Song-Type Sharing in Song Sparrows—Implications for Repertoire Function and Song Learning." *Behavioral Ecology & Sociobiology* 42 (1998): 437–446.

Langmore, N. E. "Functions of Duet and Solo Songs of Female Birds." *Trends in Ecology and Evolution* 13 (1998): 136–140.

Nowicki, S. "Vocal Tract Resonance in Oscine Bird Sound Production: Evidence from Birdsongs in a Helium Atmosphere." *Nature* 325 (1987): 53–55.

Podos, J. "Correlated Evolution of Morphology and Vocal Signal Structure in Darwin's Finches." *Nature* 409 (2001): 185–188.

Suthers, R. A. "Contributions to Birdsong from the Left and Right Sides of the Intact Syrinx." *Nature* 347 (1990): 473–477.

Tinbergen, N. "On Aims and Methods of Ethology." *Zeitschrift für Tierpsychologie* 20 (1963): 410–433.

Other

Nave, C. R. *Hyperphysics.* Georgia State University. 2000. <hyperphysics.phy-astr.gsu.edu/hbase/hframe.html>

Macaulay Library of Natural Sounds. Cornell Laboratory of Ornithology. <www.birds.cornell.edu/LNS/>

Michelle L. Hall, PhD

Avian flight

Advantages of flight

Birds have developed the power of flight to an extraordinary degree that sets them apart from other vertebrates, and they have done it with minimal loss of other forms of locomotion. Unlike bats, most birds can walk and run, and many can swim and dive well enough to catch fish and squid. Migrating birds fly airline distances over mountains, seas, and deserts, and thus gain access to remote habitats such as the arctic tundra, which are highly productive during a short season, but uninhabitable for several months of the year. On a shorter time scale, wading birds can exploit tidal mudflats, which are inaccessible on foot. Many food sources are accessible only to flying animals, from the "aerial plankton" of flying invertebrates to the fruits of forest trees that rely on birds and bats for dispersal of seeds. Trees, cliffs, and islands provide flying animals with nesting and roosting places where terrestrial predators cannot reach them. Although bats are supreme at catching insects in the dark, birds have the advantage in most other respects, thanks to a unique set of morphological and physiological adaptations.

The bird body plan

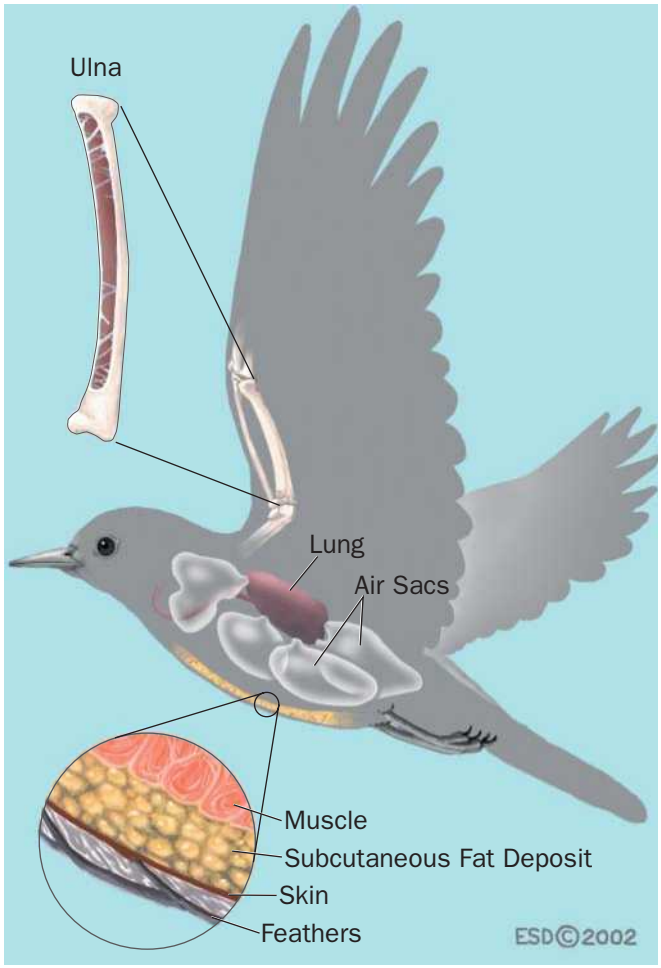
All birds share the same basic body plan, with relatively minor variations, despite being adapted to a tremendous range of habitats and lifestyles. Birds have inherited the bipedal body plan of the Archosaur branch of the reptiles, which also includes dinosaurs, pterosaurs, and crocodiles, but they have a number of distinctive modifications to the basic plan. The loss of the long balancing tail of bipedal dinosaurs means that the weight of the upper body no longer acts through the hip joint, but far ahead of it. Bipedal standing and walking with this "unbalanced hip" is made possible by the characteristic bird *synsacrum*. This is an expanded and elongated pelvis that is fused rather than articulated to the vertebrae. Postural muscles pull downward and forward on the rear end of the synsacrum, which acts as a lever holding the forward part of the body up. The bird ancestor's bipedal stance left the forelimb free to evolve into a wing that is structurally independent of the legs. Unlike bats and pterosaurs, in which the leg supports the inner end of a wing membrane, birds have been free to evolve the legs for perching, walking, running, and swimming, while also being able to use them for other functions altogether, especially catching and manipulating prey.

Birds have no diaphragm like that of mammals. Instead the curved synsacrum and sternum form the two halves of a bellows, which pumps air in and out of the body cavity. The lungs are small and compact, with "air capillaries" through which air is drawn into a system of air sacs beyond the lungs. The air and blood capillaries are arranged transversely to each other to form a "cross-current" arrangement, which is more effective than the dead-end pouches (alveoli) of mammal lungs for extracting oxygen from air at high altitudes.

The bird wing

The evolution of the small archosaur forelimb into a gliding wing required the wing span and surface area to be greatly increased, while retaining sufficient bending and torsional strength to support the weight of the body, suspended from the shoulder joints. The arm skeleton, consisting of the upper arm (humerus) and forearm (radius and ulna) provides the bending strength for the inner half of the wing only. Beyond the hand skeleton, the keratin shafts of the primary flight feathers provide the bending strength of the hand wing. Their bases are tightly bound by connective tissue to the reduced and rudimentary hand skeleton, with no freedom of movement in any direction. The bases of the secondary flight feather shafts are bound to bumps on the back side of the ulna, with some freedom to rotate downward and inward, but not upward or outward. The surface area of the hand wing is made up of the expanded vanes of the primary feathers, while the secondaries make up the area of the inner part of the wing. A leading-edge tendon with an elastic section in the middle joins the shoulder to the wrist, and supports a small triangular membrane ahead of the elbow joint. Smaller covert feathers smooth over the bases of the flight feather shafts, and seal the gaps between them. The free ends of each row of coverts overlap the feathers behind, in the manner of a tiled roof.

All of the aerodynamic force acting on a bird's wing is ultimately collected at the humerus, which has to support bending and twisting loads, with little or no compression or tension. The humerus shaft is a thin-walled, hollow cylinder of large diameter, adapted to carry these loads with a minimum amount of material. The central cavity is connected to the air sac system, and filled with air. Internal struts (trabeculae) prevent buckling of the load-bearing bony wall.



Bird adaptations for flight. (Illustration by Emily Damstra)

Likewise, the primary and secondary feather shafts are hollow, and filled with a keratin foam (parenchyma) which maintains the shape of the load-bearing keratin walls. The tail feathers are structurally similar to the flight feathers, with their bases attached to the rudimentary tail skeleton (pygostyle). They can be spread fanwise, forming an auxiliary lifting surface, which has been likened to an expandable delta wing, behind the main wing.

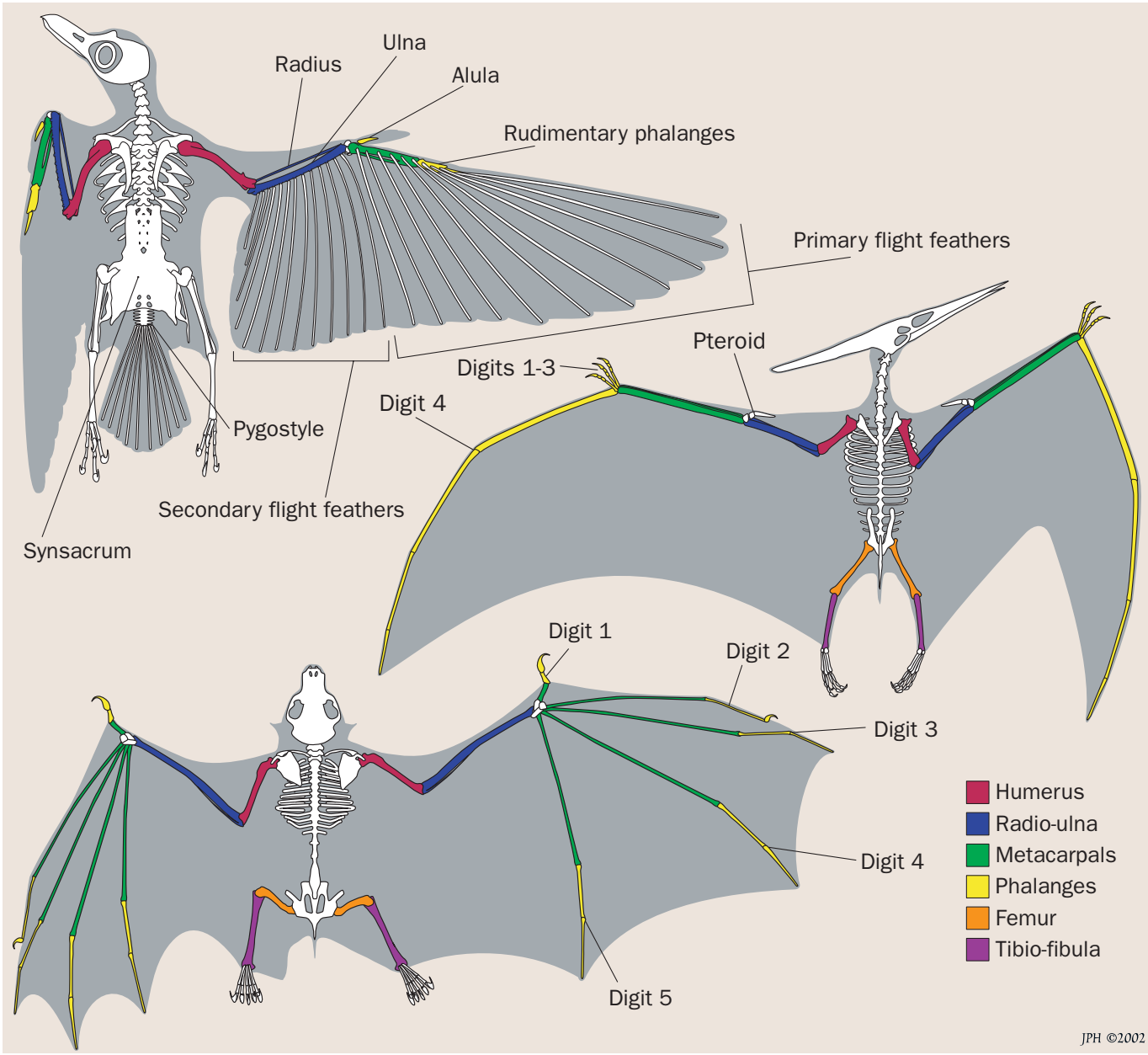
Comparison with pterosaurs

Both birds and pterosaurs originated in early Mesozoic times from the ancestral archosaur stock, which also gave rise to crocodiles and dinosaurs. They represent radically different solutions to the mechanical problems of flight, each modifying the basic archosaur body plan in a different way, unrelated to the other. All of the bending loads in a pterosaur's wing were carried by the bones of the arm and hand, ending in one enormously elongated "wing finger" (digit 4). There were no load-bearing keratin structures corresponding to the flight feather shafts of birds. Even those who interpret the parallel ridge patterns on pterosaur wing impressions as "stiffening fibers" concede that these ridges were not connected to the wing skeleton, and therefore could not transmit bending loads to the humerus. Unlike the vanes of flight feathers, the wing membrane had no bending strength, and had to be stretched between two bony supports, the wing finger and the leg. Like modern birds, later pterosaurs (pterodactyls) reduced the tail so that it lost its original function of balancing the weight of the upper body about the hip joint, but unlike birds, pterodactyls did not expand the pelvis to provide an alternative balancing mechanism for bipedal standing and walking. On the ground they must have been quadrupedal, somewhat like vampire bats, although the front "foot" was the end of the metacarpus rather than the wrist, as in bats. As judged by the wing span, pterosaurs ranged from sparrow-sized forms to 20 ft (6 m) pterodactyls. These thrived throughout the Cretaceous period, with even larger forms just at the end. However, all of them had slender bodies and large wings, somewhat like frigate birds. None were heavy-bodied like ducks or auks.

Comparison with bats

Bats are mammals, unrelated to either birds or pterosaurs, and are first known from the Eocene mammal radiation. They have a membrane wing somewhat similar to that of pterosaurs, but with all five digits contributing to the wing structure. Digit 1 (the thumb) projects forward from the wrist and is used for climbing. Digits 2 and 3 together form a stiff panel that allows the outer part of the wing to be pulled forward, creating tension that runs through the membrane to pull against the legs. Digit 3 supports the wing tip, and digits 4

Greater flamingo (*Phoenicopterus ruber*) in flight. (Photo by Art Wolfe. Photo Researchers, Inc. Reproduced by permission.)

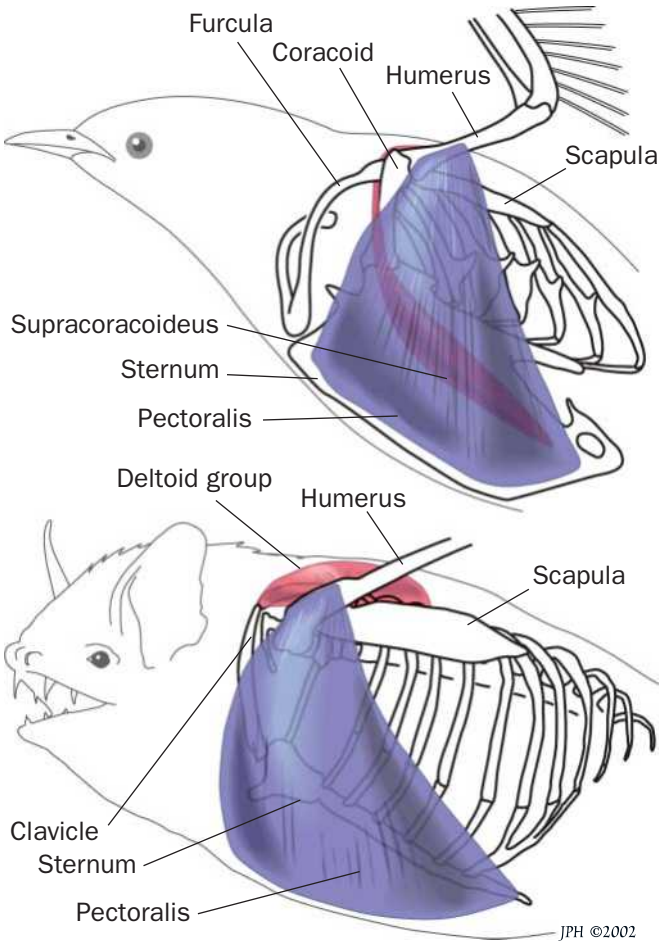


Wing comparisons of a bird (top left), pterosaur (middle right), and a bat (bottom left). (Illustration by Jonathan Higgins)

and 5 control the profile shape of the wing membrane. The ankle joints and feet are quite similar to those of pterosaurs, and are used to curl the posterior edge of the wing membrane downward. There are muscles running fore-and-aft in the membrane, which are not attached to the skeleton but are used to flatten the profile shape of the wing. Few bat species are active in full daylight, perhaps because the wing membrane is susceptible to sunburn, or because of bats' dependence on convective cooling. Many bats make seasonal migrations within continental areas, proceeding in many short stages, but bats are apparently not capable of flying as high as birds, nor of covering such long nonstop distances. Whether pterosaurs could match the performance of birds in these respects is unknown.

Flight muscles and sternum

In both birds and bats, the spherical head of the humerus articulates with the shoulder girdle, and is free to swing forward, back, up, and down, and also to rotate about its own axis, within limits set by a complicated arrangement of ligaments. The pectoralis or "breast" muscle of both birds and bats does most of the work in powered flight, by pulling the humerus downward. It inserts on the underside of a ridge that projects forward from the base of the humerus. In birds, the inner end of the pectoralis muscle is attached to the body skeleton along a prominent keel, which projects from the midline of the sternum (breastbone), and also along the outer edge of the sternum where it joins the ribs. The humerus is raised



Comparison of muscles used for flight in birds (top) and bats (bottom). (Illustration by Jonathan Higgins)

by the supracoracoideus muscle, which is attached to the sternum along the base of the keel, where it is entirely surrounded and covered by the pectoralis muscle. Its tendon runs up the coracoid, through a channel between the bones of the shoulder girdle, and curves over the shoulder joint, to insert on the top side of the humerus.

This arrangement is found only in birds, not in bats, which fly very well without an expanded keel on the sternum. In their case the two pectoralis muscles pull directly against one another, with only a small keel between them, or none at all. This shows that the keel, which is such a prominent and characteristic feature of the bird skeleton, is not a requirement for flapping flight. In bats the humerus is raised by the deltoid group of muscles on the dorsal side, as in other mammals and also in reptiles.

Heat disposal in flight

The flight muscles generate a large amount of heat in flapping flight, and this heat has to be disposed of in a controlled manner to maintain the body temperature within the required limits. Provided that the air temperature is well below the blood temperature, most or all of the excess heat can be lost by convection. Birds do this by passing a copious blood flow just below thinly insulated areas of skin that are exposed to the air flow, especially the sides of the body and the undersides of the inner parts of the wings. These areas are covered when the wings are folded, thus avoiding loss of heat when the bird is not flying. If the air temperature is too high for convective cooling, the bird opens its beak and flutters the throat pouch, thereby cooling the blood by evaporating water from the upper respiratory tract. Evaporation also takes place from the lining of the air sacs, which penetrate many organs, including the interior of the pectoralis muscles. The keel of the sternum keeps these cavities open when the muscles contract, and its function is probably to permit direct evaporative cooling of the interior of the muscles.

In bats, the huge area of skin exposed to the air flow is ready-made for convective heat disposal. The wing membrane contains a system of blood vessels in which the flow is controlled to regulate body temperature. Most bats rely mainly or wholly on convective cooling, and only resort to evaporative cooling in emergencies.

Muscle power for level flight

Because a bird's body is much denser than air, the flight muscles have to work continuously, accelerating air downward so as to produce an upward reaction that balances the weight. The rate at which work is required (power) to support the weight is highest when the air speed is zero (hovering), and decreases at medium and high speeds. However, additional power is required to overcome the drag of the body, and this increases with speed. Because of their opposite trends, these two components of power produce a characteristic U-shaped curve when added together. There is a well-defined "minimum power speed" at which the mechanical power required to fly is lower than at either slower or faster speeds.

Canadian geese (*Branta canadensis*) fly during courting. (Photo by Jack A. Barrie. Bruce Coleman Inc. Reproduced by permission.)

A bald eagle (*Haliaeetus leucocephalus*) soaring. (Photo by Joe McDonald. Bruce Coleman Inc. Reproduced by permission.)

The margin of power available over power required dwindles as the size of the bird increases, eventually defining an upper limit to the mass of viable birds, which appears empirically to be in the region of 35 lb (16 kg). Modern flying birds are restricted to small sizes, when compared with the much wider size range of walking and swimming animals. Antelope-sized birds, such as ostriches and emus, exist but are necessarily flightless. Small birds have sufficient muscle power to fly over a wide range of speeds, but large birds like swans have only just enough power to fly very near the minimum power speed. Birds heavier than any living forms might have been possible under special circumstances in the past, for instance in a combination of landscape and climate that allowed reliable soaring, taking off from slopes in hang-glider fashion.

Metabolic power and aerobic capacity

Physiological experiments measure the metabolic power, which is the rate of consumption of fuel energy, as distinct from the mechanical power, which is the rate at which the muscles do work. A bird's "aerobic capacity" is the maximum sustained metabolic power of which it is capable, and this is determined by the capacity of the heart and lungs, not by the muscles. Only hummingbirds have sufficient aerobic capacity to hover continuously, although many small and medium-sized birds can hover anaerobically for short periods. Some very large birds such as condors have insufficient aerobic capacity for sustained level flight at any speed, and are forced to resort to soaring for sustained flight.

Water birds

Gulls and ducks float on the surface of the water and use their feet in a fore-and-aft rowing motion, whereas more extremely adapted water birds such as loons and grebes have the legs set far back, and swing them in a more lateral motion, using the feet as hydrofoils. Auks and diving-petrels have wings of reduced size, forcing them to fly rather fast, with high wingbeat frequencies, but they also use their wings for propulsion under water. The aquatic wing motion is quite similar to flight, but at a much reduced frequency, with the wings partly folded. Gannets, petrels, and some albatrosses can also swim under water in this manner to a limited extent, diving a few meters below the surface. Penguins and the great auk (*Pinguinus impennis*) carried this line of evolution further, with wings too small to fly, but optimized as hydrofoils. The wings of penguins beat up and down (not in a rowing motion) and are convergent on the flippers of sea lions and marine turtles. Frigate birds do not swim or alight on the water at all, although their dispersal movements show that they spend weeks or months at a time over the open ocean, flying day and night.

Takeoff and landing

To take off, a bird has to acquire sufficient air speed over the wings to sustain its weight, either from forward motion, or by flapping the wings relative to the body, or (usually) by a combination of both. Birds up to the size of pigeons or small ducks can jump into the air from a standing start, and accelerate into forward or climbing flight, but larger birds have to run to get flying speed on a level surface. Swans use their large webbed feet alternately in a running motion to help them accelerate over a water surface, while cormorants and pelicans more often use both feet together. Large birds taking off from a tree or cliff drop to convert height into air speed. All birds head into the wind when taking off from the ground or water, as the wind then supplies part of the air speed that they have to acquire. If the wind is strong enough, petrels and albatrosses simply spread their wings and levitate into the air from the crest of a wave.

Landing into wind is obligatory, but newly fledged birds have to learn this, and often make spectacular errors by attempting to land across or down wind. In light winds, most birds slow down when preparing to land, by increasing the frequency and amplitude of the wing beat, tilting the wingbeat plane until the wings are beating nearly horizontally, and spreading and lowering the tail. Any residual downward and forward velocity (relative to the ground) is absorbed by the legs. Glide landings are often possible in moderate wind strengths, even for large birds. The body and wings are tilted up as the bird flares, with one final wing beat sweeping the wings forward almost horizontally, just before the wings are folded. Auks and loons land on water at rather high speeds, lowering their bellies into the water with the feet trailing behind, whereas ducks and swans swing their feet forward and use them like water skis. Gannets often enter the water in a shallow dive rather than alighting on the surface, while petrels and albatrosses slow down while gliding, and drop gently onto the surface. Guillemots (murres) nest on cliff ledges although they are not capable of flying slowly enough to land safely in such places. Their landing technique involves diving toward the cliff at high speed, then pulling up into a near-vertical climb. If this is accurately judged, the guillemot's

Mallard duck (*Anas platyrhynchos*) in flight. (Photo by Neal & MJ Mishler. Photo Reseearchers, Inc. Reproduced by permission.)

speed drops to zero just above the landing ledge, but if not, it has to dive away from the cliff, fly out to sea, and repeat the whole procedure.

Migration

The longest known nonstop migration is that of the Alaskan bar-tailed godwit (*Limosa lapponica*), which flies from the Alaskan Peninsula across the equator to the North Island of New Zealand, a distance of about 6,400 mi (10,300 km). The godwits build up fat before they depart, at the same time reducing the mass of organs such as the digestive system and liver, until about 55% of the total mass consists of fat. Like all long-distance migrants, they supplement the primary fuel (fat) by progressively consuming protein from the flight muscles in the course of the flight, "burning the engine" as the power required decreases. Although the fuel reserves are ample for the distance, this migration is remarkable because it is a formidable feat of navigation, requiring at least eight days and nights of continuous flight. The red knot (*Calidris canutus*) is another arctic breeding wader that migrates across the equator to high southern latitudes, with nonstop stages lasting several days on some routes. Many small passerine species cross the Mediterranean Sea and the Sahara Desert without stopping, while their American counterparts fly directly from the New England coast to the Caribbean Islands. Even longer distances are flown by species that are able to feed along the way, notably the Arctic tern (*Sterna paradisaea*), in which some individuals migrate from arctic to antarctic latitudes and back again each year.

Soaring over land

"Soaring" should not be confused with "gliding," which means flight without flapping the wings. The term "soaring" refers to behavior whereby the bird extracts energy from movements of the atmosphere, and uses this in place of work done by the flight muscles. Soaring birds do usually glide, but it is also possible to soar while flapping. Soaring is obligatory for many large birds, because of marginal muscle power. Slope soaring is the simplest method, in which the bird exploits rising air that is deflected upward as the wind blows against a hillside, or some smaller obstruction such as a tree or building. Thermals are vortex structures that float along balloon-like with the wind, containing an updraft in the central core and downdrafts around the outside. A gliding bird can gain height by circling in the core, but is carried along by the wind while doing so. At the top of the thermal, the bird glides off in a straight line, losing height until it finds another thermal and repeats the climb. When thermals are marked by cumulus clouds, soaring birds climb up to the cloudbase level. Away from sea coasts, this may be as high as 7,000 ft (2,000 m) above sea level in temperate latitudes, and higher in drier parts of the tropics and subtropics. Thermal soaring is the characteristic method of cross-country flight in large soaring birds such as storks, pelicans, and migratory eagles, while many raptors also use thermals to patrol in search of food. Lee waves are stationary wave systems that form downwind of hills. They can be exploited to higher altitudes than slope lift or thermals, but the technique is difficult. Canada geese (*Branta canadensis*) are known to use lee waves when migrating, and it is possible that some migratory swans may also occasionally use this method. Being slower than direct flapping flight, soaring migration is most advantageous to large birds, in which basal metabolism is only a small fraction of the power required for flapping flight. In small birds the energy cost of basal metabolism offsets any direct gains from soaring, because of the longer flight time.

Soaring over the sea

The trade wind zones of the tropical oceans cover a vast area in which the weather is predominantly fair with small, regularly spaced cumulus clouds. These are the visible signs of thermals, which are caused by the air mass being convected toward the equator over progressively warmer water. Although weaker than thermals caused by direct solar heating of a land surface, trade-wind thermals continue reliably at all hours of the day and night, and provide frigate birds with the means to disperse across the oceans without ever alighting on the surface. The middle latitudes, where stronger winds prevail, are the home of the petrels and albatrosses, especially in the southern hemisphere. The medium-sized and large members of this group skim with no apparent effort in and out of the wave troughs, sometimes very close to the surface, sometimes pulling up to 50 ft (15 m) or so, seldom flapping their wings. A petrel or albatross replenishes its air speed with a pulse of kinetic energy each time it pulls up out of the sheltered zone in the lee of a wave, into the unobstructed wind above. As the energy comes from the relative motion between the air and the waves, birds that use this technique are confined to the interface between air and water, just above the surface. Albatrosses can also slope-soar in zero wind by gliding along the leading slopes of moving waves. Pelicans, boobies, and other pelecaniform birds soar over slopes and cliffs when they come ashore to breed, but use mainly flapping flight at sea, as do gulls and auks.

Altitude of bird flight

Most birds fly near the earth's surface most of the time, except for soaring species, which climb to cloudbase or as high as convection allows. With the exception of frigate birds, most

seabirds spend their entire lives within 100 ft (30 m) of the sea surface, except when they come to land, and soar in slope lift or thermals. Radar studies reveal that passerines typically fly at heights up to 10,000 ft (3,000 m) above sea level on long migration flights, while waders may fly as high as 20,000 ft (6000 m). The reduced air density at high altitudes requires birds to fly faster than at sea level, and to produce more muscle power, but there may be a small increase in range due to reduced wastage on basal metabolism, caused by the shorter flight time. The "cross-current" lungs of birds appear to give them an advantage over mammals (including bats), when it comes to extracting oxygen from low-density air. Lower air temperatures aloft reduce or eliminate the need for evaporative cooling, but reports of swans migrating at 27,000 ft (8,200 m) are apocryphal. Such large birds cannot climb to great heights by muscle power alone. It is conceivable that they could do so by exploiting lee waves, but air temperatures below −58°F (−50°C) would present physiological problems.

Origin of flight

Scientists realized in the nineteenth century that both birds and pterosaurs belong to the same branch of the reptiles as dinosaurs, and it is a matter of definition whether birds actually "are" dinosaurs, or whether they developed as one or more distinct strands of the original archosaur stock. Among living mammals, cobegos, flying squirrels, and their marsupial counterparts suggest an obvious route for the evolution of flying forms from arboreal ancestors. Pterosaurs and birds could have originated in a similar way, if we suppose that there were two parallel groups of small, arboreal archosaurs early in the Mesozoic. One such group, ancestral to the pterosaurs, would initially have resembled a flying squirrel, with a membrane stretched between the fore and hind limbs, and would then have extended the wing span by lengthening the wing finger. The other group, ancestral to birds, would have developed flight feathers from modified scales, extending the wing span and area without involving the legs in the wing support structure. Whether or not this is exactly what occurred, the two groups must have diverged in Triassic times, long before any of the known Jurassic birds or birdlike reptiles.

Flight in past times and on other planets

The two physical factors that most strongly constrain flying animals are gravity and air density. On a planet with stronger surface gravity than Earth, the maximum size of flying animals would be even more restricted than it is here, while a higher air density would ease this limit, irrespective of the atmospheric composition. It is likely that the Mesozoic atmosphere was indeed denser than the modern one, and this helps to explain the prolonged success of pterosaurs with 20 ft (6 m) wing spans. However, the largest pterodactyls, which flourished briefly in the last days of the Cretaceous period, would appear to require a reduction in gravity to make them feasible, and that is more difficult to explain.

Resources

Books

Alerstam, T. *Bird Migration.* Cambridge: Cambridge University Press, 1990.

Burton, R. *Bird Flight.* New York: Facts on File, 1990.

Norberg, U. M. *Vertebrate Flight.* Berlin: Springer, 1990.

Pennycuick, C. J. *Animal Flight.* London: Edward Arnold, 1972.

Pennycuick, C. J. *Bird Flight Performance.* Oxford: Oxford University Press, 1989.

Rüppell, G. *Bird Flight.* New York: Van Nostrand Reinhold, 1977.

Tennekes, H. *The Simple Science of Flight.* Cambridge, MA: MIT Press, 1996.

Wellnhofer, P. *The Illustrated Encyclopedia of Pterosaurs.* London: Salamander Books, 1991.

Periodicals

Pennycuick, C. J. "Mechanical Constraints on the Evolution of Flight." *Mem. California Acad. Sci.* 8 (1986): 83–98.

Colin Pennycuick, PhD, FRS

Struthioniformes

(Tinamous and ratites)

Class Aves

Order Struthioniformes

Number of families 6 families of living birds

Number of genera, species 15 genera; 58 species

Photo: Southern cassowaries (*Casuarius casuarius*). (Photo by Eric Crichton. Bruce Coleman Inc. Reproduced by permission.)

Evolution and systematics

While most birds fly, there are several groups of birds that do not fly and have anatomical adaptations for a life on land. Some of the largest living birds make up the group of flightless birds generally called the ratites. Historically, some taxonomists have placed most of these large birds in the order Struthioniformes. Many recent taxonomists have divided the ratite group into separate orders and others into separate suborders or families. Most recently the *Handbook of the Birds of the World* has once again placed these birds in one large order, Struthioniformes, with several families: Struthionidae, the ostriches; Rheidae, the rhea; Casuariidae, the cassowaries; Dromaiidae, the emus; and Apterygidae, the kiwis. Additionally, the extinct moas, genus *Dinornis* (Dinornithidae), from New Zealand and the elephant birds, genus *Aepyornis* (Aepyornidae), from Madagascar and Africa were probably closely related and have been placed in separate orders or families as well. The tinamous, which are included with the Struthioniformes here, may now be considered to be in the group called Tinamiformes. Unlike ratites, tinamous have a keeled sternum and can fly, although weakly. Ratites are mostly located in central and southern Africa, central and southern South America, New Guinea and surrounding achipelagos, Australia, and New Zealand.

Ratites were considered to be very ancient birds, more primitive than most other birds. Their anatomical features, once thought to be primitive, led early taxonomists to believe that ratites descended from birds prior to the development of flight. However, if this were true, many of the anatomical features of these birds would not make much sense. The current interpretation is that these birds evolved from birds that could fly, but have developed a number of special adaptations for a non-flying existence. Ratites have wing skeletons that are not fundamentally different from those of flying birds, but are used for purposes other than flying. Ostriches and rheas, for example, use their wings for both courtship and distraction displays. Other ratites such as cassowaries, emus, and kiwis have various degrees of degeneration of the basic wing structures, but their wings are still derived from the basic wing structure of flying birds. Ratite wings still bear flight feathers and coverts in some groups, thus clearly suggesting an origin from flying birds and not directly from bipedal dinosaurs. The increase in size of most ratites has resulted in significant changes in bones, muscles, and plumage. The long, muscular legs of large ratites are well adapted for running.

Early taxonomists considered ratite birds to be a good example of convergent evolution on all the southern continents, but as the theory of continental drift emerged and evolved into plate tectonics, it became much easier to assume that ratites arose from common ancestors which became isolated as the continents drifted apart. Most families have evolved in isolation from the others. The only exception to this are the cassowaries and emus, which evolved on the same continent, Australia, but separately in different habitats, so they did not evolve in direct competition with each other. The emu, following the pattern of the ostrich and rhea, lives in more open grassland, while the cassowary lives primarily in dense rainforest. The debate on the origin and relationship of ratites continues, focusing on the exact level of relationship at the order or a higher level. Taxonomists generally agree that ratites are closer to each other and to tinamous than they are to any other bird groups. One question that has not been adequately answered is why these large flightless birds evolved in only the Southern Hemisphere. The answer to this question may well lie in the fact that major mammal predators evolved mostly in the Northern Hemisphere. Small flightless birds are very vulnerable as has been demonstrated when predators are introduced to islands with flightless birds. Ancestors of ratites had to evolve into larger and faster animals since they could not escape by flying, and this would have been much easier with a minimal number of large mammalian predators. The one exception to this is the kiwi, which evolved as a secretive forest

The emu (*Dromaius novaehollandiae*) is found throughout Australia. (Photo by Janis Burger. Bruce Coleman Inc. Reproduced by permission.)

bird in New Zealand, where the lack of large mammals may have allowed it to maintain its small size. The large number of moa species that also developed in New Zealand, and follow the pattern of ostriches, rheas, and emus, fell prey to humans when they arrived, just as the elephant birds did in Madagascar. The evolution of ratites in the absence of large mammalian predators seems to make sense. However, as with everything there is one major exception, the ostrich. Ostriches must have evolved in Africa with large mammal predators, but to compensate, they developed very large size, acute eyesight, and great speed. However, the ostrich may have evolved in very arid areas where the numbers and varieties of large predators were greatly reduced. Ostriches are also the only ratite to have spread into the Northern Hemisphere even though they have since disappeared from most of their range north of the equator. Fossil records show that ostriches once occurred from Greece to southern Russia, India, and Mongolia.

Physical characteristics

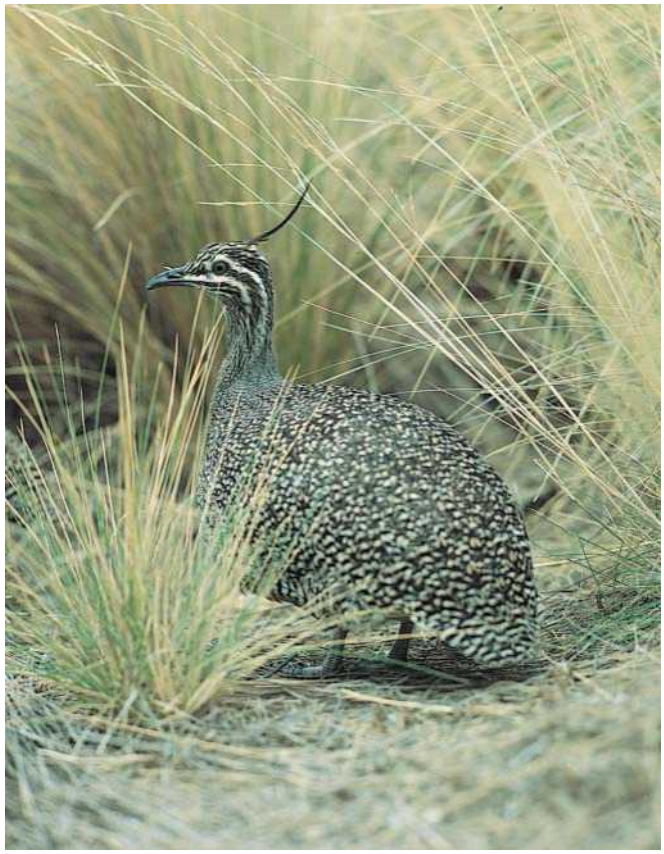
The basic characteristics of the ratite group include the following: degenerated breast muscles, lack of a keel of the sternum, an almost absent wishbone (furcula), a simplified wing skeleton and musculature, strong legs, leg bones without air chambers except in the femur, flight and tail feathers that have retrogressed or have been converted to decorative plumes, and a loss of feather vanes, which means that oiling the plumage is not necessary, and as a result there is no preen gland. There is also no separation of skin bearing contour feathers, or feather tracts (pterylae), and the area of skin devoid of contour feathers (apteria). Ratites have a palaeognathous (meaning "old jaw") palate which is found in no other bird groups except the tinamous, which are considered to be the closest phylogenetically to the ratites and probably evolved from a common ancestor.

Ostriches show the greatest dimorphism with males being generally black with white plumes and the females being brown instead of black. Rheas show some dichromatism during the breeding season when the males' color grows darker black and their posture also changes. Emus have little dimorphism except the males are usually a little larger than females and their posture during the breeding season can be used to identify the sex. Cassowaries are dimorphic in size with the females being larger and more aggressive than the males. Kiwis have little dimorphism other than a small size difference.

While ratites share features such as the strong development of feather aftershafts that are often nearly as large as the main shaft, there are also many differences between families and species as well. Ostriches have their toe number reduced to two, and one is much more prominent than the other. Ostriches are also the tallest and heaviest of modern ratites. Cassowaries have developed long inner toenails that can be used defensively. While the largest cassowaries can weigh almost as much as some ostriches, they are not nearly as tall. Ostriches and rheas both have prominent wings, which, along with flight feathers, play a significant role in courtship displays. They also use their wings in distracting displays and maneuvers to evade predators or draw them away from their nests. These behaviorisms are shared with a number of ground-nesting birds that can fly, which also probably suggests their ancestry among flying birds.

Feeding ecology and diet

Ratites also share a number of other similar behavioral and ecological adaptations. Ratite eggs are very thick-shelled and difficult for most predators to break. Chicks are well developed and can walk or run within a very short time after hatching. The diets of chicks are much more insectivorous and omnivorous than are the diets of adults. While the ostrich, rhea, and emu seem to share similar ecological habitats, the digestive tract of each shows a basic difference in diet. The ostrich has the longest digestive tract, up to 46 ft (14 m) in length, suggesting an almost exclusive vegetarian diet. Ostriches are noted for eating almost anything if they have an opportunity, including stones or pebbles to help grind up the plant material in their diet. The rhea's digestive tract is the second longest, up to 25–30 ft (8–9 m) in length with the addition of large caeca (tubes branching off the junction of the small and large intestines). They are largely vegetarian as adults and eat a great variety of broad-leafed plants, including thistles and other "weeds." However, they also eat almost all varieties of agricultural crops, making them unpopular with farmers. Rhea chicks eat mostly insects in the first few days



This elegant crested tinamou (*Eudromia elegans*) is found in Argentina. (Photo by Jeff Foott. Bruce Coleman Inc. Reproduced by permission.)

of life and over the course of several months convert to a largely vegetarian diet, but will eat insects and a variety of other things when the opportunity arises. The emu's intestine is of medium length, under 22 ft (7 m), suggesting a more varied but largely vegetarian diet. Emu chicks are also largely insectivorous when small and become more vegetarian as they grow older, but all emus eat insects and other small creatures when given the chance. The cassowary has the shortest digestive tract, under 12 ft (4 m), and is clearly much more omnivorous in its diet. As chicks, cassowaries eat largely insects and fruits but will eat nearly anything as chicks and as adults. Kiwis are adapted to feeding on earthworms, insects, and other similar creatures, and as a result they also have relatively short digestive tracts.

Reproductive biology

The social structures of these groups have similarities and differences, but generally support the close relationship among groups. Ostriches have a social system wherein one dominant pair has a nest, but additional females may lay eggs in it and assist with incubation and chick rearing. Males incubate at night and females during the day. Both parents rear the chicks although the females dominate in the care of young. Rheas show a reversal of sex roles where the male incubates and cares for the chicks, even though the male initially gathers a harem of up to 10 or 12 females. Female rheas move from one male to the next during the breeding season. Emus are relatively close to rheas in their system where several females, usually two to four, lay eggs in one nest for a male who incubates and rears the chicks. Cassowaries are similar, with the male incubating the eggs and rearing the chicks, but usually only one or two females lay in each male's nest. Tinamous are quite similar to rheas in this reversed role of the sexes. Kiwis are monogamous and nocturnal, which differentiate them from other ratites. However, like other ratites, the males generally incubate the eggs. The larger ratites—ostriches, rheas, and emus—tend to congregate in flocks during the non-breeding season and some yearling birds remain in flocks until they become sexually mature.

Significance to humans

Ratite eggs have been used by humans for centuries. Ostrich eggs have been used as water containers by local bushmen and Sudanese. They are also used to make bracelets and necklaces and are considered to have mystical powers by some local peoples. Ratite eggs are carved and decorated by artists around the world. People also have used feathers of ratites for centuries. During the eighteenth century the soft white feathers of the male ostrich wings and tail came into fashion for ladies hats. This led to widespread hunting of the wild birds, and as a result, large declines in populations. Ostrich farms developed in southern Africa and many remain today. Ostrich farming spread to Australia, North America, and eventually around the world as use of the feathers, eggs, meat, and hides became popular. Emu farms also sprang up for similar reasons and for emu oil as well. Rhea feathers have long been used for feather dusters, and their eggs and meat are used to feed chickens and pets in South America. Hides of ratites are used to produce shoes and other leather products. Ostriches that have escaped from farms in Australia have thrived in some arid habitats there.

Resources

Books

Bertram, B. C. R. *The Ostrich Communal Nesting System.* Princeton: Princeton University Press, 1992.

Brown, L. H., E .K. Urban, and K. Newman.*The Birds of Africa.* Vol. 1. New York: Academic Press, 1982.

Bruning, D. F., and E. P. Dolenzek. "Ratites (Struthioniformes, Cassuariiformes, Rheiformes, Tinamiformes, and Apterygiformes)." In *Zoo and Wild Animal Medicine*, edited by M. E. Fowler. Philadelphia: W. B. Saunders Co., 1986.

del Hoyo, et al., eds. *Handbook of the Birds of the World.* Vol. 1. Barcelona: Lynx Edicions, 1992.

Resources

Periodicals

Bruning, D. F. "Social Structure and Reproductive Behavior in the Greater Rhea." *Living Bird* (1974): 251–294.

Other

Laufer, B. "Ostrich Egg-shell Cups of Mesopotamia and the Ostrich in Ancient and Modern Times." *Leaflet No. 23.* Chicago: Field Museum of Natural History, 1926.

Museum of Paleontology. U of California, Berkley. 1 Jan. 1996 (20 Jan. 2002). <http://www.ucmp.berkeley.edu/diapsids/birds/palaeognathae.html>

Viegas, Jennifer. "DNA Reveals Ancient Big Birds." *Discovery News* 13 Feb. 2001 (20 Jan. 2002). <http://dsc.discovery.com/news/briefs/20010212/moa.html>

Donald F. Bruning, PhD

Tinamous
(Tinamidae)

Class Aves
Order Struthioniformes
Suborder Tinami
Family Tinamidae

Thumbnail description
Small to medium-sized ground-dwelling birds with fully developed wings and capable of flight; cryptically colored in grays and browns, with three or four toes

Size
8–21 in (20–53 cm), 0.09–5 lb (43–2,300 g)

Number of genera, species
9 genera; 47 species

Habitat
Rainforest, secondary forest, savanna woodland, montane steppe, grassland, and cropland

Conservation status
Critically Endangered: 2 species; Vulnerable: 5 species; Near Threatened: 4 species

Distribution
South and Central America, as far north as Mexico

Evolution and systematics

In older natural history books, the description of birds usually began with ratites, including rheas, ostriches, cassowaries, kiwis, and the extinct moas and elephant birds of Madagascar. Because these large flightless birds have no keel on the sternum (breastbone), they are known as flat-chested birds, in contrast to all modern keel-breasted (Carinatae) birds. Today we know that the ratites descended from flying keel-breasted ancestors. Tinamous (Tinamidae) are a still-living primitive bird family that may be close to the ancestral group of ratites.

Physical characteristics

Length 8–21 in (20–53 cm), weight 0.09–5 lb (43–2,300 g). Tinamous are ground birds with a compact form, a slender neck, a small head, and a short, slender bill that curves slightly downward. The wings are short and capacity for flight is poor. The feet are strong; there are three well-developed forward toes, and the hind toe is in a high position and either retrogressed or absent. The tail is very short and in some species it is hidden under tail coverts; this and abundant rump feathering give the body a rounded shape. Powder down and a preen gland are present. In contrast to gallinaceous birds, they do not scratch for food with their feet, but do use their feet to dig nest scrapes. A copulatory organ is present. The plumage is inconspicuous, although crown feathers of some species can be raised as a crest. Males and females have similar plumage, or females may be somewhat brighter in color and often larger than males.

Distribution

The range of tinamous has not changed significantly in recorded time. They live in tropical parts of Central and South America. In the north they live only slightly beyond the tropic of Cancer (Zimttao in northwest Mexico), but in South America they are widespread, distributed throughout the continent. One species has been successfully introduced to Easter Island in the Pacific.

Habitat

Many species live in dense forest, especially those in the genera *Tinamus*, *Nothocercus*, and *Crypturellus*. Other species live in savanna, on grassland, and in the montane or puna re-

gions, at high altitudes. Some grassland forms have established themselves successfully in cropland; others can live on ranches among grazing cattle.

Behavior

Walking or running, tinamous move almost exclusively on the ground. When approached by people, they hide in thick ground cover or steal away unobserved. When hard-pressed in open country, they crawl into holes dug by other animals. Some species are very reluctant to fly. When surprised by a larger animal or when followed too closely, they rise suddenly with loud, frightening wing beats, and often they call. They disappear swiftly and alight in thick vegetation. Before a surprised hunter can bring up his gun, they have disappeared.

The initial burst of wing fluttering is often followed by a long glide and again by renewed wing beats. Although many tinamous cover long distances on foot rather than in flight, D. A. Lancaster observed a brushland tinamou (*Nothoprocta cinerascens*) that regularly flew 660 ft (200 m) from nest to feeding place. In other species, flights of 660–4,900 ft (200–1,500 m) have been observed. In Patagonia, the elegant crested tinamou (*Eudromia elegans*) forms strings of six to 30 or more birds. But most adult tinamous live singly except during the reproductive season. Many tinamous roost on the ground, but in some—especially those in the genus *Tinamus*—the hind surface of the tarsus is rough. These birds roost in trees, squatting with the tarsus across a branch rather than gripping the branch with their toes as songbirds do.

Hearing tinamou calls is one of the most unforgettable experiences one can have in tropical America. In contrast to most tinamous, the male highland tinamou (*Nothocercus bonapartei*) utters a rough crowing or barking call that can be heard for several miles (kilometers) through mountain forests. In some species, males and females are distinguishable by their calls. Tinamous sing mainly during the breeding season; they are noisiest in early morning and late evening. When startled, they fly off or follow one another, hoarsely shrieking or crowing.

Feeding ecology and diet

Tinamous eat mainly small fruits and seeds that they pick from the ground or from plants they can reach from the ground; they may jump up 4 in (10 cm) to reach a particularly tempting fruit. Seeds with wing-like appendages that make swallowing difficult are beaten against the ground or vigorously shaken. They also eat opening buds, tender leaves, blossoms, and even roots. For variety they catch insects and their larvae, worms, and, in moist places, mollusks. They swallow small animals whole; they first peck at larger ones, then shake them or beat them against the ground. When searching for food, they scatter fallen leaves and other ground cover with their bills, but do not scratch with their feet. When searching for worms or larvae in moist places, many species fling the earth aside with their bills, digging down 0.7–1.2 in (2–3 cm).

A puna tinamou (*Tinamotis pentlandii*) nest in the high Andes of Peru. (Photo by F. Gohier. Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

In ornate and highland tinamous, and in taos and many other species, there are about as many females as males. But in the variegated tinamou there may be four times as many males as females.

Reproductive behavior differs from that of most other birds. Only males care for eggs and young. In the few species that are adequately studied, males live in polygyny and females in polyandry. A male in breeding condition attracts two, three, or more females by continually calling. Females lay in the same nest and leave incubation to the male. Females leave to lay eggs in the nests of other males. When the male has raised his young or lost the eggs, he begins to call again and attracts new hens that supply him with another nest full of eggs. This breeding behavior has been observed in such different species as the highland tinamou, the brushland tinamou, and the slaty-breasted tinamou (*Crypturellus boucardi*). The variegated tinamou (*Crypturellus variegatus*) cares for only a single egg; the clutch of four to nine eggs incubated by the male ornate tinamou (*Nothoprocta ornata*) seems to come from a single female. In this mountain species, the

Highland tinamou (*Nothocercus bonapartei*) with hatching chicks in Costa Rica. (Photo by Michael Fogden. Bruce Coleman Inc. Reproduced by permission.)

larger and more aggressive female defends the breeding territory; in other tinamous this is done by males.

Tinamous almost always nest on the ground, often in densest herbage or between projecting root buttresses of large trees. Many tinamous lay their eggs directly on the ground or on leaves that happen to be on the chosen spot. Ornate tinamous build a proper nest base of dry earth, or a mixture of earth and moss turf. On this they erect a firm structure of grass that is worked into the base to form a circle. Shiny tinamou eggs are among the most beautiful natural products known. They may be green, turquoise blue, purple, wine red, slate gray, or a chocolate color, and often have a purple or violet luster. They are always uniformly colored, without spots or blotches. Their shape is oval or elliptical.

Incubating male tinamous sit continuously on eggs for many hours. In most species they leave the clutch once a day to look for food, usually during mornings or in the afternoon, depending on the weather, and are away from the nest for 45 minutes up to five hours.

Although the eggs are conspicuous and have no protective coloration, some tinamous do not cover the eggs when leaving the nest. A brushland tinamou covers its eggs only when they are about to hatch. The ornate tinamou regularly covers the eggs with feathers, giving them some protection from the harsh climate in the 13,000-ft (4,000-m) Peruvian puna. In the warm forests of Central America, a slaty-breasted tinamou always threw leaves toward the nest quite carelessly; often more than half the eggs were left uncovered.

Incubating tinamous sit so firmly on the nest that one can approach very closely. Although they will not let themselves be touched by a hand, an observer can sometimes touch them with the end of a long stick. If someone approaches, some species—including the ornate tinamou and several *Crypturellus* species—press head and body close to the ground and raise the hind end, sometimes until the stumpy tail and lower tail coverts stand almost vertically. This posture resembles that assumed by certain tinamous in courtship display or when they are alarmed while walking. It seems to serve no special purpose in the incubating cocks, because raising the hind end may expose the shiny eggs. If one approaches an incubating tinamou cock too closely, it flies off the nest and out of sight in a burst of speed. An exception is the tataupa (*Crypturellus tataupa*), which flutters over the ground as if hurt and unable to fly when displaced from its eggs.

Newly hatched tinamous are densely covered with long soft down that in some species is marked in dulled colors. On the first day after hatching, the male leads the young out of the nest, moving slowly and calling them with repeated soft whistles or whining tones. Now and then he picks up an insect from the ground and moves it in his bill, then lays the insect before one of the young to be picked up. On leaving the nest, chicks of the small tinamous are very delicate, but they move so skillfully through the dense vegetation that little is known about them after they leave the nest. They probably develop rapidly and soon leave their father. A slaty-breasted tinamou at 20 days differed little in color and size from adults.

Conservation status

Eleven species are threatened, mainly because clearing and development have fragmented their habitats. The rarest are the Magdalena tinamou (*Crypturellus saltuarius*), known from one specimen, and Kalinowski's tinamou (*Nothoprocta kalinowskii*), not seen for many years. Both of these species are considered Critically Endangered by the IUCN. The dwarf tinamou (*Taoniscus*) and the lesser nothura (*Nothura minor*) are badly affected by development—IUCN considers these species Vulnerable. Three other species with very small ranges are also considered Vulnerable—the black tinamou (*Tinamus osgoodi*), the Choco tinamou (*Crypturellus kerriae*), and Taczanowski's tinamou (*Nothoprocta taczanowskii*). Four additional species are listed as Near Threatened—the yellow-legged tinamou (*Crypturellus noctivagus*), the pale-browed tinamou (*Crypturellus transfasciatus*), the Colombian tinamou (*Crypturellus columbianus*), and the solitary tinamou (*Tinamus solitarius*).

Significance to humans

Tinamous are hunted for food by humans throughout their range. A Brazilian rural family consumed about 60 nothuras a year, but this is not thought to be too severe a drain on the birds. Many attempts have been made to introduce the birds to other parts of the world, so far, except for Easter Island, without success.

1. Variegated tinamou (*Crypturellus variegatus*); 2. Female spotted nothura (*Nothura maculosa*); 3. Highland tinamou (*Nothocercus bonapartei*); 4. Male slaty-breasted tinamou (*Crypturellus boucardi*); 5. Male thicket tinamou (*Crypturellus cinnamomeus*); 6. Red-winged tinamou (*Rhynchotus rufescens*); 7. Elegant-crested tinamou (*Eudromia elegans*); 8. Female brushland tinamou (*Nothoprocta cinerascens*); 9. Black tinamou (*Tinamus osgoodi*); 10. Great tinamou (*Tinamus major*). (Illustration by Bruce Worden)

Species accounts

Black tinamou
Tinamus osgoodi

TAXONOMY
Tinamus osgoodi Conover, 1949, Curzo, Peru. Two subspecies.

OTHER COMMON NAMES
French: Tinamou noir; German: Schwartztinamu; Spanish: Tinamú Negro.

PHYSICAL CHARACTERISTICS
17 in (43 cm). Females are slightly larger. Sooty brown belly; vent is chestnut with black speckling.

DISTRIBUTION
Known only from two restricted and widely separated localities—the upper Magdalena valley in southern Colombia (subspecies *T. o. hershkovitzi*) and the Marcapata valley in southeastern Peru (*T. o. osgoodi*).

HABITAT
Humid, high-altitude tropical forest, 5,000–7,000 ft (1,500–2,100 m), where epiphytes, tree ferns, bromeliads, and moss abound.

BEHAVIOR
The call is a simple, descending whistle.

FEEDING ECOLOGY AND DIET
Not known.

REPRODUCTIVE BIOLOGY
The only nest found was on the ground and contained two glossy blue eggs.

CONSERVATION STATUS
Vulnerable. Threatened by habitat destruction.

SIGNIFICANCE TO HUMANS
None known. ◆

Tinamus osgoodi
Resident

Great tinamou
Tinamus major

TAXONOMY
Tinamus major Gmelin, 1789, Cayenne.

OTHER COMMON NAMES
English: Mountain hen; French: Grand tinamou; German: Großtinamu; Spanish: Tinamú Oliváceo.

PHYSICAL CHARACTERISTICS
17.5 in (44 cm), 2.5 lb (1.1 kg). Female slightly larger. Overall color ranges from light to dark olive brown. Whitish on throat and center of belly.

Tinamus major
Resident

DISTRIBUTION
Widely distributed, with seven subspecies in Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, French Guiana, Honduras, Mexico, Nicaragua, Panama, and Venezuela.

HABITAT
Dense tropical and subtropical forest, preferably with an open floor, at altitudes of 1,000–5,000 ft (300–1,500 m).

BEHAVIOR
Usually solitary, maintaining a home range. The call is a series of musical, tremulous whistles.

FEEDING ECOLOGY AND DIET
Feeds on the forest floor, taking fruits and seeds, especially of the Lauraceae, Annonaceae, Myrtaceae, and Sapotaceae.

REPRODUCTIVE BIOLOGY
The breeding season is long, extending from mid-winter to late summer. The nest, built between buttresses of a forest tree, contains 3–6 glossy turquoise or violet eggs. The male alone incubates eggs and rears the brood.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
It is hunted as a game bird, especially around towns, but has survived better than other game species. The great tinamou has various roles in native American folklore in Brazil, Colombia, and Panama. ◆

Highland tinamou
Nothocercus bonapartei

TAXONOMY
Nothocercus bonapartei Gray, 1867, Aragua, Venezuela. Five subspecies.

OTHER COMMON NAMES
English: Bonaparte's tinamou; French: Tinamou de Bonaparte; German: Bergtinamu; Spanish: Tinamú Serrano.

PHYSICAL CHARACTERISTICS
15 in (38.5 cm), 2 lb (925 g). Mottled or barred with black and cinnamon on back and wings. Throat is variable rufous color.

DISTRIBUTION
Colombia, Costa Rica, Panama, and Venezuela.

HABITAT
Tropical and subtropical forest, mainly above 5,000 ft (1,500 m), favoring damp areas, especially those with bamboo thickets.

BEHAVIOR
The call is loud and hollow, repeated many times, given by the male from his home range, which he occupies throughout the year.

FEEDING ECOLOGY AND DIET
Feeds on fallen fruits and small animals.

REPRODUCTIVE BIOLOGY
The male defends a small territory in his home range, attracting one or more females with calls and a display known as "follow feeding." The nest, which may contain eggs from several females in a clutch of four to 12, is concealed in ground vegetation. Incubation is by the male alone.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted as a game bird; populations in Costa Rica and Peru have declined as a result. ◆

Thicket tinamou
Crypturellus cinnamomeus

TAXONOMY
Crypturellus cinnamomeus Lesson, 1842, La Union, El Salvador.

OTHER COMMON NAMES
English: Rufescent tinamou; French: Tinamou cannelle; German: Beschtinamu; Spanish: Tinamú Canelo.

PHYSICAL CHARACTERISTICS
10.8 in (27.5 cm), 1 lb (440 g). Barred black on back and flanks; white throat and cinnamon or rufous cheeks and breast.

DISTRIBUTION
This tinamou, with nine subspecies, is widespread in Central America and has populations in Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua. Its distribution extends farther north than that of any other tinamou.

HABITAT
Thick undergrowth, with an overstory—a foliage layer in a forest canopy including the trees in a timber stand—ranging from arid scrub to secondary forest.

Crypturellus cinnamomeus

Resident

Crypturellus boucardi

Resident

BEHAVIOR
The monotonous call sounds like a steam whistle when heard at close quarters. The bird lives singly, in pairs, or in family parties. When disturbed it walks, rather than flies, away.

FEEDING ECOLOGY AND DIET
Feeds on fruit, seeds, and insects, searching for food in small parties that attract attention by crackling dry leaves as they feed.

REPRODUCTIVE BIOLOGY
The nest is placed on the ground at the base of a tree. The clutch is usually three, but may be up to seven glossy purplish eggs. Hybrids have been found between this species and the slaty-breasted tinamou.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Because it is so unwilling to fly, it is not regarded as an important game bird. ◆

Slaty-breasted tinamou
Crypturellus boucardi

TAXONOMY
Crypturellus boucardi Sclater, 1859, Oaxaca, Mexico. Two subspecies.

OTHER COMMON NAMES
English: Boucard tinamu; French: Tinamu de Boucard; German: Graukehltinamu; Spanish: Tinamú Pizarroso.

PHYSICAL CHARACTERISTICS
10.8 in (27.5 cm), 1 lb (470 g). Pink to bright red legs; slaty breast, blackish head, and white throat. Back is blackish to chestnut. Female has barring on wings.

DISTRIBUTION
Belize, Costa Rica, Guatemala, Honduras, Mexico, and Nicaragua.

HABITAT
Sea level to 6,000 ft (1,800 m), sometimes favors thick undergrowth. Also humid forest with little undergrowth at ground level. Sometimes common in regenerating plantations and is often in damp areas, especially near forest edges.

BEHAVIOR
The call has three notes and is lower than the calls of many tinamous. It may be given in long bouts, up to five hours in one case. Calls of individual males are recognizable, and mellower and less variable than female calls. It is solitary, remaining in its home range throughout the year.

FEEDING ECOLOGY AND DIET
Feeds on fruits and seeds, tossing leaves aside with its bill in its search. It takes insects, including ants and termites.

REPRODUCTIVE BIOLOGY
In the breeding season it establishes a small territory in its home range, attracting two to four females to lay in a nest at the base of a tree or in thick vegetation. The male alone incubates; females leave to mate with another male.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Hunted as a game bird and has become rare in some of its range, but is elsewhere still common. ◆

Variegated tinamou
Crypturellus variegatus

TAXONOMY
Crypturellus variegatus Gmelin, 1789, Cayenne.

OTHER COMMON NAMES
French: Tinamou varié; German: Rotbrusttinamu; Spanish: Tinamú Abigarrado.

PHYSICAL CHARACTERISTICS
11.5 in (29.5 cm), 0.8 lb (380 g). Black head; neck and breast rufous. Light barring on underparts.

DISTRIBUTION
Belize, Brazil, Colombia, Ecuador, Guiana, Peru, and Venezuela.

HABITAT
Tropical forest with dense undergrowth at moderate altitudes, 300–4,300 ft (100–1,300 m).

BEHAVIOR
The call is a series of five evenly pitched tremulous notes, often merging to a trill, with the first note descending and distinct from the rest of the trill.

FEEDING ECOLOGY AND DIET
Mainly seeds and fruits, with few insects.

REPRODUCTIVE BIOLOGY
The female establishes a territory, attracts a male, lays one egg in a rudimentary nest, and leaves the male incubating while she departs to establish another territory and repeat the process.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
The bird does not appear to be important as a game species. ◆

Red-winged tinamou
Rhynchotus rufescens

SUBFAMILY
Rhynchotinae

TAXONOMY
Rhynchotus rufescens Temminck, 1815, São Paulo, Brazil. Four subspecies.

OTHER COMMON NAMES
French: Tinamou isabelle; German: Pampahuhn; Spanish: Tinamú Alirrojo.

PHYSICAL CHARACTERISTICS
16 in (41 cm), 1.8 lb (830 g). Female slightly larger. Black patch on crown; rufous primaries. Light grayish brown to whitish underneath. May be black barring on flanks, abdomen, and vent.

DISTRIBUTION
Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

HABITAT
At low altitudes, below 3,300 ft (1,000 m), it lives in damp grassland and woodland edges; at higher altitudes it is found in semiarid scrub and cereal fields.

BEHAVIOR
The call, given only by males, is a long, ringing single whistle followed by shorter, mournful whistles. The birds live dispersed in the dense vegetation, and are most active in the heat of the day.

FEEDING ECOLOGY AND DIET
It is sedentary, feeding on the ground on seeds, tubers, and fruit. In the summer it takes more animal food, including earthworms, termites, and other insects. It digs for food with its bill, and so is unpopular on newly sown cropland.

REPRODUCTIVE BIOLOGY
The red-winged tinamou has many displays, the male attracting one or more females by follow feeding, and always accompanies the female to the nest when she is to lay. He alone incubates the eggs and broods the chicks.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A popular game bird and hunted out in some regions, but elsewhere common. Because it will live in cropland it has extended its range alongside agricultural development. ◆

Brushland tinamou
Nothoprocta cinerascens

TAXONOMY
Nothoprocta cinerascens Burmeister, 1860, Tucumán, Argentina. Two subspecies.

OTHER COMMON NAMES
French: Tinamou sauvageon; German: Cordobasteißhuhn; Spanish: Tinamú Montaraz.

PHYSICAL CHARACTERISTICS
12.5 in (31.5 cm), 1.2 lb (540 g). Female slightly larger and darker. Black barring on back and wings.

DISTRIBUTION
Argentina, Bolivia, and Paraguay.

HABITAT
Favors dry savanna woodlands, usually below 3,300 ft (1,000 m), but will live in cropland and open thorn scrub.

BEHAVIOR
The advertising call is a series of seven to 10 clear whistled notes with considerable carrying power. Home ranges are about 50 acres (20 ha), maintained mainly by calls but often overlapping ranges of other males.

FEEDING ECOLOGY AND DIET
Feed on the ground, mostly on insects and small animals, but also take some fruit.

REPRODUCTIVE BIOLOGY
Males attract groups of two to four females, establish a nest site, and supervise females while they lay in it. When the females leave to join another male, the original male incubates the clutch and rears the brood alone.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Subject to light hunting but remains common. ◆

Spotted nothura
Nothura maculosa

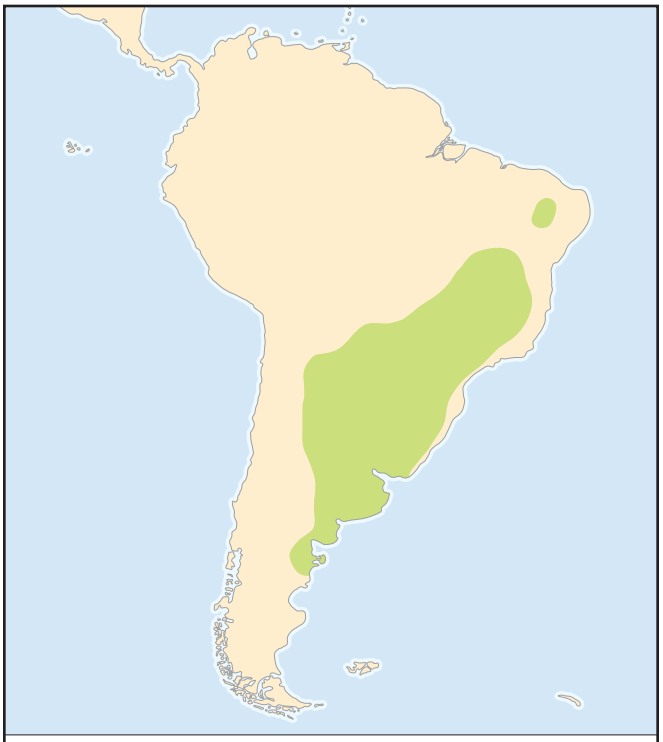
TAXONOMY
Nothura maculosa Temminck, 1815, Paraguay. Eight subspecies.

OTHER COMMON NAMES
French: Tinamou tacheté; German: Fleckensteißhuhn; Spanish: Tinamú Manchado.

PHYSICAL CHARACTERISTICS
10 in (25.5 cm), 0.6 lb (250 g). Female slightly larger. Variable appearance, sometimes very dark upperparts.

DISTRIBUTION
Argentina, Brazil, and Uruguay.

HABITAT
Most subspecies inhabit lowlands, living in open grassland, shrub steppe, and cropland. Its range is expanding as clearing takes place for agriculture.



Nothura maculosa

Resident

Eudromia elegans

Resident

BEHAVIOR
The call is a series of brief, high-pitched piping notes, often given in response to other calling birds. Populations may be very dense in favorable country, up to a bird to every 2.5 acres (1 ha).

FEEDING ECOLOGY AND DIET
The spotted nothura feeds on vegetable and animal matter, taking more insects than plants in Argentina, but elsewhere feeding mainly on seeds, including those of pasture plants, crops, and weeds.

REPRODUCTIVE BIOLOGY
The species has a very high reproductive rate; females can mature at two months of age and have 5–6 broods in a year. Males take longer to mature, or at least to establish nests. As with other tinamous, males undertake all incubation and parenting, often attracting more than one female to lay in a single nest.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A very popular game bird, but a high reproductive rate and early maturity ensure that it remains common. ◆

Elegant crested-tinamou
Eudromia elegans

TAXONOMY
Eudromia elegans Geoffroy St. Hillaire, 1832, South America. Eight subspecies.

OTHER COMMON NAMES
French: Tinamou élégant; German: Perlsteißhuhn; Spanish: Martineta Común.

PHYSICAL CHARACTERISTICS
15.5 in (39 cm), 1.3 lb (600 g). Leg color pale bluish to grayish brown. Lacks hind toe. Crest is long, normally carried backwards.

DISTRIBUTION
Throughout Argentina and Chile.

HABITAT
Arid and semiarid grassland and savanna, favoring open sites, ranging from sea level to 8,000 ft (2,500 m) in altitude.

BEHAVIOR
The call is a loud melancholy whistle. Unlike many tinamous, this species forms small flocks, especially in winter when it invades alfalfa crops. In spring and summer it may still be found in pairs and small groups.

FEEDING ECOLOGY AND DIET
In winter it feeds mainly on seeds and leaves of plants; in summer it takes many insects and invertebrates, including termites.

REPRODUCTIVE BIOLOGY
Breeding systems are polyandrous and polygynous, although males undertake all incubation and parenting.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
It is hunted intensely and remains common only in remote areas. ◆

Resources

Books

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

del Hoyo, J., A. Elliot, and J. Sargatal, eds. *Handbook of the Birds of the World.* Vol. 1, *Ostrich to Ducks.* Barcelona: Lynx Editions, 1992.

Periodicals

Beebe, W. "The Variegated Tinamou *Crypturus variegatus* (Gmelin)." *Zoologica* 6 (1925): 195–227.

Lancaster, D. A. "Life History of the Boucard Tinamou in British Honduras." *Condor* 66 (1964): 165–81, 253–76.

Lancaster, D. A. "Biology of the Brushland Tinamou *Nothoprocta cinerescens*." *Bulletin of the American Museum of Natural History* 127 (1964): 271–314.

S. J. J. F. Davies, ScD

Rheas
(Rheidae)

Class Aves
Order Struthioniformes
Suborder Rheae
Family Rheidae

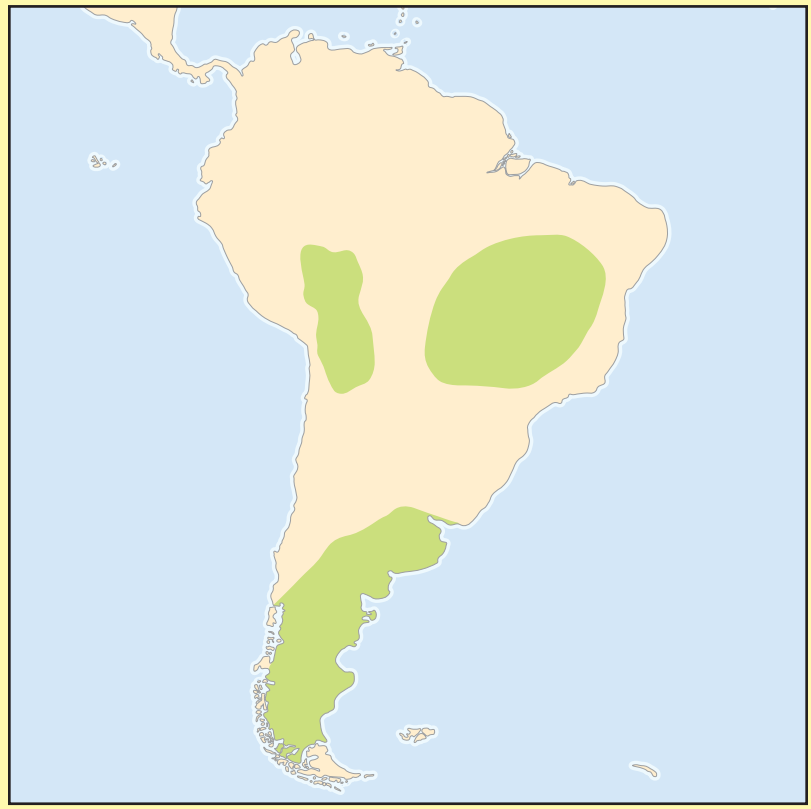
Thumbnail description
Very large flightless birds with long legs and three toes; plumage gray or spotted brown and white; wings used only in display, reduced with long soft feathers; no tail feathers and no casque on the head

Size
36.4–55 in (92–140 cm); 33–88 lb (15–40 kg)

Number of genera, species
2 genera; 2 species

Habitat
Savanna, grassland, and high mountain plains

Conservation status
Not threatened. Populations are now fragmented and numbers have declined, but still abundant in some areas



Distribution
Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay

Evolution and systematics

Rheas belong to the group of large, flightless birds known as the ratites, which all lack a keel to the sternum and a distinctive palate. The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Whereas it used to be thought that ratites had a southern origin, in the old continent of Gondwana, new fossil evidence has shown flying ratites inhabited the northern hemisphere in the Paleocene and Eocene, 40–70 million years ago. The present southern hemisphere distribution of ratites probably results from the spread of flying ancestors of the group from the north. Fossil rheas have been found in the Upper Pleistocene of Argentina. They lived there about two million years ago; it is thought that rheas are related to Tinamidae.

Physical characteristics

Rheas are smaller and more slender than ostriches: standing upright they reach 5.6 ft (1.7 m). They may weigh up to 88 lb (40 kg), the head, neck, rump, and thighs are feathered, and their plumage is soft and loose. There are three front toes, and the hind toe is absent. The tarsus has horizontal plates in front. The gut and the caeca are very long. Urine is stored in an expansion of the cloaca and is eliminated in liquid form. The copulatory organ is extrudable. In the greater rhea (*Rhea americana*) total height reaches 5.6 ft (1.7 m); height of the back is 3.3 ft (100 cm), wingspan reaches 8.2 ft (250 cm), tarsal length is 12–14.5 in (30–37 cm), and bill length is 3.5–4.7 in (9–12 cm). Males are larger than females. The tarsus has about 22 horizontal plates in front. The lesser rhea (*Pterocnemia pennata*) is smaller than the greater with a height at the back of 3.0 ft (90 cm). The tarsus is 11.0–11.8 in (28–30 cm) and has about 18 horizontal plates.

Distribution

Rheas are confined to South America—Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay.

Habitat

Rheas are birds of grassland, the greater rhea and one subspecies of lesser rhea, *Pterocnemia pennata pennata*, of lowland grassland or pampas. The other two subspecies of lesser rhea live in the puna zone of the Andes, inhabiting deserts, salt puna, heath, and pumice flats. Although *P.p. pennata* feeds on lowland grassland in the non-breeding season, it usually

The lesser rhea (*Pterocnemia pennata*) with chicks on their nesting ground just north of Punta Arenas, Chile. (Photo by N.H. [Dan] Cheatham. Photo Researchers, Inc. Reproduced by permission.)

breeds in upland areas where bunch grass grows, around 5–6,000 ft (2,000 m).

Behavior

Rheas are silent except as chicks, when they give a plaintive whistle, and during the breeding season when males make a deep booming call, sometimes described as like the last tone of a siren or as a di-syllabic grunt. In any case one of the renditions of the call "nandu" has become a common name for the bird. Males perform an elaborate display while giving these calls, raising the front of the body, with the neck held stiffly upwards and forward and the plumage greatly ruffled. Wings are raised and extended, and after calling the bird may run some distance, sometimes flipping the wings up and down alternately. Usually this display, the call display, is given near females and may be followed by the wing display, that is directed at a specific female. The male spreads his wings, lowers his head, and walks in this posture beside or in front of a female, holding the display for 10 minutes or more. Females seem to be attracted to a male displaying in this way. As the display becomes more intense the male waves his neck from side to side in a figure-eight pattern, often attracting females to watch him for several minutes before they move off to feed. If a female remains beside a displaying male, she may solicit and copulation follows.

During the non-breeding season the greater rhea forms flocks of 10–100 birds, while the lesser rhea lives in smaller flocks than that. As in the ostrich, birds in small flocks are more vigilant than those in large flocks. They are also more vigilant when in tall grass environments than on open plains. Rheas feed most of the day in these flocks, although males show mild aggression to each other from time to time. When fleeing in alarm, a rhea will follow a zigzag course, often raising one wing, apparently to act as a rudder and help it to turn rapidly. Dust bathing is common in captive birds. Flocks break up in the winter for the breeding season.

Feeding ecology and diet

Both species of rhea are mainly herbivores. Both take a few small animals—lizards, beetles and grasshoppers—but not in any significant quantity. Most of the present range of the greater rhea is used for cattle ranching, with the result that pastures have been seeded with fodder grasses and forbs. The greater rhea takes much alfalfa and maize. The Lesser rhea lives in less developed areas, but is mainly herbivorous, taking forbs like saltbush and fruits of cactus.

Reproductive biology

Much information has been gathered about the reproductive behavior of the greater rhea, both in the wild and in captivity. It is a polygamous bird, meaning both males and females take two or more mates. When the winter comes, the flocks break up into three types of groups—single males, flocks of

A male greater rhea (*Rhea americana*) sits on its nest. (Photo by F. Gohier. Photo Researchers, Inc. Reproduced by permission.)

two to 15 females, and large flocks of yearlings. Males soon begin posturing and challenging each other, behavior that becomes intense as the spring and summer breeding season arrives. Males attempt to attract harems of females, building a nest and leading females toward it. When a harem has chosen a male, one female will approach the nest. The male may stand but usually remains sitting or crouching, twisting his neck to follow the movements of the female as she walks around the nest. The male, at first acting aggressively and spreading his wings to cover the eggs, gradually relaxes and replaces head-forward movements with head-bobbing and neck swinging. The female crouches and lays her egg at the rim of the nest and the male rolls the egg beneath himself. In this way, with eggs from as many as 15 females, he may build up a clutch of 50 or more eggs in a week. Then he begins to incubate in earnest. As in the ostrich some eggs remain outside the nest, and these seem to act to dilute the clutch, so that it is less likely that the eggs being incubated are taken by predators, because they first take the eggs outside the nest. Recent work has shown that some males have male partners. A subordinate male may take over the clutch from the first harem of females that the dominant male attracts, incubate them, and parent the chicks. Meanwhile the dominant male attracts another harem, or the same one to another nest, incubates the second clutch and rears the second brood. Measurements show that both dominant and subordinate males are equally successful at incubating and raising broods.

The mean clutch size of the greater rhea in Argentina is 24.9 eggs and the incubation period 36–37 days. The male alone incubates, leaving the nest from time to time to feed. As in other birds, chicks in the eggs are able to communicate with each other and synchronize hatching, so that the male stays no more than 36 hours on the nest once hatching begins. Breeding success is usually low, about 20%, but in some years breeding success is greater than this. Some nests are deserted when bad eggs explode during incubation, and in other cases armadillos dig under the nest and eat the eggs. Predation also accounts for the loss of many small chicks; birds of prey follow broods until one chick straggles and then snatch it. Much less is known about the breeding biology of the lesser rhea, but it appears to have a similar breeding system, clutch size, and incubation period.

Conservation status

The greater rhea is farmed in some areas for its meat and leather, but the range available for wild birds is shrinking, and many are taken by hunters. Similarly the lesser rhea suffers from development of its environment by the construction of roads that allow hunters access to country that was previously inaccessible. Both species need large, well protected reserves if they are to survive as wild populations.

Significance to humans

Feathers of rheas have always been taken for use as dusters. Skins are used as cloaks in their dried state and as fashion leather when fully tanned. Rhea meat has long been a staple food for South Americans, who are now able to hunt the birds more effectively with rifles than they were when they had only the bolas, a weapon made of three thongs of leather tied together centrally. At the outer end of each thong a small stone is attached. The bolas is whirled around by the hunter and thrown with great skill and accuracy at the running bird. The thongs wrap around the birds legs and bring it to the ground, effectively immobilizing it. The bolas is still used, even by scientists who want to catch the birds alive.

1. Lesser rhea (*Pterocnemia pennata*); 2. Greater rhea (*Rhea americana*). (Illustration by Patricia Ferrer)

Species accounts

Greater rhea
Rhea americana

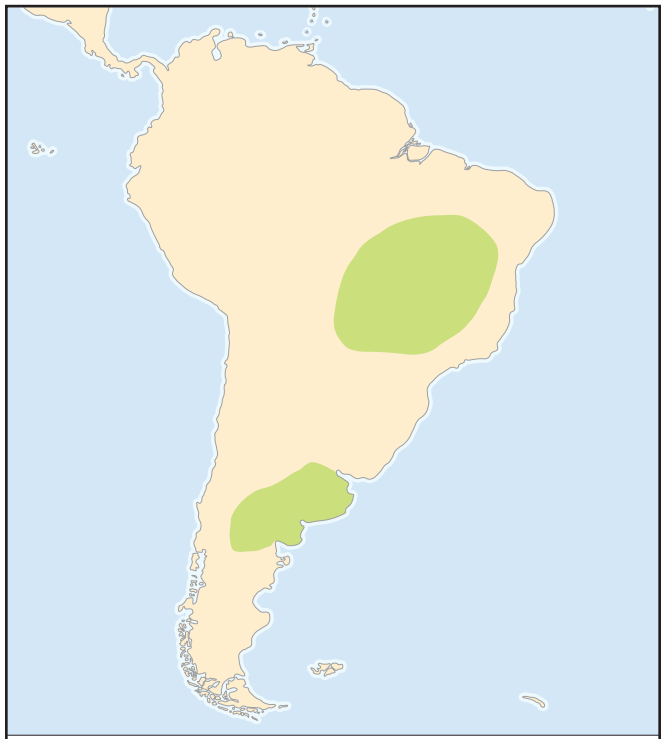
TAXONOMY
Rhea americana Linnaeus, 1758, Sergipe and Rio Grande do Norte, Brazil. Five subspecies.

OTHER COMMON NAMES
English: Common rhea; French: Nandou d'Amérique; German: Nandu; Spanish: Ñandú.

PHYSICAL CHARACTERISTICS
50–55 in (127–140 cm); 44–88 lb (20–40 kg). General color gray or grayish brown above, whitish below without spotting in both sexes. The head and neck of the male are black or largely black. The female is paler. Unlike the lesser rhea, the whole length of the tarsus is bare and covered with transverse scutes.

DISTRIBUTION
Brazil, Uruguay, Paraguay, and Bolivia. The form in eastern Brazil, *Rhea americana americana* is the nominate, or first named, form. *R. a. intermedia* comes from southeastern Brazil and Uruguay, *R. a. nobilis* from Paraguay, *R. a. araneiceps* from Paraguay and Bolivia, and *R. a. albescens* from Paraguay and, possibly, Bolivia.

HABITAT
Grassland and pampas.



BEHAVIOR
Greater rheas live at densities of 0.002–0.076 birds per acre (0.05–0.19 birds/ha). In the nonbreeding season they live in flocks of 20–50 birds. Once the breeding season starts, males establish a nest site and defend its immediate vicinity, attracting groups of females to lay in the nest.

FEEDING ECOLOGY AND DIET
Herbivore, feeds on grasses and forbs.

REPRODUCTIVE BIOLOGY
Males incubate eggs laid by harem of females in a nest on the ground. The mean clutch size is 26, the eggs coming from up to seven different females. Females are attracted to the nest by male displays in which the wings are prominently displayed. The male leads the female to the nest and often sits on it while she lays outside it. He then rolls the egg into the nest. Eggs are greenish yellow color, 5 by 3.5 in (13 by 9 cm). Incubation period is 29–43 days, by the male only.

CONSERVATION STATUS
Population fragmented by agricultural development.

SIGNIFICANCE TO HUMANS
Hunted for meat, leather, and feathers; now farmed. ◆

Lesser rhea
Pterocnemia pennata

TAXONOMY
Pterocnemia pennata d'Orbigny, 1834, Lower Río Negro, south of Buenos Aires. Three subspecies.

OTHER COMMON NAMES
English: Darwin's rhea; French: Nandou de Darwin; German: Darwinstrauss; Spanish: Ñandú Overo.

PHYSICAL CHARACTERISTICS
36–39 in (92–100 cm); 33–55 lb (15–25 kg). The plumage is spotted brown and white. The upper part of the tarsus is partly feathered, but the rear and lower part is bare, covered with transverse scutes.

DISTRIBUTION
Argentina, Chile, Peru, and Bolivia. The nominate form, *Pterocnemia pennata pennata*, lives in southern Chile and Argentina, while *P. p. tarapacensis* lives in the Andes of Chile and *P. p. garleppi* lives in the Andes of Peru, Bolivia and northwestern Argentina.

HABITAT
Grassland, high Andes in the puna zone.

BEHAVIOR
Lives in flocks of 2–30 individuals at a mean density of 0.28 birds per mi^2 (0.11 birds/km^2). Males defend nest sites during the breeding season. A male attracts groups of females to a

Pterocnemia pennata

Resident

nest site and lay there, leaving the male to incubate the eggs alone.

FEEDING ECOLOGY AND DIET

Feeds on fruits and leaves of forbs, the items taken varying by place and season. In some places grasses are prominent, in others shrub foliage and fruits are mostly taken.

REPRODUCTIVE BIOLOGY

Males incubate eggs laid by harem of females in a nest on the ground. The greenish yellow eggs measure 4.9 by 3.4 in (12.6 by 8.7 cm) and are incubated for 30–44 days. Clutch size varies from five to 55 eggs, depending on the region. The birds mature in their third year.

CONSERVATION STATUS

Two isolated populations subject to severe hunting pressure.

SIGNIFICANCE TO HUMANS

Hunted for meat and leather. ◆

Resources

Books

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

del Hoyo, J., A. Elliot, and J. Sargatal, eds. *Ostrich to Ducks.* Vol. 1 of *Handbook of the Birds of the World.* Barcelona: Lynx Edicions, 1992.

Periodicals

Bruning, D. F. "The Social Structure and Reproductive Behavior in the Greater Rhea." *Living Bird* 13 (1974): 251–94.

Codenotti, T. L., and F. Alvarez. "Cooperative Breeding Between Males in the Greater Rhea *Rhea americana*." *Ibis* 139 (1997): 568–71.

S. J. J. F. Davies, ScD

Cassowaries
(Casuariidae)

Class Aves
Order Struthioniformes
Suborder Casuarii
Family Casuariidae

Thumbnail description
Large flightless birds with tiny wings terminating in long spines, shiny black plumage, three toes, a casque on the head (also called a helmet or a crown), and colorful bare skin on the neck

Size
40–67 in (102–170 cm); 30–130 lb (14–59 kg)

Number of genera, species
1 genus; 3 (possibly 4) species

Habitat
Rainforest and adjacent dense vegetation

Conservation status
Potentially endangered by logging and forest clearing and by competition from feral pigs and dogs

Distribution
Cape York (Australia), New Guinea, and some surrounding islands

Evolution and systematics

Cassowaries belong to the group of large flightless birds known as the ratites that have in common a distinctive palate and the lack of a keel to the sternum. The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Whereas it was previously thought that ratites had a southern origin, new fossil evidence has shown flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, between 40 million and 70 million years ago. The present Southern Hemisphere distribution of the ratites probably results from the spread of flying ancestors of the group from the north. The cassowaries differ from the rheas and ostriches in their structure and way of life. All cassowary feathers consist of a shaft and loose barbules; there are no rectrices (tail feathers) nor a preen gland and only five to six large wing feathers. On the strongly retrogressed wing, the lower arm and hand are only half as long as the upper arm. The furcula (wishbone) and coracoid (shoulder blade) are degenerate. There is a special palatal structure, and the palatal bones and sphenoids touch one another. Cassowaries are known from fossils of the Pliocene (about three million to seven million years ago) in New Guinea. Although not formally described until the nineteenth century, the first living cassowary to reach Europe was transported to Amsterdam in 1597.

Physical characteristics

Cassowaries are large, long-legged, cursorial (running) birds, with distinctive head casques of trabecular (fibrous and cordlike) bone or calcified cartilage up to 7 in (18 cm) high. The colorful skin of the neck is bare, and long neck wattles adorn two species. The birds weigh 37–130 lb (17–59 kg). Cassowary wings are small, but the shafts of five or six primary feathers remain as long curved spines. Of the three toes, the inner one is armed with a long sharp claw, an effective weapon that is capable of disemboweling an adversary—even a human. Like the emu, the aftershaft of the cassowaries' coarse, black feathers is as long as the main shaft, so that each feather appears double—almost like extremely thick hair.

Male southern cassowary (*Casuarius casuarius*) on its nest with eggs. (Photo by Frith Photo. Bruce Coleman Inc. Reproduced by permission.)

Distribution

The eastern side of Cape York in northern Australia, throughout New Guinea, New Britain, Seram, and Aru, Japen, Salawati, and Batanta islands. Humans have introduced the birds to some of these islands, and their natural distribution is uncertain.

Habitat

Cassowaries are birds of the rainforest but often stray into adjoining eucalypt forest, palm scrub, tall grassland, savanna, secondary growth, and swamp forest.

Behavior

Except during courtship and egg-laying, cassowaries are solitary birds, seldom seen in groups, and then usually at some source of abundant food such as a fruiting tree. Each bird occupies a home range, moving around within it to find food. Each species has a characteristic territorial boom call, a threatening roar, given with the head bent down under the body. The birds are able to move quietly through the rainforest until disturbed. The noise of their hasty departure as they crash through the undergrowth is often the first indication of their presence. They swim well and have been recorded reaching an island a mile and a half (2.4 km) from the coast.

Feeding ecology and diet

Cassowaries feed on the fruits of rainforest trees and shrubs. The birds collect most of these from the ground, using their bill and sometimes their casque to unearth the fallen fruit from the litter of the forest floor. As the cassowaries travel, they disperse the seeds of these fruits throughout the rainforest, thus ensuring the continuance of more than 150 species of rainforest plants. In a study of the southern cassowary in north Queensland, Australia, the fruits of laurels, myrtles, and palms were most important. Opportunistically, the birds will take fungi, insects, and small vertebrates, but the basic diet consists of fruit. Disturbance of the forest can have serious consequences for cassowaries. Selective logging can remove almost all of one species of tree, so that the crop of fruit from that species is missing from the forest. If the fruit of this tree forms a significant part of the cassowary's diet, it will be left without food for weeks or months and suffer accordingly. Selective logging damages the bird's habitat more subtly than clear cutting, but equally seriously.

Reproductive biology

Cassowaries nest on a pad of vegetation on the ground. The clutch contains three to eight bright green or greenish blue eggs. Incubation lasts for 50–52 days, and is performed by the male alone. Chicks remain with the male for some months before gaining independence.

A male southern cassowary (*Casuarius casuarius*) on its nest with a 1-day-old chick. (Photo by Cliff Frith. Bruce Coleman Inc. Reproduced by permission.)

Conservation status

Disturbance of the forest is the main factor causing a decline in cassowary numbers. In Australia the cassowary population is estimated at 1,300 to 2,000 adults. Information on the status of New Guinea species is scant. The birds are so secretive—and the political situation so uncertain in West Irian—that any assessment is mere guesswork. It can only be said that the birds, or signs of them, can still be found whenever they are sought.

Significance to humans

Although they do not breed well in zoos, many cassowaries are kept in New Guinea villages. They are caught as chicks and raised to be killed and eaten when mature. Some of these captive birds have caused serious injury, even death, to village people tending them. They attack unexpectedly, slashing with powerful forward kicks, tearing the bodies of opponents with the long sharp claws of the inner toes with such accuracy that they are much feared.

1. Bennett's cassowary (*Casuarius bennettii*); 2. One-wattled cassowary (*Casuarius unappendiculatus*); 3. Southern cassowary (*Casuarius casuarius*). (Illustration by Marguette Dongvillo)

Species accounts

Southern cassowary
Casuarius casuarius

TAXONOMY
Casuarius casuarius Linnaeus, 1758, Seram.

OTHER COMMON NAMES
English: Double-wattled cassowary, two-wattled cassowary, Australian cassowary, kudari; French: Casoar à casque; German: Helmkasuar; Spanish: Casuario Común.

PHYSICAL CHARACTERISTICS
50–67 in (127–170 cm); female 128 lb (58 kg), male 64–75 lb (29–34 kg). Distinguished from the other cassowaries by having two wattles hanging from the neck. The bare skin of the head and neck is vividly colored in blue and red, and the legs are gray-green to gray-brown. The species has an especially long inner toenail or spike up to 5 in (12 cm) in length. Chicks are longitudinally striped with black, brown, and cream, and they have a chestnut head and neck for their first three to six months. Immatures have dark brown plumage and small casques, acquiring their colorful necks toward the end of their first year, and glossy adult plumage in about three years.

DISTRIBUTION
The Australian populations are all north of Townsville, Queensland, on the eastern side of Cape York. It is widespread in southern, eastern, and northwestern New Guinea, the Aru Islands, and Seram. The population on Seram has probably been introduced.

HABITAT
The southern cassowary lives mainly in lowland rainforest, below 3,600 ft (about 1,100 m).

BEHAVIOR
Although usually shy, some birds will become tame enough near settlements to approach places where food is regularly put out for them. Adults are territorial, no more than two associating together, except that the chicks stay with their father for about nine months.

FEEDING ECOLOGY AND DIET
The southern cassowary feeds on the fallen fruits of rainforest trees, fungi, and a few insects and small vertebrates.

REPRODUCTIVE BIOLOGY
In Australia the southern cassowary breeds in the winter—June and July—coinciding with the abundance of forest fruit, especially laurels (of the family *Lauraceae*). The nest, on the ground, is often close to the roots of a large tree, and the clutch consists of up to four lime green eggs. Males and females hold separate territories except for a few weeks at laying time. Incubation, by the male alone, 47–61 days, with variation thought to be a response to ambient temperature. Polyandrous females may take on another male or two before mating season ends, providing a clutch of eggs for each of her partners. The chicks stay with the male for up to nine months.

CONSERVATION STATUS
The status of the southern cassowary is uncertain. It requires large areas of undisturbed rainforest to flourish. As these are logged or disturbed by roadmaking and settlement, the bird's future is put at risk. Some are killed on the roads. Feral animals such as pigs and dogs disturb the nests in their search for eggs, causing the population to shrink. In New Guinea the bird is hunted and snared for food, but while large tracts of forest remain, it is secure.

SIGNIFICANCE TO HUMANS
Both in Australia and New Guinea the southern cassowary is incorporated into the mythology of the indigenous peoples, but it is still hunted by them, and the chicks captured, to be kept in pens in the villages until they are large enough to eat. ◆

Bennett's cassowary
Casuarius bennettii

TAXONOMY
Casuarius bennettii Gould, 1857, New Britain.

OTHER COMMON NAMES
English: Dwarf cassowary, little cassowary, mountain cassowary; French: Casoar de Bennett; German: Bennettkasuar; Spanish: Casuario Menor.

Casuarius bennettii

Resident

PHYSICAL CHARACTERISTICS
Height 39–53 in (99–135 cm); weight 39 lb (about 18 kg). A small cassowary with a flat, low casque and a less colorful neck than the other species. A distinctive form lives on the west side of Geevink Bay, West Irian, and may merit recognition as a species, *C. papuanus*.

DISTRIBUTION
New Guinea, New Britain, and Japen Island.

HABITAT
Lives in forest and secondary growth, favoring hilly and mountainous country to 10,800 ft (3,300 m). On New Britain, where other species are absent, it lives in lowland forest as well.

BEHAVIOR
Usually solitary or in small family groups, traversing steep slopes and thick vegetation. Its call is higher pitched than that of the other species.

FEEDING ECOLOGY AND DIET
Bennett's cassowary feeds mainly on fallen fruits in the rainforest but also takes fungi, insects, and small vertebrates.

REPRODUCTIVE BIOLOGY
The clutch consists of four to six eggs. Incubation 49–52 days.

CONSERVATION STATUS
Not threatened. Although it is hunted extensively it remains widespread at low densities.

SIGNIFICANCE TO HUMANS
Widely kept as a pet and, when small, traded between localities. ◆

One-wattled cassowary

Casuarius unappendiculatus

TAXONOMY
Casuarius unappendiculatus Blyth, 1860, aviary in Calcutta.

OTHER COMMON NAMES
English: Northern cassowary; French: Casoar unicaronculé; German: Einlappenkasuar; Spanish: Casuario Unicarunculado.

PHYSICAL CHARACTERISTICS
Height 65–69 in (165–175 cm); weight females 128 lb (58 kg); males 81 lb (about 37 kg). A large cassowary with coarse black plumage, a tall casque, a colorful neck, and one central wattle.

DISTRIBUTION
Northern New Guinea, from western Vogelkop, West Irian, to Astrolabe Bay, Papua New Guinea, and on Satawati, Batanta, and Japen islands.

HABITAT
Mostly lowland areas of rainforest and swamp forest, up to 1,600 ft (490 m).

BEHAVIOR
Assumed to be similar to other cassowaries.

FEEDING ECOLOGY AND DIET
Feeds on fallen forest fruits.

REPRODUCTIVE BIOLOGY
Birds in breeding condition have been collected in May and June, but nothing else has been reported about its breeding.

Casuarius unappendiculatus

Resident

CONSERVATION STATUS

The status of the cassowary is uncertain. It requires large areas of undisturbed rainforest to flourish. It is hunted and snared for food, but where large tracts of forest remain, it is secure.

SIGNIFICANCE TO HUMANS

The cassowary is incorporated into the mythology of the indigenous peoples, but it is still hunted by them, and the chicks captured, to be kept in pens in the villages until they are big enough to eat. ◆

Resources

Books

Coates, B. J. *The Birds of Papua New Guinea.* Alderly, Australia: Dove, 1985.

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

del Hoyo, J., A. Elliott, and J. Sargatal, eds. *Handbook of the Birds of the World.* Vol. 1, *Ostrich to Ducks.* Barcelona: Lynx Edicions, 1992.

Marchant, S., and P. J. Higgins. *Handbook of Australian, New Zealand and Antarctic Birds.* Vol. 1, *Ratites to Ducks.* Oxford: Oxford University Press, 1990.

Periodicals

Crome, F. H. J. "Some Observations on the Biology of the Cassowary in Northern Queensland." *Emu* 76 (1976): 8–14.

Davies, S. J. J. F. "The Natural History of the Emu in Comparison with That of Other Ratites." *Proceedings of the Sixteenth International Ornithological Congress* (1976): 109–20.

Organizations

Birds Australia. 415 Riversdale Road, Hawthorn East, Victoria 3123 Australia. Phone: +61 3 9882 2622. Fax: +61 3 9882 2677. E-mail: mail@birdsaustralia.com.au Web site: <http://www.birdsaustralia.com.au>

Other

Bredl, Rob. "Cassowaries." *Barefoot Bushman.* 5 Dec. 2001 <http://www.barefootbushman.webcentral.com.au/cassowaries.htm>

"The Cassowary." *The Living Museum: Wet Tropics.* Wet Tropics Management Authority Official Web Site. 5 Dec. 2001 <http://www.wettropics.gov.au/lm/The_Cassowary.htm>

"Double-wattled cassowary." *Zoo Discovery Kit.* Los Angeles Zoo. 5 Dec. 2001 <http://www.lazoo.org/learnfiles/ZooDiscoveryKit/Cassowaryfacts.html>

S.J.J.F. Davies, ScD

Emus
(Dromaiidae)

Class Aves
Order Struthioniformes
Suborder Casuarii
Family Dromaiidae

Thumbnail description
Large, flightless birds with tiny wings, three toes, and brown-black plumage

Size
60–75 in (150–190 cm); 75–110 lb (35–50 kg)

Number of genera, species
1 genus; 3 species

Habitat
Forest, woodlands, savanna, heath, and grasslands

Conservation status
Extinct: 2 species; Not threatened: 1 species

Distribution
Continental Australia and, formerly, Tasmania, King, and Kangaroo Islands

Evolution and systematics

Emus belong to the group of large, flightless birds known as the ratites that have in common massive, muscular legs, small wings, and a distinctive palate. Their inability to fly is due to the lack of a keel to the sternum, which in flying birds serves as the attachment point of flight muscles. The term "ratites" is derived from the Latin "ratis" for "raft", a boat without a keel. The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Whereas it used to be thought that the ratites had a southern origin, in the old continent of Gondwana, new fossil evidence has shown flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, 40–70 million years ago. The present Southern Hemisphere distribution of the ratites probably results from the spread of flying ancestors of the group from the north. The first evidence of ratites in Australia comes from the Eocene and the first recognizable Dromaiidae from the Miocene, 20 million years ago. The emu, *Dromaius novaehollandiae*, appears in the Pleistocene, only 2 million years ago.

Physical characteristics

Emus are large, cursorial, flightless birds, with long, scaly legs, three toes, and no preen gland. Weighing 51–120 lb (23–55 kg) and standing 6.5 ft (2 m) tall, emus are second only to ostriches in bird size. Although emus usually walk, their long, muscular legs are adapted to running, and they can run up to 30 mph (48 km/h), reaching strides of 9 ft (2.7 m) long. Their plumage is dark brown just after the annual molt, but fades during the year to pale brown. The wings are small, only one tenth the length of the body, and are hidden by the plumage. The main shaft and aftershaft of the feathers are equal in length so that every feather appears double. Pale blue skin shows clearly through the sparse feathers of the long neck. Females are slightly larger than males, weighing 90 lb (41 kg) versus male weights of 80 lb (36 kg). The females have a stronger blue coloration on the bare skin of the neck and head.

The sexes can be further distinguished during the laying period. The hen molts before laying and is a dark bird at this time, whereas the male does not molt until he is incubating,

Emu (*Dromaius novaehollandiae*). (Illustration by Patricia Ferrer)

and is paler than the female. New chicks are striped longitudinally with black, brown, and cream. They weigh 1 lb (0.5 kg) and stand approximately 5 in (12 cm) tall. Birds in their first year have black feathers covering their heads and necks, and the bare skin of the adult appears during their second year of life.

In the 15 ft (4.5 m) gut the gizzard is very muscular, capable of grinding, with the help of ingested stones, hard seeds and nuts. The emu bill is broad and soft, adaptable for grazing. The emu has a tracheal pouch, part of its air sac system, which is used for communication. The pouch is over 12 in (30 cm) long, very thin-walled, and allows the emu to produce deep guttural grunts. The pouch develops fully during breeding season and is used for courtship.

Distribution

Emus lived on Australia, Tasmania, and on King and Kangaroo islands. The only surviving species is confined to the Australian mainland. Because emus are nomadic and all members of the populations respond to the same environmental cues, large movements can occur. In Western Australia a fence has been built to protect the agricultural areas from emus moving towards the southern winter rains. Movements are often seen in Western Australia, where they can be detected on this fence, and also occur in eastern Australia, when emus swim the Murray River in large numbers.

Habitat

Emus are omnivores, at home in eucalypt forest and woodland, acacia woodland, savanna and heath, pine woodland, coastal heath, open spinifex and other tussock grassland, and in remnant vegetation along salt watercourses and on high alpine plains. They swim well and have been found on islands up to 3 mi (5 km) off the coast. Emus drink frequently, probably every day, taking 0.2–0.4 gal (600–1,500 ml) of water at a time. The chicks also need water, but usually obtain it from the leaves of succulent plants that they eat.

Behavior

Behavior has been studied only in the surviving species *Dromaius novaehollandiae*. Many accounts describe emus as flock birds but this is an artifact of observations on captive and semi-captive birds. In open country emus live as pairs in home ranges of about 12 mi^2 (30 km^2). They will defend significant parts of these areas, but usually try to avoid meeting other emus. In confrontations, they use kicking as a defense. The members of a brood may stay together for some months after they are deserted by their father, but will eventually break up and form pairs, rather than remain as a flock.

Emus have two basic calls, each of which can vary greatly in intensity. The grunt is given mainly by the male and has an aggressive message. The drum or boom is given mainly by females and has a territorial motivation. For the drum, the bird uses the tracheal pouch as a resonating chamber and the low frequency call carries 0.6 mi (1 km). Chicks have a piping call until their voice breaks, at about five months old, when a hole opens in their trachea, and communication with the air sac in the neck is established. Emus display by fluffing out their neck while they drum and, at other times, by stretching themselves up to their full height and grunting with vigor.

An emu (*Dromaius novaehollandiae*) tends its nest. (Photo by J.P. Ferrero/Jacana. Photo Researchers, Inc. Reproduced by permission.)

Emus (*Dromaius novaehollandiae*) in a field in the Grampian Mountains area of Australia. (Photo by Joy Spurr. Bruce Coleman Inc. Reproduced by permission.)

Feeding ecology and diet

Emus feed on nutritious parts of plants, fruits, seeds, flowers, and green shoots. They also take grasshoppers, beetles, and caterpillars, often in great quantities. In order to grind up hard material, emus eat pebbles and stones. Individual stones may weigh 0.1 lb (45 g) and individual gizzards may contain 1.6 lb (745 g) of mineral material. Experiments in a zoo, where emus were fed marbles, showed that such hard materials could be retained in the gizzard for over 100 days. It was thought that this might be a useful method of marking the birds, getting them to eat marbles of different colors at different sites, but the method failed because the bird's bill was too weak to pick up the marbles. Emus also eat quantities of charcoal, but the function of this material is unknown. Emus exhibit very strong specific search images, concentrating on one food even though alternative foods are readily available. They also move great distances searching for food.

Reproductive biology

Reproductive biology has been studied only in the surviving species *D. novaehollandiae*. In southern Australia emus usually lay in autumn, on a platform 3.3 ft (1 m) in length consisting of sticks, grass, and debris on the ground. The clutch varies with the rainfall, from eight to 20 eggs, which are dark green and have a pimply texture. Each egg weighs 1.5 lb (0.7 kg), is 5–6 in (13–15 cm) high, and the shells are 0.03 in (0.8 mm) thick. Incubation is by the male alone, although in captivity hens have been observed to sit for short periods. The male chases the female from the nest when the clutch is completed; she may mate with another male, move away on migration, or remain in the territory, defending it for some weeks. Wild males do not leave the vicinity of the nest, unless disturbed, and do not eat, drink or defecate during incubation. They lose 10–20 lb (5–9 kg) during this period. The chicks hatch after about 56 days, often over four days, and the male then leaves the nest area with them. They stay with their father for 5–7 months. Emus can lay at a year old, but most do not breed until they are two. Wild birds live only six or seven years, although captive ones may live much longer. Under captive conditions some males will have two mates, but this is rare in the wild.

Conservation status

The emu is secure on the Australian mainland and has been reintroduced to Tasmania. The Tasmanian emu, a subspecies of *D. novaehollandiae*, died out in 1865, and the dwarf species *D. ater* of King Island and *D. baudinianus* of Kangaroo Island were exterminated by human activity before 1810 and 1827 respectively. Fears have long been expressed for the survival of the emu on mainland Australia. In fact the bird is surviving well and will continue to do so while two thirds of Australia is unoccupied or used only as rangeland. It seems to be one of those species that can sustain very large population fluc-

An emu (*Dromaius novaehollandiae*) drinking in western New South Wales, Australia. (Photo by Jen and Des Bartlett. Bruce Coleman Inc. Reproduced by permission.)

tuations. On an area of 1,000 mi^2 (2,500 km^2) in Western Australia, the number of birds fluctuated between five and 970 over ten years. Estimates of the total population of emus in Australia vary from half to one million. Emus are vulnerable as eggs and hatchlings. Buzzards eat the eggs, and young emus are hunted by dingoes, eagles, non-native foxes, dogs, and cats.

Significance to humans

The emu is the national bird of Australia and appears on that country's coat of arms. For the Australian Aborigines the emu was as central to their existence as was the American buffalo to Native Americans. The emu provided food, and their fat and organs were also used for medicine. The bird was incorporated into their rituals and mythology. Emus were killed for meat by early European settlers. Later emus damaged crops in some areas, leading to organized campaigns to eradicate the birds, including the brief 1932 "emu war" in which machine guns were used. Bounties were paid on their heads in some areas, but recently fences have been used to keep emus out of areas where they might cause damage. Europeans have attempted to farm emus, because they reproduce well in captivity and grow fast, but so far have been unable to establish stable markets for any commercially viable quantity of product. Emu farming began in Australia in the 1970s. The insular species were killed for food by settlers, sealers, and whalers until they became extinct.

Species accounts

Emu
Dromaius novaehollandiae

TAXONOMY
Casuarius n. hollandiae Latham, 1790, New Holland (=Sydney, Australia).

OTHER COMMON NAMES
French: Émeu d'Australie; German: Emu; Spanish: Emú.

PHYSICAL CHARACTERISTICS
60–75 in (150–190 cm); female 57–106 lb (26–48 kg), male 39–103 lb (18–47 kg). The plumage is brown, sometimes ticked, the feathers long and shaggy.

DISTRIBUTION
Away from settled areas, the emu can be seen anywhere in Australia, but it visits the arid zone only when good rains have fallen there.

HABITAT
Emus are able to live in all types of native Australian vegetation.

BEHAVIOR
Emus live as pairs in large territories; young birds remain with their male parent for about seven months, and may then form small flocks until maturity.

FEEDING ECOLOGY AND DIET
The emu feeds on nutritious parts of plants, fruits, seeds, flowers, and green shoots.

REPRODUCTIVE BIOLOGY
Emus breed as pairs in natural conditions, the female laying up to 20 eggs that she leaves the male to incubate. The male also guards the chicks for about seven months.

CONSERVATION STATUS
Not threatened. The emu is secure in mainland Australia.

SIGNIFICANCE TO HUMANS
The emu has been seen as a pest in some areas and elsewhere as a potential farm animal from which meat, leather and fat can be harvested. ◆

King Island emu (extinct)
Dromaius ater

TAXONOMY
Dromaius ater Vieillot, 1817, King Island, Tasmania.

OTHER COMMON NAMES
English: Black emu; French: Émeu noir; German: Emu King Island; Spanish: El Emú de King Island.

PHYSICAL CHARACTERISTICS
Height 55 in (140 cm); 51 lb (c. 23 kg). A small, black emu, with grayish juveniles and striped chicks.

DISTRIBUTION
King Island, Tasmania.

HABITAT
Not known.

BEHAVIOR
Not known.

FEEDING ECOLOGY AND DIET
Ate berries, grass, and seaweed.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Extinct.

SIGNIFICANCE TO HUMANS
Source of food to sealers and settlers. ◆

Kangaroo Island emu (extinct)
Dromaius baudinianus

TAXONOMY
Dromaius baudinianus Parker, 1984, Kangaroo Island, South Australia.

OTHER COMMON NAMES
English: Dwarf emu; French: Ému de Baudin; German: Emu Kangaroo Island; Spanish: El Emú de Kangaroo Island.

PHYSICAL CHARACTERISTICS
A small, black emu, slightly larger than the King Island emu.

DISTRIBUTION
Kangaroo Island, South Australia.

HABITAT
Not known.

BEHAVIOR
Not known.

FEEDING ECOLOGY AND DIET
Not known.

REPRODUCTIVE BIOLOGY
Not known.

CONSERVATION STATUS
Extinct.

SIGNIFICANCE TO HUMANS
Source of food to sealers and settlers. ◆

Resources

Books

Bird, David M. *The Bird Almanac: The Ultimate Guide to Essential Facts and Figures of the World's Birds.* Buffalo: Firefly Books, 1999.

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

del Hoyo, J., A. Elliot, and J. Sargatal, eds. *Ostrich to Ducks.* Vol. 1, *Handbook of the Birds of the World.* Barcelona: Lynx Edicions, 1992.

Marchant, S., and P. J. Higgins. *Ratites to Ducks.* Vol 1, *Handbook of Australian, New Zealand and Antarctic Birds.* Oxford: Oxford University Press, 2001.

Whitfield, P., ed. *The MacMillan Illustrated Encyclopedia of Birds.* New York: Collier Books, 1988.

Periodicals

Davies, S. J. J. F. "The food of emus." *Australian Journal of Ecology* 3 (1978): 411–22.

Davies, S. J. J. F. "Nomadism in response to desert conditions in Australia." *Journal of Arid Environments* 7 (1984): 183–95.

Grice, D., G. Caughley, and J. Short. "Density and distribution of emus." *Australian Wildlife Research* 12 (1985): 69–73.

Organizations

Birds Australia. 415 Riversdale Road, Hawthorn East, Victoria 3123 Australia. Phone: +61 3 9882 2622. Fax: +61 3 9882 2677. E-mail: mail@birdsaustralia.com.au Web site: <http://www.birdsaustralia.com.au>

Emu Farmers Federation of Australia. c/o Secretary, Arthur Pederick, P.O Box 57, Wagin, Western Australia 6315 Australia. Phone: +61 8 9861 1136.

S. J. J. F. Davies, ScD

Kiwis
(Apterygidae)

Class Aves
Order Struthioniformes
Suborder Apteryges
Family Apterygidae

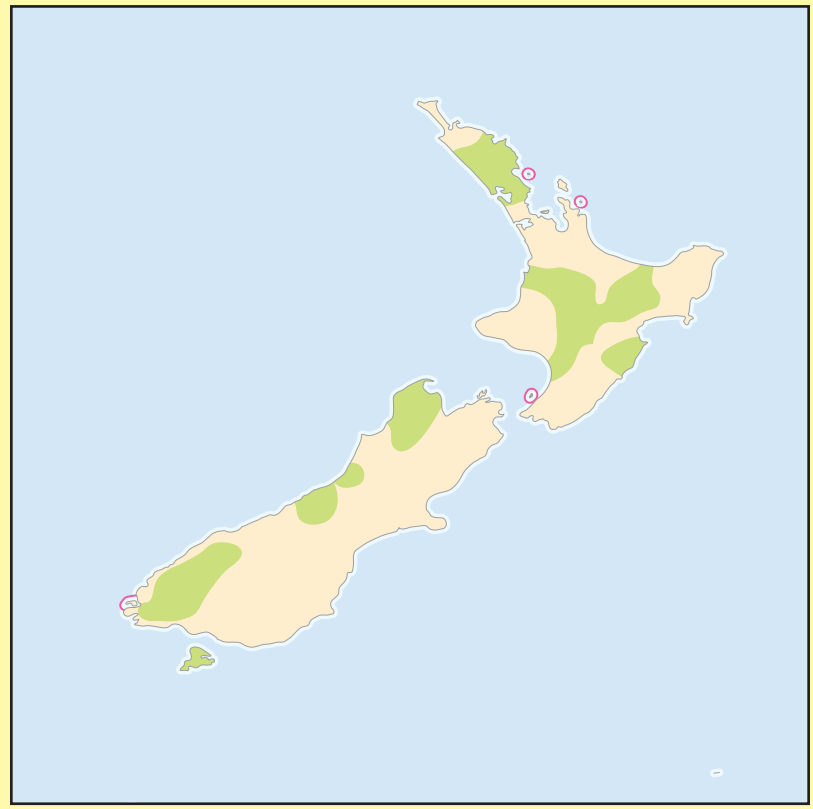
Thumbnail description
Chicken-sized birds, the smallest of the ostrich-like birds (ratites); only ratite with four toes; stout legs and feet, vestigial wings, long and curved bill with nostrils near tip; brown-black "hair-like" plumage

Size
14–22 in (35–55 cm); 2.6–8.6 lb (1.2–3.9 kg)

Number of genera, species
1 genus; 3 species

Habitat
Sub-tropical and temperate forest, woodlands, coastal heath, pasture, and tussock grasslands

Conservation status
Endangered: 2 species; Not threatened: 1 species



Distribution
New Zealand

Evolution and systematics

Kiwis (genus *Apteryx*) belong to the group of large, flightless birds known as the ratites that have in common the lack of a keel on the sternum and a distinctive palate. The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Whereas it used to be thought that the ratites had a southern origin, in the old continent of Gondwana, new fossil evidence has shown flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, 40–70 million years ago. The present Southern Hemisphere distribution of the ratites probably results from the spread of flying ancestors of the group from the north. Anatomical evidence suggests that the kiwis' closest relatives were the extinct moas of New Zealand. Biochemical evidence is conflicting.

Physical characteristics

Kiwis are medium-sized, flightless birds, with stout legs, four toes, and no preen gland. They weigh 2.6–8.6 lb (1.2–3.9 kg). The bill is long, pliable, and sensitive to touch, and the nostrils are lateral at the tip. The eye interior has a much-reduced pectin, which normally serves to supply nutrients and oxygen to the retina and tends to be smaller in nocturnal birds. The feathers have no aftershaft and lack barbules (hooks on the barbs); therefore, the feathers are loose and project out much like coarse hair. There are large vibrissae, stiff feathers that usually have tactile function, around the gape, and there are 13 flight feathers, which are only a little stronger than the other feathers. The second finger is absent. There is no tail, only a small pygostyle (similar to a tailbone). The legs are strong but short, and the claws are sharp. The gizzard is weak. The caeca, which aid in digestion, are long and narrow. The young are colored like the adults but with softer plumage.

Distribution

Kiwis live on the North and South Islands of New Zealand and on Stewart Island. Although formerly widespread, only the brown kiwi (*Apteryx australis*) remains common, inhabiting several areas of North Island, some parts of South Island and most of Stewart Island. The other two species are confined to a few island sanctuaries and a small area of the northwest of South Island.

Brown kiwis (*Apteryx australis*) are largely nocturnal, and roost in sheltered areas at ground level during the day. (Photo by I. Visser/VIREO. Reproduced by permission.)

Habitat

Kiwis favor subtropical and temperate podocarp and beech forest, but settlement and forest clearing has left little forest for them to use. The brown kiwi has successfully occupied plantations, even of exotic pines, as well as the fringes of farmland, sub-alpine scrub and tussock grassland. The other two species are now confined to mountainous regions and islands, but in the past they were probably widespread in podocarp forests of both lowlands and highlands.

Behavior

Most kiwis are nocturnal, but the Stewart Island form of the brown kiwi is active during the day. They form monogamous pairs, probably lasting for life, moving about their territory singly and indulging in frequent calling, sometimes as duets between males and females. Territories seem to be maintained by calling, although aggressive behavior has been observed, involving vigorous encounters and chases at territorial boundaries. Territory sizes vary with locality and species from 5 to 111 acres (2–45 ha). Only the weak, shrill "kee wee" or "kee kee" whistles of the male and the hoarse "kurr kurr" of the female betray their presence. Males call more frequently than females. Both sexes call in an upright position, with bill raised and neck and legs fully stretched. Apart from calling, few displays accompany mating, which may last 1–2 minutes. Kiwis roost alone during daylight in shallow burrows and sheltered places, mostly at ground level.

Feeding ecology and diet

Kiwis feed on invertebrates, especially earthworms, spiders, and insects from the ground and litter. They take some plant material, but the quantity is insignificant compared with their intake of animal food. The sense of smell of kiwis is very acute so that most of their food is located by scent. Sight and sound play only minor roles in food searching. While probing for hidden worms and insect larvae in the soft forest floor, they use their long bills in the same manner as snipes (family Scolopacidae). The bill is thrust deeply into the ground when feeding and the resulting characteristic holes betray the presence of the birds. Distended gizzards may contain 2 oz (50 g) of material. As in other birds, their gizzards also contain some grit that helps to grind up the food.

Reproductive biology

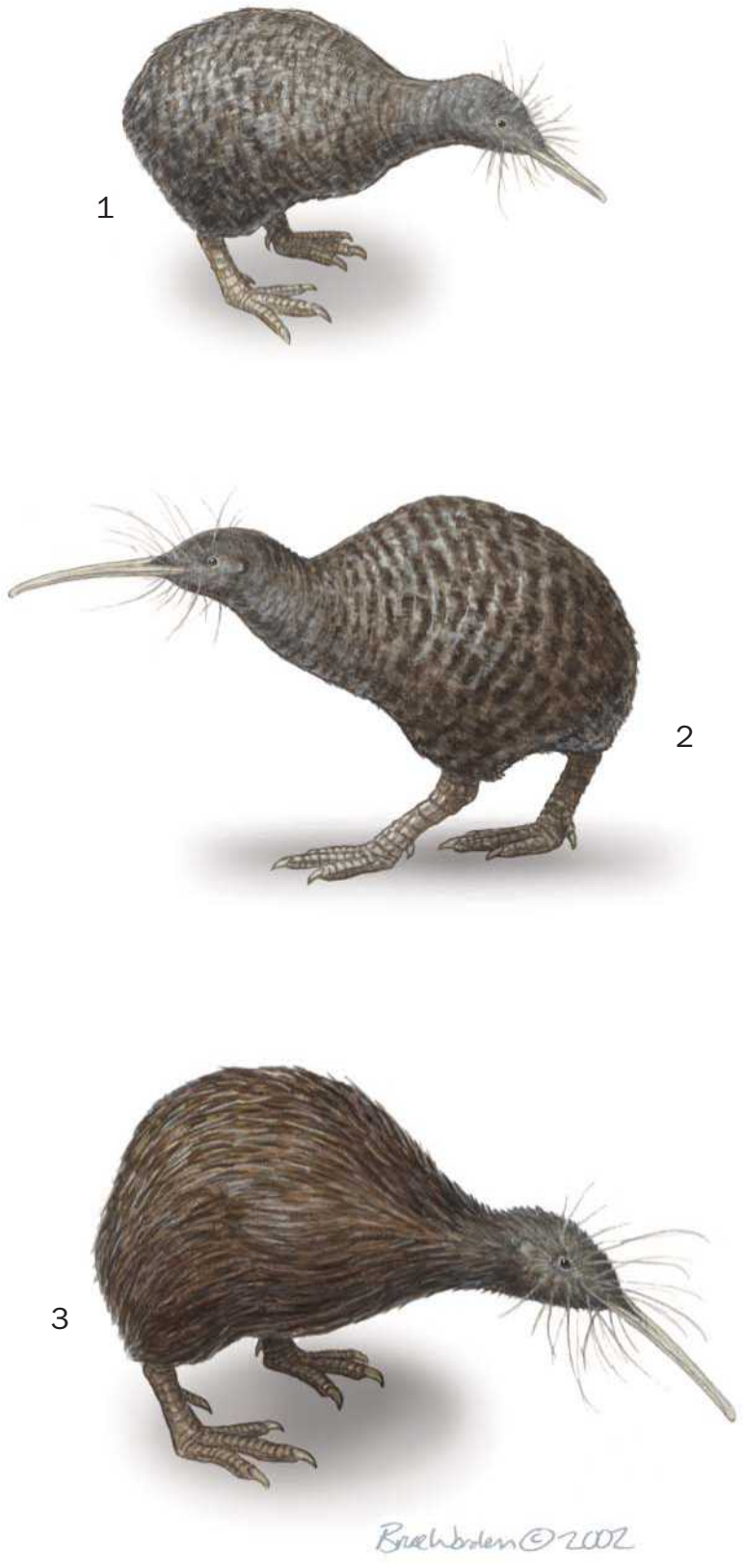
Kiwis are unique in the bird world in having paired functional ovaries. In most other birds, only the left ovary is functional, although some individuals of a few raptor species also have a functional right ovary. In kiwis, both ovaries function regularly, but only the left oviduct is developed, the eggs from both ovaries passing down it. The eggs are of great size, up to 1 lb (450 g), each egg a fifth to a quarter the weight of the female. Often only one egg is laid, but some two-egg clutches have been found. It may be 20–60 days between the laying of eggs in two-egg clutches. For its nest, the bird digs a burrow or selects and remodels a den in some sheltered spot. Incubation is by the male, except in the great spotted kiwi (*A. haastii*), where both sexes regularly incubate the egg(s). The incubation period lasts 63–92 days. The chick hatches in adult plumage, remains inactive in the nest burrow for some days while feeding on its yolk sac, and then emerges to feed independently.

Conservation status

New Zealand has no native mammals, but the introduction of rats, dogs, pigs, and mustelids (stoats and weasels) has caused severe predation on kiwis. Apart from the clearing of native forest, predation has been blamed for the decline of the populations of all three kiwi species. The effect has been worst on the spotted kiwis; the brown kiwi seems able to survive in spite of the presence of dogs and introduced mammals. The little spotted kiwi (*A. owenii*) is now confined to four island sanctuaries from which predators have been or are being removed. The great spotted kiwi population suffers from traps set to catch introduced possums; for example, up to half of some populations have fractured or amputated toes. Captive breeding and translocations are being undertaken by New Zealand conservation agencies.

Significance to humans

Kiwis are the national bird of New Zealand, but are of no other special significance to other people. In former times, Maoris used kiwi skins to make cloaks and they and the early European settlers hunted kiwis for food.



1. Little spotted kiwi (*Apteryx owenii*); 2. Great spotted kiwi (*Apteryx haastii*); 3. Brown kiwi (*Apteryx australis*). (Illustration by Bruce Worden)

Species accounts

Brown kiwi
Apteryx australis

TAXONOMY
Apteryx australis Shaw and Nodder, 1813, Dusky Sound, South Island, New Zealand.

OTHER COMMON NAMES
English: Common kiwi; French: Kiwi austral; German: Streifenkiwi; Spanish: Kiwi Común.

PHYSICAL CHARACTERISTICS
18–22 in (45–55 cm); female: 4.6–8.5 lb (2.1–3.9 kg), male: 3.6–6.1 lb (1.6–2.8 kg). Medium-sized, rotund, flightless bird, with no tail. Body cone-shaped, tapering to a small head with a long, slightly down-curved bill. Streaked rufous plumage, shaggy and hair-like, obscuring short wings that end in a claw. Female larger than male.

DISTRIBUTION
On North Island mainly in Northland and Taranaki, although still occurs in small pockets elsewhere. On South Island mainly in Fiordland, with small populations in Westland. Widespread on Stewart Island.

HABITAT
Subtropical and temperate forests and shrublands. Most common in dense forest but able to maintain populations in regenerating bush, pasture, and pine forest.

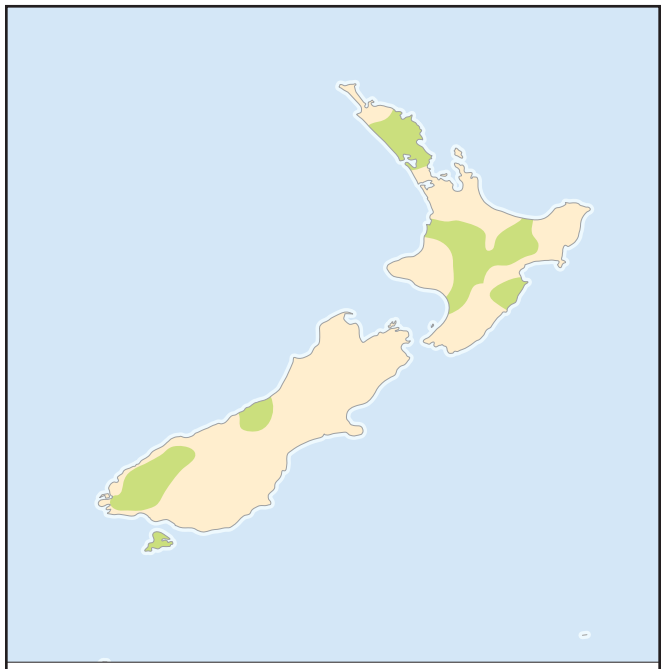
BEHAVIOR
Nocturnal, usually seen alone; roosts in dens or burrows by day. The name "kiwi" comes from the sound of one whistled call that has also been rendered as "ah-eel". Males call most often, with duets between partnered males and females at times.

FEEDING ECOLOGY AND DIET
The brown kiwi feeds on soil invertebrates such as earthworms, beetle larvae, snails, spiders, centipedes, and orthoptera. It uses its sense of smell to find food, probing ceaselessly into the ground, leaving characteristic cone-shaped holes in the substrate.

REPRODUCTIVE BIOLOGY
Live as monogamous pairs in territories of 12–106 acres (5–43 ha), depending on location. Nests are made in burrows, sheltered places, and beneath thick vegetation. The female lays one or two large eggs that the male incubates for up to 90 days. The young hatch in adult plumage and, after a few days in the nest, come out to feed independently. There is little evidence of parental care, but the chick may be found near its parents for up to a year.

CONSERVATION STATUS
Not threatened. Although the brown kiwi is the most common of the group, it suffers from attacks by dogs and is often caught in traps set for the introduced possum. Large populations live in Northland and on Stewart Island, but elsewhere fragmentation has reduced population sizes below sustainable levels.

SIGNIFICANCE TO HUMANS
The Maori formerly ate the birds and made cloaks from their skins. Apart from being New Zealand's national bird, the species is of no economic significance to humans now. ◆



Little spotted kiwi
Apteryx owenii

TAXONOMY
Apteryx owenii Gould, 1847, New Zealand.

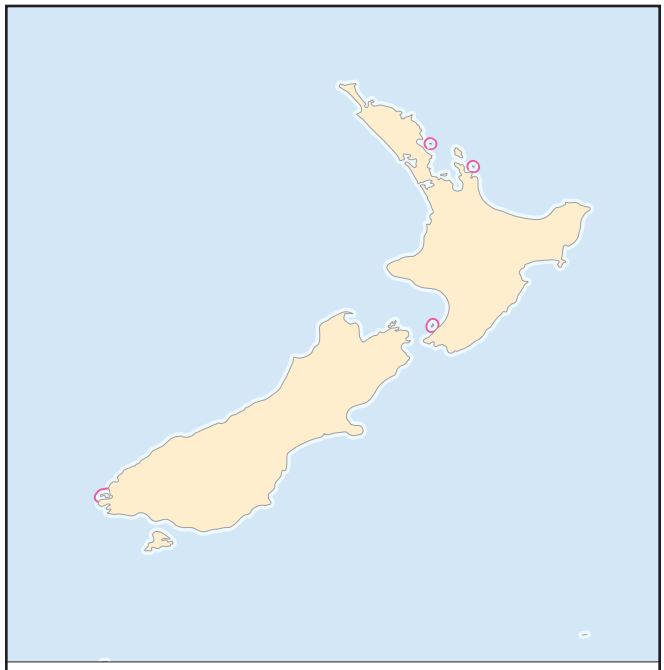
OTHER COMMON NAMES
English: Little gray kiwi; French: Kiwi d'Owen; German: Zwergkiwi; Spanish: Kiwi Moteado Menor.

PHYSICAL CHARACTERISTICS
Length 13.8–17.7 in (35–45 cm); males 2–2.9 lb (0.9–1.3 kg), females 2.2–4.2 lb (1.0–1.9 kg). Medium-sized, flightless, nocturnal bird with pale-mottled, gray, shaggy plumage. The body is pear-shaped with a long neck and bill.

DISTRIBUTION
Surviving on only four islands: Kapati, Red Mercury, Hen, and Long.

HABITAT
Evergreen, broadleaf forest and margins of forest up to 3,000 ft (1,000 m) with over 40 in (100 cm) annual rainfall. Favors wet forest, with rotten logs and dense undergrowth.

BEHAVIOR
Nocturnal, pairs hold territories of about 10 acres (4 ha). Pair formation in second year and maintained for life. Chases



Apteryx owenii

Resident

occur in defense of territory, but most displays are vocal, using high-pitched whistles that have distinct male and female versions.

FEEDING ECOLOGY AND DIET

Omnivorous, but eats mostly soil and litter invertebrates, such as earthworms, millipedes, larval beetles, as well as moths, crickets, and spiders, supplemented with some fruit.

REPRODUCTIVE BIOLOGY

Nest in burrows dug by the pair. Sometimes there is no nest material, but in other burrows some leaves and twigs have been gathered. Most clutches are composed of one egg, but about 15% have two. Only the male incubates, sitting for 63–76 days. The chick is tended (probably fed) for about four weeks after it hatches. Unlike the brown kiwi, the chick of the little spotted kiwi may stay in the nest for two to three weeks before emerging.

CONSERVATION STATUS

Endangered with a total population of about 1,000 individuals. Even on its island sanctuaries it suffers predation on its eggs from native rails (wekas) and rats.

SIGNIFICANCE TO HUMANS

None known. ◆

Great spotted kiwi

Apteryx haastii

TAXONOMY

Apteryx haastii Potts, 1872, Westland, New Zealand.

OTHER COMMON NAMES

English: Great gray kiwi; French: Kiwi roa; German: Haastkiwi; Spanish: Kiwi Moteado Mayor.

PHYSICAL CHARACTERISTICS

Length 17.7–19.7 in (45–50 cm); males 2.6–5.7 lb (1.2–2.6 kg), females 3.3–7.3 lb (1.5–13.3 kg). Medium-sized, flightless, nocturnal bird with pale, mottled-gray, shaggy plumage. The body is pear-shaped with a long neck and bill. Females larger than males, and with longer bills. Larger than the little spotted kiwi and about the size of the brown kiwi.

DISTRIBUTION

Two isolated populations in the northwest of South Island, in Nelson and Westland.

HABITAT

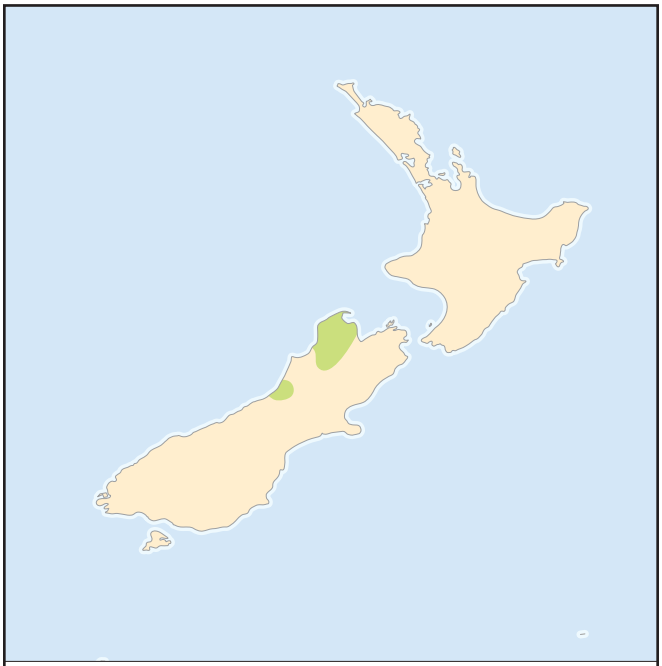
Densest population above 2,000 ft (700 m) in wet beech forest in mountain ranges running parallel to the coast. Also in tussock grassland, podocarp, and hardwood forests, and sometimes in coastal pasture.

BEHAVIOR

Nocturnal, pairs holding territories of about 49 acres (20 ha) or more. Most displays are vocal, using high-pitched whistles that have distinct male and female versions—the male shriller than the female. Roost in dens during the day, into which some vegetation is taken by the bird to form a small mat. A kiwi may have 100 dens in its territory, using a different one each day.

FEEDING ECOLOGY AND DIET

Omnivorous, but eats mostly soil and litter invertebrates, such as earthworms, millipedes, and larval beetles, as well as moths, crickets, and spiders, supplemented with some fruit. Crayfish



Apteryx haastii

Resident

are eaten when they leave flooded streams, and some food is taken above the ground when the bird can walk out along leaning branches.

REPRODUCTIVE BIOLOGY
Pairs maintained for life with some indication of polyandry in lowland populations. Mostly nest in natural hollows and sheltered places, but a few nests are in short burrows dug by the pair. Some moss lichen, leaves, and twigs are gathered to form a thick nest. Most clutches are composed of one egg, but two eggs have been reported. Both sexes incubate, usually the male by day and the female by night. The incubation period is not known.

CONSERVATION STATUS
Endangered, declining in lowland forests and vulnerable to traps set for possums and to attacks by dogs.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Books

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

Folch, A. "Apterygidae (Kiwis)." In *Handbook of the Birds of the World.* Vol. 1, *Ostrich to Ducks*, edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal. Barcelona: Lynx Edicions, 1992.

Marchant, S., and P. J. Higgins. *Ratites to Ducks.* Vol. 1, *Handbook of Australian, New Zealand and Antarctic Birds.* Oxford: Oxford University Press, 1990.

Reid, B., and G. R. Williams. "The Kiwi." In *Biogeography and Ecology in New Zealand*, edited by G. Kuschel. The Hague, 1975.

Periodicals

Wenzel, B. M. "Olfactory Sensation in the Kiwi and Other Birds." *Annals of the New York Academy of Sciences* 188 (1971): 183–93.

Organizations

Birds Australia. 415 Riversdale Road, Hawthorn East, Victoria 3123 Australia. Phone: +61 3 9882 2622. Fax: +61 3 9882 2677. E-mail: mail@birdsaustralia.com.au Web site: <http://www.birdsaustralia.com.au>

Ornithological Society of New Zealand. c/o Secretary, P.O. Box 12397, Wellington, North Island New Zealand. E-mail: OSNZ@xtra.co.nz Web site: <http://osnz.org.nz>

S. J. J. F. Davies, ScD

Moas
(Dinornithidae)

Class Aves
Order Struthioniformes
Suborder Dinornithes
Family Dinornithidae

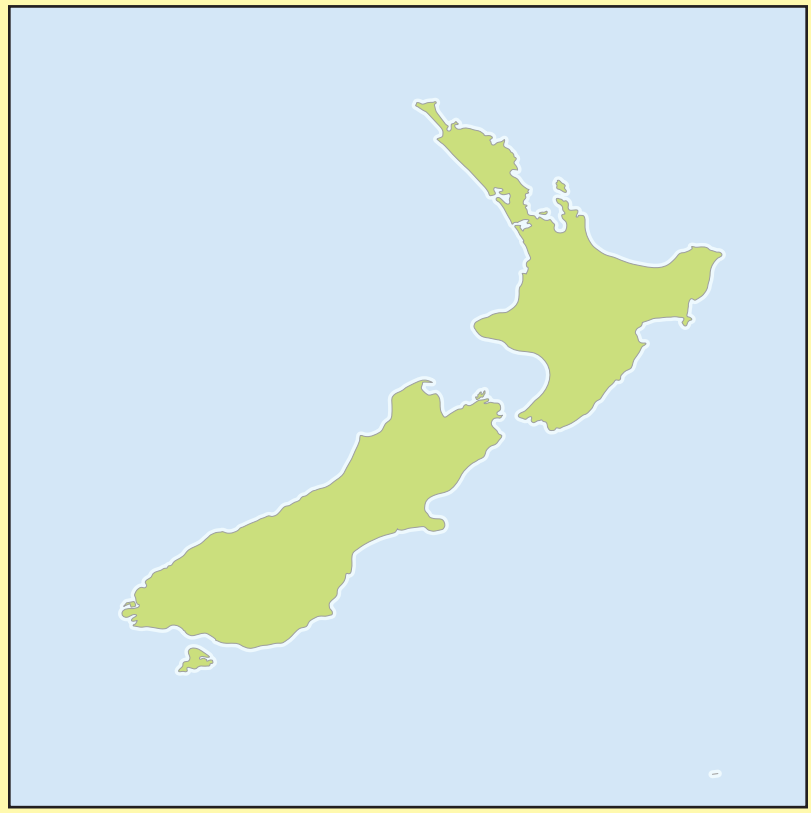
Thumbnail description
Large, flightless cursorial birds with no visible wings, long legs, long necks, and four toes

Size
3–12 ft (0.9–3.7 m); 48–506 lb (22–230 kg)

Number of genera, species
6 genera; 10 species

Habitat
Forest, woodland, heath, and grassland

Conservation status
Extinct



Distribution
New Zealand

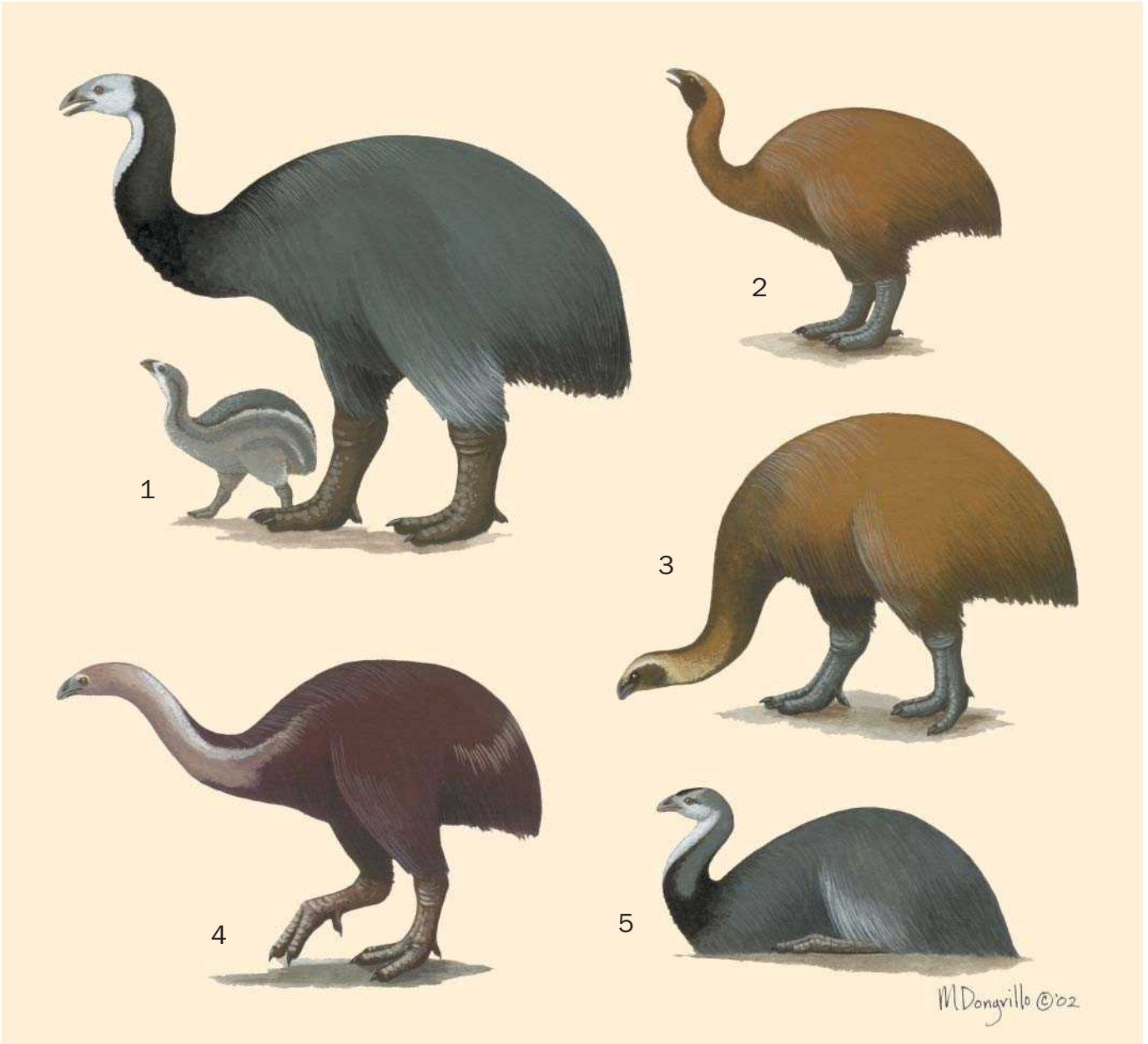
Evolution and systematics

Moas belong to the group of large, flightless birds known as ratites. Ratites have a distinctive palate, and a sternum (breastbone) with no keel, so there is no anchor for the strong musculature needed for powered flight. The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Ratites were once thought to have a southern origin in the ancient continent of Gondwana, but new fossil evidence shows that flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, 40–70 million years ago. The present Southern Hemisphere distribution of ratites probably resulted from the spread of flying ancestors of the group from the north.

The earliest remains of moas in New Zealand are from the Upper Pliocene, about 1.5 million years ago. By then they were recognizably moas, but it is thought that the two subfamilies—the tall, graceful Dinornithinae and the short, stout-bodied Anomalopteryginae—may be descended from two different flying ratites that invaded New Zealand during the Tertiary. Many different classifications have been proposed for moas; some authors list as many as 27 species, others only 10. The lower figure is adopted here, following a detailed review by Atholl Anderson, because many earlier classifications depended on small differences in subfossil bone size and shape that could be due to sexual dimorphism or age differences.

Physical characteristics

There are no accounts of living moas. All information is derived from subfossil material recovered from swamps, caves, and river beds. Moas were very large, flightless birds with long necks and long legs. Unlike surviving large ratites, the tibial bone of moa legs was longer than the tarsus, and they moved slowly. Except for bats, no mammals inhabited New Zealand, so moas had no predators before the Polynesians arrived and no need to flee swiftly. The height of the birds (to the back) was 3–12 ft (0.9–3.7 m) and they weighed 48–506 lb (22–230 kg). The three *Dinornis* species and *Pachyornis elephantopus* were the largest, weighing 257–506 lb (117–230 kg). Surviving feather and skin fragments indicate that, apart from the legs, the birds were fully feathered, although they had no visible wings. Each feather was double, with a well-developed aftershaft, and was brownish, sometimes with pale edging.



1. *Pachyornis elephantopus*; 2. *Euryapteryx curtus*; 3. *Euryapteryx geranoides*; 4. *Emeus crassus*; 5. *Pachyornis mappini*. (Illustration by Marguette Dongvillo)

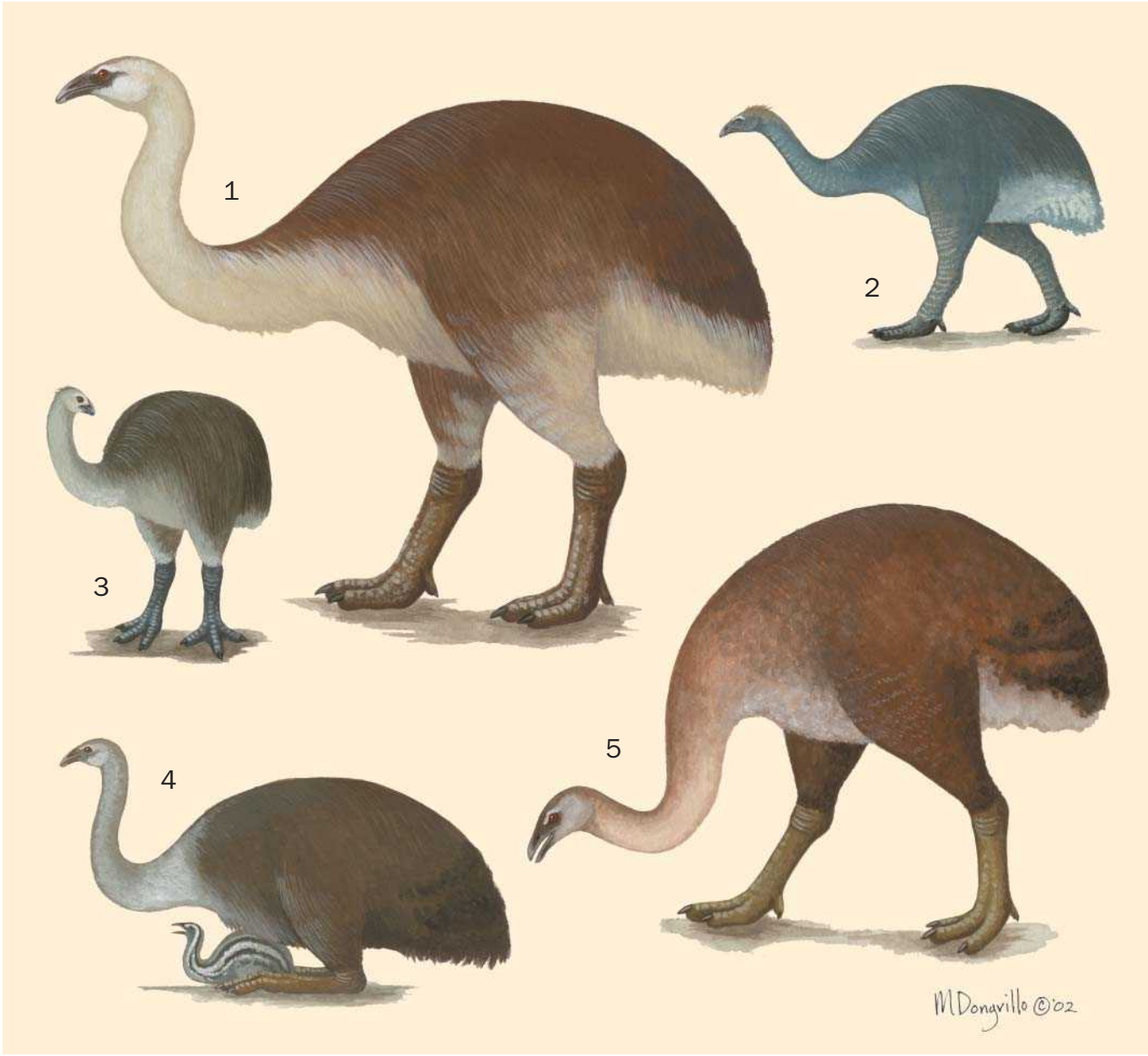
Evidence indicates that in at least some species females were larger than males.

Distribution

Moas lived only in New Zealand. Five species (*Anomalopteryx didiformis*, *Euryapteryx geranoides*, *Dinornis struthoides*, *D. novaezealandiae*, and *D. giganteus*) were common to North and South Island, two have been found only on North Island (*Euryapteryx curtus* and *Pachyornis mappini*), and three only on South Island (*Megalapteryx didinus*, *Emeus crassus*, and *P. elephantopus*). At least one species (*Euryapteryx geranoides*), and possibly two, also lived on Stewart Island. There is debate about the total numbers of moas, with estimates ranging from millions to thousands. Using the most recent evidence, Atholl Anderson has argued that if all 10 species were combined, there were probably only tens of thousands in total—twice as many in South Island as in North Island—with the greatest concentration on the eastern side of South Island.

Habitat

Moas apparently lived in all New Zealand environments, using coastal dunes, forest fringes, podocarp (seed-producing conifers) forests, beech forests on limestone, shrubland, and grassland up to 6,600 ft (2,000 m). *A. didiformis*, *D. struthoides*,



1. *Dinornis giganteus*; 2. *Megalapteryx didinus*; 3. *Anomalopteryx didiformis*; 4. *Dinornis struthoides*; 5. *Dinornis novaezealandiae*. (Illustration by Marguette Dongvillo)

and *D. novaezealandiae* lived in dense lowland conifer and broad-leaved forest, and beech forest. *M. didinus* lived only in high-altitude beech forest. *Emeus crassus*, *Euryapteryx* species, *Pachyornis* species, and *D. giganteus* lived in the lowlands—dunelands, forest fringes, and forest, shrub, and grassland mosaics.

Behavior

Most moas were probably diurnal, living in small groups rather than large flocks. There is no hard evidence about their daily lives.

Feeding ecology and diet

A number of moa gizzards have been found and analyzed, showing that the birds fed on plants, taking seeds, twigs, and leaves from different species. Nineteen gizzards from two different sites showed that the birds took plants that grew in the forest and those from open country, suggesting they often fed along the boundary between the two environments. About 80% of the material was twigs, but seeds and leaves were also abundant. It may be that the tough twigs stayed longer in the gizzard than other plants and were over-represented in the sample.

It is now clear that moas did not exist solely on ferns, as some early authors suggested, but used a number of different

plant species as food. Seeds of the shrub *Comprosma* and the tree *Podocarpus* were abundant, but 29 different species were represented in 19 samples. All gizzards contained pebbles, up to 11 lb (5 kg) in a large *Dinornis*. From the nature of these pebbles, which were the kinds of rock found where the gizzard was collected, it can be deduced that moas were sedentary. Had they been migratory or nomadic, pebbles in the gizzard would have included rocks of many kinds because such pebbles remain in the gizzard for months, and would have reflected different landscapes. More information will gradually come to light about the diversity of the moa diet, because the shapes and sizes of their bills differ considerably, suggesting that various species must have selected different foods.

Reproductive biology

Moas laid small clutches, perhaps only one egg. It is thought, on very slight evidence, that males incubated, as is the case in most other ratites, but nothing is known of their routines, not even the incubation period. Some supposed nests of sticks around scrapes in the ground have been found in caves and rock shelters associated with egg shell fragments. The eggs are large—up to 9 in (23 cm) long and 7.6 in (19.5 cm) wide—and green, at least in some species.

Conservation status

Extinct. The last moas probably died out in the seventeenth century.

Significance to humans

Moa is the Maori word for a group of large, flightless birds. A great deal of thought has been given to the interaction of Maoris and moas. More than 300 sites have been identified at which moas were butchered by Maoris, some (according to carbon dating) as old as A.D. 1000. The sites provide evidence that the Maoris killed and ate moas systematically. Some sites are very large, but Atholl Anderson has analyzed their location and size to show that they fall into two classes. Sites near the coast are adjacent to large rivers and usually contain remains of many moas. This suggests that expeditions were made up river and the birds brought downstream by boat for butchering. Small sites are mostly in the mountains, or where water transport would not be available, suggesting that they represent the catch of one hunting party, the birds being butchered on the spot and probably eaten there too. Moas would provide a very valuable protein resource in a land where other game was scarce.

The evidence of such extensive hunting has been used to suggest that moas were hunted to extinction. However, the Maoris also cleared the land, mainly by burning vegetation; such habitat alteration may have contributed significantly, perhaps fatally, to the extermination of many species. There are other puzzles, too. Many moa bones are found aggregated in beds of former and existing swamps. There is much to discover about the interactions between moas and Maoris. It is known that Maoris used moa skins as cloaks and carved tools from the bones. It is surprising, considering the significance the birds must have had, how little mythology about them has survived.

Resources

Books

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

Anderson, A. *Prodigious Birds, Moas and Moa-hunting in prehistoric New Zealand.* Cambridge: Cambridge University Press, 1989.

Periodicals

Anderson, A. "Habitat Preferences of Moas in Central Otago, A.D. 1000–1500, According to Palaeobotanical and Archaeological Evidence." *Journal of the Royal Society of New Zealand* 3 (1982): 321–36.

Rudge, M. R., ed. "Moas, Mammals and Climate in the Ecological History of New Zealand." *New Zealand Journal of Ecology* Supplement 12 (1989): 1–169.

Organizations

Ornithological Society of New Zealand. P.O. Box 12397, Wellington, North Island New Zealand. E-mail: OSNZ@xtra.co.nz Web site: <http://osnz.org.nz>

S. J. J. F. Davies, ScD

Ostriches
(Struthionidae)

Class Aves
Order Struthioniformes
Suborder Struthiones
Family Struthionidae

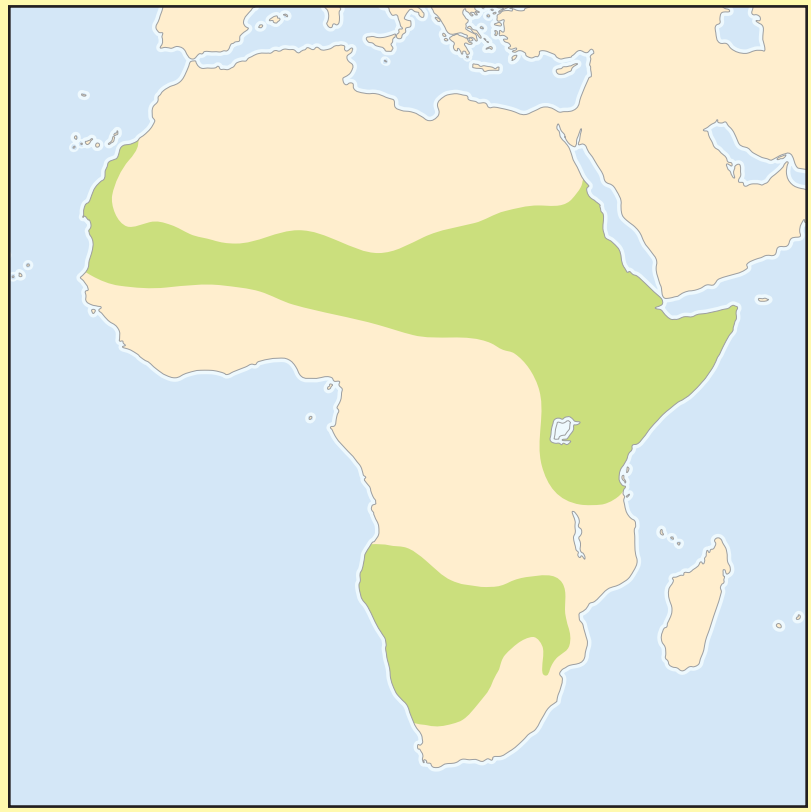
Thumbnail description
Very large flightless birds with large, loose-feathered wings, two toes, and black-and-white (male) or gray-brown (female) plumage

Size
5.7–9.0 ft (175–275 cm); 139–345 lb (63–157 kg)

Number of genera, species
1 genus; 1 species

Habitat
Open woodlands, savanna, arid shrubland, desert, and grasslands

Conservation status
Secure: 1 species



Distribution
Africa, excluding tropical forest belt adjacent to the equator

Evolution and systematics

The ostrich (*Struthio camelus*) belongs to the group of large, flightless birds known as ratites. Ratites have in common a distinctive palate and the lack of a bony keel to the sternum (breastbone), to which the powerful musculature required for flight would be attached.

Ratites were once thought to have a southern origin in the ancient continent of Gondwana, but recent fossil evidence discovered in North America and Europe shows that flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, 40–70 million years ago. The current Southern Hemisphere distribution of ratites was likely due to the spread of flying ancestors from the north.

The ostrich is the only living representative of suborder Struthiones, family Struthionidae. Eight extinct species all belonged to the same genus. Fossil bones and egg shells show that ostrich ancestors probably originated in the Eocene (40–55 million years ago) in the Asiatic steppes as small flightless birds. In the lower Pliocene (about 12 million years ago) they developed into gigantic forms that were distributed as far as Mongolia and, later, South Africa. The present-day ostrich is somewhat smaller and originated as a new species in the Pleistocene (one to two million years ago); some of its early remains were found at home sites of prehistoric humans.

Physical characteristics

A large bird, cursorial with long legs and neck. At 5.7–9 ft (1.8–2.8 m) and 139–345 lb (63–157 kg), the ostrich is the largest living bird. Males are larger than females. The head and about two-thirds of the neck are sparsely covered with short, hair-like, degenerated feathers, making the bird appear nude. The skin is variably colored, depending on the subspecies. The legs are particularly strong and long. The tarsus in sexually mature males has red horn plates; in sexually mature females they are black. The foot has two toes: a large, strongly clawed third toe and a weaker, generally clawless fourth (outside) toe. The first and second toes are absent. The feathers have no secondary shaft or aftershaft. There are 50–60 tail feathers. The wing has 16 primaries, four alular, and 20–23 secondary feathers. Wing feathers and rectrices have changed to decorative plumes.

Ostrich (*Struthio camelus*). (Illustration by Patricia Ferrer)

The penis-like copulatory organ is retractable and can be as long as 8 in (20 cm). Food passes through three stomach segments; the gut can be as long as 46 ft (14 m). The rectum is especially expanded, and the caecae—cul-de-sac-like structures at the lower end of the gastrointestinal tract—are about 28 in (70 cm) long. Urine is concentrated in the large cloaca but, in contrast to all other living birds, is secreted separately from the feces. Unlike other birds, ostriches have pubic bones that are fused toward the rear and support the gut. The wishbone is absent, and palate formation is different from that of other ratites. Sphenoid and palatal bones are unconnected.

Distribution

The ostrich formerly occupied Africa north and south of the Sahara, east Africa, Africa south of the rainforest belt, and much of Asia Minor. Its distribution has now shrunk to Africa south of the Sahara and parts of east Africa, but most existing populations are in game parks.

Habitat

The ostrich is an open-country bird. In northern Africa it lives in the dry beds of watercourses in broad valley bottoms and in desert-savanna plains, rarely above 300 ft (100 m). In eastern Africa it is in savanna; in southern Africa it is in open grassland with some shrubs. In southwest Africa its habitat is semidesert or true desert, with patches of open, stunted woodland.

Behavior

An ostrich population often becomes a mixed society of flocks, families, and individuals of all age groups whose composition changes with the season. In a series of ostrich sightings in east Africa, 49% of the sightings were of single birds, 35% were of two birds together, and 16% were of groups of three to five birds. In rainless periods, when wandering, in common grazing grounds, and at watering places, they form peaceful aggregations of hundreds of birds, but individual flocks remain recognizable. Social contacts between birds of different groups are initiated when one bird approaches another in a submissive posture, with head lowered and tail down. Often a family of one herd adopts the chicks or young of another. Single cocks may join together and form "schools" of half-grown ostriches, which then wander about for days or weeks. For communal sand baths, each flock seeks out a sandy depression.

The ostrich is diurnal but may sometimes be active on moonlit nights. It loafs and roosts by squatting on the ground, and is most active early and late in the day. Its normal walking pace is 2.5 mph (4km/hr), but when running in alarm it can reach speeds of 45 mph (70 km/hr). It is very vigilant when feeding, continually raising its head to look around. It feeds more frequently in small flocks than in large ones. The territorial call of the male ostrich is a roar, far-carrying and

A male ostrich (*Struthio camelus*) displays his courting dance. (Photo by Leonard Lee Rue, III. Photo Researchers, Inc. Reproduced by permission.)

Ostrich (*Struthio camelus*) drinking at Kalahari Gemsbok National Park, South Africa. (Photo by Nigel J. Dennis. Photo Researchers, Inc. Reproduced by permission.)

resembling the roar of a lion. A soft "booh" is used as a contact call and hisses are given in threat displays.

Feeding ecology and diet

The ostrich grazes on green grass and browses on shrubs, succulents, and seeds. A few animals are taken, particularly when swarms of insects, such as the plague locust, are active.

Reproductive biology

Males are polygynous, taking more than one mate at a time. In the initial phase of courtship, the cock displays by alternating wing beats in front of the flock to attract or separate out the chosen hens. He chases yearlings away with the help of his major hen. Then the birds move together to the breeding territory, an area of 1–6 mi^2 (2–14 km^2).

During the courtship of a specific hen, the cock always drives her away from the others. Both move to a remote spot and graze, while their behavior becomes increasingly synchronized. The feeding evidently becomes secondary and evolves into a ritual that further synchronizes the partners' behavior. The smallest disruption in their movements leads promptly to a premature end of the preliminary display. When the courtship continues undisturbed, the cock excitedly and alternately flaps the right and left wings. Both birds then slow their steps and each begins to poke its bill into the ground on a sandy spot and pull out grasses. The cock then throws himself to the ground and stirs up the sand with tremendous wing beats; this seems to be a symbolic hollowing of a nest bowl. Simultaneously, he turns and winds his head in a rapid spiral motion. He continually repeats his muted courtship song while the hen circles in front of or around him in submissive posture, dragging her wings. Suddenly the cock jumps up, the hen drops to the ground and, beating his wings, the cock mounts for copulation.

The breeding season varies regionally, often correlating with the rainy season. The first female to lay in a nest becomes the major hen of the male that owns the nest; she dominates other hens, minor hens, that may also lay in it. As the time of incubation approaches the major hen discards some of the eggs of minor hens, so that the clutch is kept to a size that a bird can incubate effectively. The male incubates by night and the female by day. The clutch of wild birds averages 13 eggs and takes, on average, 42 days to hatch. Both parents care for the chicks, but as they grow, broods may amalgamate, and finally the young from one region gather into an immature flock. Breeding success is low, of the order of one chick per incubated nest, the eggs and chicks being subject to attacks from many predators, hyenas, jackals, and vultures.

Conservation status

The ostrich has declined greatly in abundance and distribution in the last 200 years. Most surviving birds are in game parks or on farms. Only in remote desert regions do truly wild birds persist, but farms and game parks ensure the preservation of the species.

Significance to humans

The ostrich has inspired human thought, religion, and art since ancient times, as indicated by 5,000-year-old records from Mesopotamia and Egypt. For today's Kalahari bushman, its egg is still a valuable vessel in which he keeps scarce water, and from the shells he makes beautiful jewelry for his wife and children. Ostriches are also farmed for feathers, meat, eggs, and leather.

A crèche of 3-ft (90-cm) tall ostrich (*Struthio camelus*) chicks is escorted by an adult across the shortgrass plains of the Serengeti in Tanzania. (Photo by Gregory G. Dimijian. Photo Researchers, Inc. Reproduced by permission.)

Resources

Books

Bertram, B. C. R. "The Ostrich Communal Nesting System." In *Monographs in Behavior and Ecology*, edited by J. R. Krebs and T. H. Clutton-Brock. New Jersey: Princeton University Press, 1990.

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

del Hoyo, J., A. Elliot, and J. Sargatal, eds. *Handbook of the Birds of the World.* Vol. 1, *Ostrich to Ducks.* Barcelona: Lynx Edicions, 1992.

Periodicals

Bertram, B. C. R. "Ostriches Recognize Their Own Eggs and Discard Others." *Nature* 279 (1979): 233–4.

Bolwig, N. "Agonistic and Sexual Behavior of the African Ostrich (*Struthio camelus*)." *Condor* 75 (1973): 100–5.

Sauer, E. G. F., and E. M. Sauer. "The Behavior and Ecology of the South African Ostrich." *Living Bird* Supplement 5 (1966): 45–75.

Organizations

BirdLife South Africa. P. O. Box 515, Randburg, 2125 South Africa. Phone: +27-11-7895188. Web site: <http://www.birdlife.org.za>

S. J. J. F. Davies, ScD

Elephant birds
(Aepyornithidae)

Class Aves
Order Struthioniformes
Suborder Aepyornithes
Family Aepyornithidae

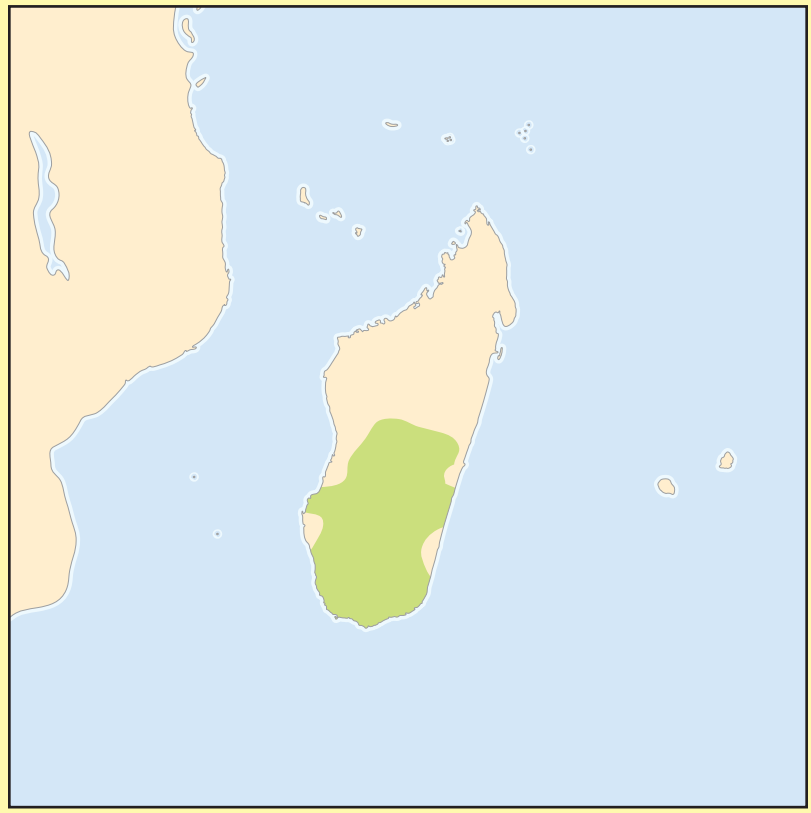
Thumbnail description
Extinct, large, flightless birds of massive build, known only from fragmentary fossil remains

Size
Some species probably 10 ft (3 m), 880 lb (400 kg)

Number of genera, species
2 genera; 7 species

Habitat
Thought to have inhabited woodland and forest in southwest Madagascar

Conservation status
Extinct



Distribution
Madagascar

Evolution and systematics

Elephant birds belong to the group of large, flightless birds known as ratites. Ratites had a distinctive palate, and a sternum (breastbone) with no keel, so there was no anchor for the strong musculature needed for powered flight.

The origin of these birds has recently been clarified by the discovery of numerous good fossils in North America and Europe. Ratites were once thought to have a southern origin in the ancient continent of Gondwana, but new fossil evidence shows that flying ratites inhabited the Northern Hemisphere in the Paleocene and Eocene, 40–70 million years ago. The present Southern Hemisphere distribution of ratites probably resulted from the spread of flying ancestors of the group from the north.

Another indication that ancestors of elephant birds reached Madagascar as flying birds is that no fossils of ratites or elephant birds are found in India. In the process of separation of Gondwana into multiple continents, Madagascar and India remained joined for millions of years after breaking away from Gondwana. If elephant birds had walked to Madagascar, they would surely also have reached India. On the other hand, numerous remains of birds from genera such as *Mullerornis* and *Aepyornis* are known from the Quaternary period of Madagascar. They were found in rock strata that are at most two million years old.

Elephant birds seem most closely related to present-day ostriches. Two fossil birds, *Eremopezus eocaenus* and *Stromeria fajumensis*, from the lower Tertiary of Egypt are sometimes placed in the Aepyornithidae, but opinion is divided about their relationships and they are omitted from the family in this treatment.

Seven separate species of elephant bird are known to have existed: *Mullerornis betsilei*, *Mullerornis agilis*, *Mullerornis rudis*, *Aepyornis maximus*, *Aepyornis medius*, *Aepyornis hildebrandti*, and *Aepyornis gracilis*.

Physical characteristics

No precise estimate can be made of the size and weight of these birds. Some were very large, up to 10 ft (3 m) tall, and weighed 880 lb (400 kg). Others were probably smaller, but more fossil material is needed to give good size-range estimates. When x-rayed, some eggs reveal embryonic elephant

Elephant bird (*Aepyornis maximus*). (Illustration by Bruce Worden)

birds, giving clues about the form of the whole bird, or at least its chick. The middle bone of the leg, the tibia, is longer than the lowest bone, the tarsus, indicating the birds were not fast runners. They had no need to run because other animals on Madagascar were no larger than a cat.

Distribution

Most early reports and recent fossil material have come from southwestern Madagascar. Two intact elephant bird eggs were found on the beaches of western Australia, on the far side of the Indian Ocean from Madagascar. It was concluded that these eggs were laid near the sea, washed into the sea by rivers or brought to the coast by human inhabitants of Madagascar, and floated to western Australia. Their survival on a journey of at least 5,000 mi (8,000 km) is remarkable.

Habitat

Étienne de Flacourt, the first French governor of Madagascar, was the first to report to scientists about elephant birds. He stated that a giant bird called "vouron patra" was still frequently found in the southern half of the island in the mid-seventeenth century. It is thought that elephant birds lived in the forests and woodlands of southwestern Madagascar. When human inhabitants arrived on the island about 2,000 years ago, they fragmented and burned these environments, causing the birds to lose their livelihood and become extinct soon after Flacourt's report.

Behavior

Nothing is known of the behavior of these birds. An account by Marco Polo in which large birds seized elephants, flew into the sky, then dropped the elephants to kill them and feast on them is a delightful fairy tale that may have given elephant birds their name.

Feeding ecology and diet

Elephant birds are thought to have fed on forest fruits. They may have been important in the dispersal of some fruit-bearing plants on the island—plants that are now known only from a few very old individual trees.

Reproductive biology

It is likely that elephant birds laid small clutches, perhaps of only one egg, and therefore reproduced slowly. The first scientific data on elephant birds was a report on their eggs made when a traveler named Sganzin sent a sketch of one of the giant eggs to collector Jules Verreaux from Madagascar in 1832. The eggs would have weighed about 13 lb (6 kg) and would be some of the largest single cells ever known.

Conservation status

Extinct.

Significance to humans

Flacourt reported that the natives used remains of elephant bird eggs as vessels. The shells are several millimeters thick; they may be more than 12 in (30 cm) long, and their volume is given as more than 1.6 gal (6 l). This corresponds to more than six ostrich eggs or more than 150 chicken eggs. Even today, many broken eggshells litter the beaches of southwestern Madagascar. The eggs and the birds that laid them must have been a great food resource for local people.

Resources

Books

Davies, S. J. J. F. *Ratites and Tinamous.* Oxford: Oxford University Press, 2002.

Feduccia, Alan. *The Origin and Evolution of Birds.* New Haven and London: Yale University Press, 1996.

Heuvelmans, Bernard. *On the Track of Unknown Animals.* London: Hart-Davis, 1959.

Periodicals

Brodkorb, P. "Catalogue of Fossil Birds. Part 1." *Bulletin of the Florida State Museum (Biological Sciences)* 7 (1963): 205–7.

Wetmore, A. "Re-creating Madagascar's Giant Extinct Bird." *National Geographic* 132 (1967): 488–93.

S. J. J. F. Davies, ScD

Procellariiformes

(Tubenosed seabirds)

Class Aves

Order Procellariiformes

Number of families 4 families

Number of genera, species 23 genera; 108 species

Photo: Northern fulmar (*Fulmarus glacialis*) at Kilt Rock on the Isle of Skye, Scotland. (Photo by Art Wolfe. Photo Researchers, Inc. Reproduced by permission.)

Introduction

Procellariiformes are exclusively marine birds. Also commonly known as petrels, tubinare, or tube-noses, this order is extremely diverse: from the massive, yet majestic, wandering albatross (*Diomedea exulans*) to the tiny, wave-dancing least storm-petrel (*Halocyptena microsoma*).

Traditionally there are four families within the order Procellariiformes: the Diomedeidae (albatrosses); the Procellariidae (giant petrels, fulmars, gadfly petrels, and shearwaters); the Hydrobatidae (storm-petrels); and the Pelecanoididae (diving-petrels). These four families include 23 genera and 108 species.

Evolution and systematics

The oldest Procellariiform fossil is from the early Paleocene, some 60 million years ago. However, a DNA-based study published in 1997 suggests that the order is even older and was distinct from penguins (order Sphenisciformes) and divers (order Gaviiformes) prior to the end of the Cretaceous. Thus, like many early avian groups, the Procellariiformes survived the mass extinction event at the end of Cretaceous about 65 million years ago. The fossil record of the Procellariiformes is generally poor, but a few sixteen million-year-old fossils show that even then albatrosses and shearwaters were very similar to modern-day species.

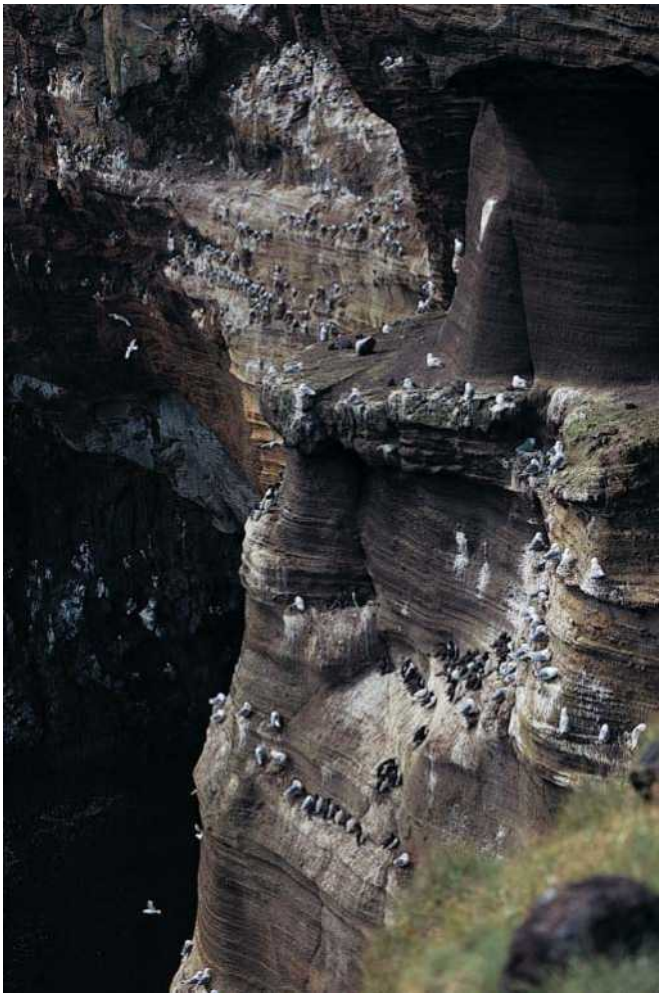
Procellariiformes are thought to have first evolved in the Southern Hemisphere and two-thirds of extant species are still found in this region. Surprisingly, most Procellariiform fossils have been found north of the equator. Many albatross fossils from the Pliocene (2 to 5 million years ago) have been recovered from Europe, North America, and Japan. This northern bias may simply reflect relative effort and the greater amount of landmass in the Northern Hemisphere. A few fossils from Australia, South Africa, and Argentina do confirm, however, the presence of albatrosses in the southern oceans over five million years ago.

DNA-DNA hybridization and DNA sequencing have confirmed the common ancestry of all Procellariiformes, but the taxonomy within the order is complex and subject to constant revision. John Warham, in his detailed book *The Petrels*, states that "the classification and systematics of Procellariiformes have long been the subject of controversy and a general agreement on species' limits in the near future seems unlikely." His prediction proved to be accurate. For example, in 1997 it was suggested that the number of albatross species should be revised from 14 to 24.

Physical characteristics

The unifying characteristic of Procellariiformes is their tubular nostrils. In the albatrosses (Diomedeidae) the tubular nostrils protrude from each side of the bill whereas in the three other Procellariiform families the nostrils are fused and sit prominently at the base of the upper bill. Unlike most other birds, petrels are thought to have a have a highly developed sense of smell, which they use to locate food and breeding sites. The tubular nostrils may enhance this sense or the tubes could simply act to keep the salty solution produced by the nasal glands away from the face and eyes.

Another unique feature of this order is the structure of the bill. Unlike any other birds, the bills of Procellariiformes are split into seven to nine distinct horny plates. The hooked bill of petrels is formed by a plate on the upper bill called the maxillary unguis. The hooked, stout, and very sharp unguis can firmly hold slippery food items such as fish and squid. In



Kittiwakes, murres, and fulmars share this bird-nesting cliff on the Snæfellsnes Peninsula in Iceland. (Photo by Kenneth W. Fink. Bruce Coleman Inc. Reproduced by permission.)

smaller Procellariiformes the cutting edges of the plates in the lower bill (tomia) are more comb-like and form filters for feeding on plankton and other small items of food.

Procellariiformes show the greatest range in body size of any avian order. The smallest species is the least storm-petrel (*Halocyptena microsoma*), which weighs less than 1 oz (20 g) and has a wingspan of 12.5 inches (32 cm). The largest species, the wandering albatross (*Diomedea exulans*), can weigh over 24 pounds (11 kg) and has a wingspan of up to 12 feet (3.6 m).

The plumages of Procellariiformes are generally quite plain and are composed of black, brown, gray, or white feathers. The legs and feet are usually black, but some are flesh-colored or mottled. In prions, diving-petrels, and little shearwaters (*Puffinis assimilis*) the feet and legs are blue. The bills of Procellariiformes are usually dark gray or black although some have yellow, orange, or pink coloration.

Also peculiar to Procellariiformes is stomach oil. This pale oil mainly contains wax esters and triglycerides and has a dietary origin. It is stored in the large, sac-like proventriculus that separates the esophagus and gizzard. Enzymes secreted within the proventriculus allow Procellariiformes to metabolize the wax esters. The oil is used by both chicks and adults as an energy-rich food source during the potentially long periods between meals. The oil has a strong smell and may give the Procellariiformes their characteristic musty odor. Giant petrels (Genus *Macronectes*) are particularly pungent, hence their nickname "stinkers."

The oil has a second function. If chicks or ground-nesting adults are threatened, the oil can be regurgitated from the proventriculus and sprayed over a considerable distance. When the oil cools it has a wax-like consistency and can damage the plumage of predatory birds such as skuas (Laridae; Stercorariinae).

Distribution

Procellariiformes have the widest distribution of any avian order. Antarctic petrels (*Thalassoica antarctica*) and snow petrels (*Pagodroma nivea*) breed so far south that birds have to fly over a hundred miles from their inland colony before they reach the coastline of the Antarctic continent. In the Northern Hemisphere, fulmars (*Fulmaris glacialis*) nest on the northeastern tip of Greenland, as far into the Arctic as any land reaches. Petrels occur in all oceans but are most numerous in the Southern Hemisphere and are least abundant in the tropics.

Habitat

Petrel colonies are mostly found on remote islands away from land-based predators. Those that nest on larger islands or mainland continents do so in areas with low numbers of predators, such as deserts or mountainsides.

The breeding sites of the larger petrels must be windswept. Albatrosses and other large petrels cannot take off or forage widely for food without the help of strong winds. The subantarctic islands so favored by Procellariiformes are in latitudes referred to by sailors as the 'Roaring Forties' and 'Furious Fifties' because of the powerful, westerly winds that blow throughout the year.

Outside the breeding season, Procellariiformes spend virtually all their time at sea. Their distribution is largely governed by the availability of food, which is in turn influenced by the distribution of currents, upwellings, and weather conditions. However, some Procellariiformes, such as short-tailed shearwaters (*Puffinus tenuirostris*) and Manx shearwaters (*Puffinus puffinus*), make predictable return migrations between the Northern and Southern Hemispheres. Although migrating at the same time and in the same direction, these two species do not breed in the same hemisphere. The Manx shearwater favors the northern summer whereas the short-tailed shearwater, like most petrels, breeds during the summer months of the Southern Hemisphere. Research published in 2000 has shown that wandering albatrosses (*Diomedea exulans*) also have predictable migrations. Adults that nest on the Crozet Islands near South Africa return to the same patch of ocean at the end of each breeding cycle. However, the favored area could be as far away as Australia and may be different for each adult albatross.

Behavior

Most petrels are gregarious. At sea they can occur in large multi-species flocks around natural food sources or fishing boats. Squabbles are common and the large, aggressive albatrosses and giant petrels usually displace other species.

Petrels are also gregarious during breeding and can form huge colonies. Surface-nesters usually build their nests just beyond the pecking distance of their nearest neighbor. Larger albatrosses and the northern giant petrel (*Macronectes halli*) nest on the ground but not in dense colonies. More commonly their nests are loosely scattered along hillsides, headlands, or mountain ridges. Smaller petrels nest in dense, single-species colonies but usually excavate burrows or squeeze behind rocks.

Many petrels have elaborate display rituals in order to choose a mate or maintain a pair bond. Diurnal species such as albatrosses perform terrestrial dances or synchronized "aerial-ballet" routines. The courtship display of other petrels can be equally impressive. The display of the black-winged petrel (*Pterodroma nigripennis*) consists of swooping aerial chases and loud high-pitched calls. Species that return to their breeding sites after dusk tend to have less elaborate displays but can still be extremely vocal.

Most Procellariiformes are silent at sea unless competing for food. On land, various piping calls, shrieks, croaks, and other calls are produced at the nest or burrow. Albatrosses produce a variety of calls that accompany their complex displays. Shearwaters are renowned for the eerie human-like cries they produce from within their burrows.

Feeding ecology and diet

Among seafarers, albatrosses were well known for their ability to effortlessly follow ships for thousands of miles. By gliding on long, narrow wings, albatrosses, fulmars, petrels, and shearwaters can use the ocean winds to cover vast distances in search of food. However, not all Procellariiformes fly so economically. The short, stubby wings and rounded, penguin-like body of diving-petrels is more adapted to a life under the water than above it.

Typically petrels search for their patchily distributed food either offshore or beyond the continental shelf. Their search can take them thousands of miles from their breeding colony. Studies using satellite-tracking devices have shown that some albatrosses breeding on the Crozet Islands forage up to 1,600 mi (2,600 km) away from their nest. In contrast, diving-petrels predominantly search for food in inshore waters close to their breeding sites.

Petrels usually find their food close to or on the surface of the ocean although shearwaters, diving-petrels, and even some albatrosses can dive more than 30 ft (10 m) below the surface. Squid is the principal food source for most large petrels, although they will opportunistically eat other seabirds and carrion. Carcasses of seals, whales, and cuttlefish will attract hungry albatrosses while other Procellariiformes such as gadfly petrels and storm-petrels will mop up any scraps. Only giant petrels regularly forage for food on land. Petrels also exploit the actions of whales, dolphins, sharks, and tuna.

Least storm-petrel (*Oceanodroma microsoma*). (Photo by J. Hoffman/VIREO. Reproduced by permission.)

These marine predators will push schools of fish close to the surface and within reach of the shallow-diving-petrels. Storm-petrels and prions eat zooplankton such as copepods, amphipods, and fish eggs, which they delicately pluck from the surface of the ocean.

Concentrations of sea life occur where upwellings bring nutrient-rich waters closer to the surface. But even in these regions the abundance of food is largely unpredictable and the physiology of Procellariiformes reflects the ephemeral nature of their food sources. At 100°F (38°C), the body temperature of petrels is lower than most birds (105°F; 41°C). Therefore, less energy is required to maintain body temperature and less heat is lost. When food is plentiful, layers of subdermal fat and stomach oil can store excess energy until it is needed. The digestive tract of Procellariiformes is unusual in that the esophagus passes unrestricted into the proventriculus, which fills a large proportion of the abdominal cavity. The size of the proventriculus allows very large meals to be consumed and stored.

Reproductive biology

Procellariiformes are long-lived, very slow breeders. None can breed in the first year, and the largest petrels wait over a decade before breeding for the first time. In each breeding attempt, all Procellariiformes lay a single white egg. The egg is large relative to body size and can be up to 28% of the mother's body weight. Incubation in petrels is prolonged (6 to 11 weeks): about twice as long as gull (Laridae) eggs of a similar size. A petrel chick takes between two and nine months to fledge, twice as long as gulls of the same body mass. The reasons behind such a slow growth rate are thought to be associated with breeding sites and the parents' ability to feed

the young. Terrestrial predators are usually absent from the islands where petrels breed, which removes the pressure to fledge a chick quickly. Also, food is rarely abundant close to breeding sites, so a fast growing chick would be more likely to starve during the potentially long periods between meals.

All Procellariiformes form exclusive social pairings, but behavioral and DNA-based studies have shown that infidelity does occur and males are not always the genetic fathers of the chick they help to raise. Copulations occur at the nest and are often preceded by complex behaviors or mutual allopreening.

Both sexes build or excavate the nests, incubate the egg, and provision the chick. Initially, surface-nesting petrels protect the chick from potential predators. Later, both parents leave the chick while they forage for food. A healthy chick can defend itself by regurgitating the stomach oil stored in its proventriculus.

Petrels receive little or no post-fledging care. They spend their first 2–11 years at sea before returning to their natal site to breed. Rarely, a young bird will return to a different island or colony to make its first breeding attempt.

Conservation

There are 108 extant species of Procellariiformes. Of these, 23 are threatened with extinction. Only one species, the Guadalupe storm-petrel (*Oceanodroma macrodactyla*), has become extinct since 1600. The principal threats to petrels are mammalian predators introduced to breeding islands and interactions with fishing vessels.

Humans have accidentally or deliberately introduced cats, rodents, possums, pigs, mustelids, rabbits, goats, foxes, and other mammals to petrel breeding sites. They usually have a severe impact. On Marion Island in the Indian Ocean, the 2000 or so feral cats targeted diving-petrels and killed nearly half a million seabirds each year. Eradication schemes have now successfully removed mammalian predators from many petrel breeding sites. On Australia's subantarctic Macquarie Island, an intensive effort to remove cats saw immediate success when in 2000 gray petrels (*Procellaria cinerea*) bred successfully on the main island for the first time in 40 years.

Before being banned in 1991, drift-net fisheries were thought to be responsible for killing up to 500,000 seabirds each year. Currently, the greatest threat to foraging seabirds are long-line and trawl fishing boats that annually kill thousands of petrels and have been linked to the decline of many albatross populations. One study published in 1991 estimated that 44,000 albatrosses are killed by the Japanese longline fishery each year. Longline fishers are now expected to use bird-scaring lines and other bycatch mitigation measures in an attempt to reduce the death toll of seabirds.

Significance to humans

Not surprisingly, Procellariiformes have been of most significance to fishermen, whalers, and other seafarers. They are sometimes used to pinpoint fish shoals or a surfacing whale and are the subject of many superstitions. Some thought albatrosses were good omens and to kill one would bring ill fortune. At other times, to see an albatross or touch a storm-petrel was considered to be bad luck. Procellariiformes were also seen as the embodiment of the souls of cruel captains or drowned sailors that were destined to wander the seas for all time.

Petrels have long been used as a source of food for humans and have been found among archaeological remains around the world. Petrels have also sustained many a sailor shipwrecked in the southern oceans. In Alaska, Kodiak Islanders harpooned short-tailed albatrosses (*Diomedea albatrus*) from canoes, and royal albatross chicks (*Diomedea epomophora*) were highly prized by New Zealand tribes. Until the late 1980s, the inhabitants of Tristan Island in the Indian Ocean harvested the eggs of yellow-nosed mollymawks (*Diomedea chlororhynchos*) and sooty albatrosses (*Phoebetria fusca*). In many places, humans harvested shearwater chicks, also known as "muttonbirds." Tasmanian aborigines ate short-tailed shearwaters (*Puffinus tenuirostris*) at least 2000 years ago and a highly regulated harvest continues today. In New Zealand, there is a traditional harvest of sooty shearwater chicks (*Puffinus griseus*). Meticulous records track the number of Manx shearwaters (*Puffinus puffinus*) harvested from colonies on the Isle of Man in the United Kingdom. In the mid 1600s, the annual harvest was 10,000 chicks. However, like most petrel colonies, this population was vulnerable to introduced predators. By 1789, the colony disappeared after a shipwreck introduced rats to the island.

Many places where albatrosses and other petrels breed or forage now attract humans that simply wish to marvel at their size, elegance, and beauty.

Resources

Books

del Hoyo, J., A. Elliot, and J. Sargatal, eds. "Ostrich to Ducks." Vol. 1 of *Handbook of the Birds of the World.* Barcelona: Lynx Edicions, 1992.

Marchant, S., and P.J. Higgins, eds. "Ratites to Ducks." Vol. 1 of *Handbook of Australian, New Zealand and Antarctic Birds.* Melbourne: Oxford University Press, 1990.

Tickell, W.L.N. *Albatrosses.* Sussex: Pica Press, 2000.

Robertson, G., and R. Gales, eds. *Albatross Biology and Conservation.* Chipping Norton: Surrey Beatty, 1998.

Warham, J. *The Petrels.* London: Academic Press, 1990.

Periodicals

Brothers, N. "Albatross Mortality and Associated Bait Loss in the Japanese Longline Fishery in the Southern Ocean." *Biological Conservation* 55 (1991): 255-268.

Resources

Cooper, A., and D. Penny. "Mass Survival of Birds across the Cretaceous-Tertiary Boundary: Molecular Evidence." *Science* 275 (1997): 1109-1113.

Huyvaert, K. P., D.J. Anderson, T.C. Jones, W.R. Duan, and P.G. Parker. "Extra-pair Paternity in Waved Albatrosses." *Molecular Ecology* 9 (2000): 1415-1419.

Nunn, G.B. and S.E. Stanley. "Body Size Effects and Rates of Cytochrome b Evolution in Tube-nosed Seabirds." *Molecular Biology and Evolution* 15 (1998): 1360-1371.

Roby D.D., J.R.E. Taylor, and A.R. Place. "Significance of Stomach Oil for Reproduction in Seabirds: an Interspecies Cross-fostering experiment." *The Auk* 114 (1997): 725-736.

Weimerskirch, H., N. Brothers, and P. Jouventin. "Population Dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and Their Relationships with Long-line Fisheries - Conservation Implications." *Biological Conservation* 79 (1997): 257-270.

Weimerskirch, H. and R.P. Wilson. "Oceanic Respite for Wandering Albatrosses." *Nature* (2000): 955-956.

Michael Colin Double, PhD

Albatrosses
(Diomedeidae)

Class Aves
Order Procellariiformes
Family Diomedeidae

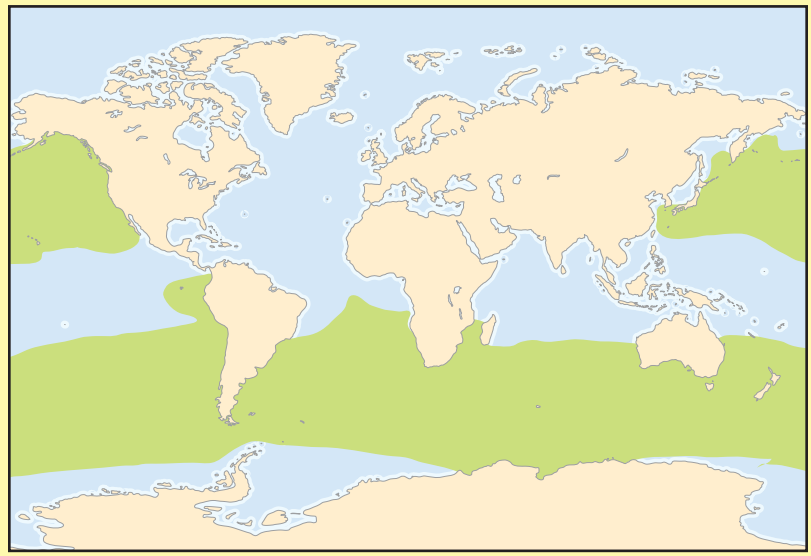
Thumbnail description
The largest flying seabirds, with exceptionally long narrow wings adapted for gliding and distinctive hooked bill and plumage ranging from all dark to mostly white

Size
Wingspan 62.3–106 in (190–323 cm); 3.74–26.25 lb (1.7–11.9 kg); length: 20–80 in (50–200 cm)

Number of genera, species
4 genera; 14 species

Habitat
Oceanic, generally only approach land for breeding on remote islands

Conservation status
Critically Endangered: 1 species; Vulnerable: 8 species; Lower Risk: 4 species; Data Deficient: 1 species.



Distribution
The north and south Pacific, Indian, and south Atlantic oceans

Evolution and systematics

A range of fossil albatrosses are evidence of a wider and more cosmopolitan distribution than those extant today. The earliest identified are from the Oligocene in Germany and South Carolina. Species approaching the characteristics of modern albatrosses are from the Northern Hemisphere (Europe and both coasts of North America) in the Miocene and Pliocene, but deposits are known from Australia, South Africa and Argentina in the predominantly marine Southern Hemisphere. Albatrosses were probably widespread in the north Atlantic until the late Tertiary.

The taxonomic status of albatrosses was fragmented and confusing until long-term field studies started during the 1930s. The collation of morphological, biological, and distribution data from breeding locations, with various genetic analyses from the 1990s, suggests a division into 4 genera and 24 taxa, a term that applies to both the species and subspecies of this order (*Phoebastria* with three taxa; *Diomedea*, 7 taxa; *Thalassarche*, 12 taxa; and *Phoebetria*, two taxa). Most of the 24 recognizable taxa (by combined morphology and genetics) may warrant species status and can be considered as distinct conservation units. In this treatment, however, the more traditional count of two genera will be applied: *Diomedidae*, which encompasses the proposed genera *Phoebastria* and *Thalassarche*; and *Phoebetria*, the two species of sooty albatross. A more positive resolution of the species question awaits data from poorly studied species in remote locations.

Physical characteristics

The great albatrosses (*Diomedea*) are the largest, with wingspans that can exceed 9.8 ft (300 cm). They lack a dark back except as juveniles. All have a white underwing. The upper wing of the northern royal albatross (*D. epomophora sanfordi*) is always black, while that of the wandering albatross (*D. exulans*) and the southern royal albatross (*D. epomophora*) grow increasingly white with age, especially among males. When Antipodean (*D. antipodensis*) and Amsterdam albatrosses (*D. amsterdamensis*) breed, especially females, they are almost as dark as in as juveniles. In the wandering royal albatross (*D. exulans*), Tristan albatross (*D. dabbenena*) and Gibson's albatross (*D. gibsoni*), body plumage whitens with age, and females may retain dark markings on the chest, flank, and back. Otherwise the body is chiefly white in the royal and northern royal albatrosses. The long (5.5–7.5 in; 140–190 mm) pale, horn-colored bill has a distinctively hooked tip, and it flushes pink in adults rearing chicks.

The Northern Pacific albatrosses include four medium to small taxa with wingspans of 6.2–7.9 ft (190–240 cm), and all have short, black tails. The two largest, i.e. the short-tailed albatross (*D. albatrus*) and the waved albatross (*D. irrorata*), have distinctive yellow/golden plumage on the head and nape. Of the two smallest, the Laysan albatross (*D. immutabilis*) has a pinkish bill, white body, and dark upper wing, while the black-footed albatross (*D. nigripes*) has a black bill and is mainly dark brown, except for a white patch at the rump and a variably pale face.

Laysan albatross (*Diomedea immutabilis*) parent with chick on Midway Atoll. (Photo by Frans Lanting. Photo Researchers, Inc. Reproduced by permission.)

The mollymawks, which include 11 small to medium size taxa, are the most diverse group of albatrosses with wingspans of 5.9–8.4 ft (180–256 cm). All have black upper wings and back, variable amounts of black on the underwing, and white body. All have a variable gray eyebrow with heads and necks varying from mainly white to dark gray, some with pronounced paler cap. The shy albatross, white-capped albatross, Salvin's, and Chatham mollymawk (*D. cauta*, *D. cauta cauta*, *D. salvini* and *D. cauta eremita*) all have chiefly white underwings, while all others have variable amounts of black reaching into the underwing from the leading edge. All mollymawks have distinctive bill structures and colors which, when combined with head color, help identification. The black-browed mollymawk (*D. melanophris*) and the Campbell black-browed mollymawk (*D. impavida*) have golden yellow bills with pink tips. The gray-headed mollymawk (*D. chrysostoma*) has a dark gray head and bill, with a yellow culmen and pink nail, yellow lower mandible stripe and black intervening sides to the bill. Buller's mollymawk (*D. bulleri*) and the Pacific mollymawk (*D. platei*) have similar bills without the pink nail and have gray, with paler-capped, heads. The smallest mollymawks (*D. chlororhynchos*) have a gray washed head, and the eastern yellow-nosed mollymawk (*D. bassi*) has a chiefly white head. Both taxa have bills with a yellow culmen stripe and pink nail. All mollymawks have a colorful pink/orange fleshy facial stripe from gape to ear which is exposed during displays.

The two sooty albatrosses (*Phoebetria*), with a wing span of 6.0–7.15 ft (183–218 cm), and the longest and most pointed tails of all albatross taxa, have mainly dark bills, plumage, and legs. However, the light-mantled sooty albatross (*P. palpebrata*), normally has a paler brown mantle than the dark-mantled sooty albatross (*P. fusca*).

Distribution

Three albatrosses, namely the short-tailed, the Laysan, and the black-footed, are confined to the northern Pacific ocean. The waved albatross is tropical, mainly found from the Galápagos Islands to the coasts of Ecuador and Peru. All other albatrosses are found in the Southern Hemisphere in a circumpolar band mainly from 65°S to 20°S, but north to 15°S on the coast of southern Africa and 5°S on the west coast of South America.

Habitat

More than 70% of an albatross' life is spent on or over the ocean, while foraging, migrating, or resting. With the exception of the waved albatross, albatrosses avoid the relatively windless tropical doldrums. Though ranging widely at sea from breeding islands and during non-breeding time, significant differences in distribution can occur within and between species or between sexes. Some species are found to forage locally over continental shelves, while others roam widely to obtain food. Significant concentrations of birds can be found in areas of ocean richness near major currents, gyres and upwellings around South America (e.g. Humbolt current), Australia, New Zealand, South Africa (Benguela current) and in the north Pacific (Bering Sea and Gulf of Alaska). The remaining time is spent ashore at the usually windswept, remote island breeding locations for courtship, nesting and chick rearing. *Diomedea* species are more commonly found on grassy slopes or plains where nests are often far apart, and rebuilt each nesting attempt, but located within sight of neighbors. The northern royal albatross uses the flat scrubby tops of small rocky islets, while *Phoebetria* species are usually widely spaced along steep grassy slopes and cliff ledges.

Behavior

Albatrosses cannot fly in calm weather, needing a good breeze to effect the soaring and tacking pattern of flight which enables large distances to be covered with little effort. Generally silent at sea, or in social resting or washing flocks. However, breeding colonies (especially close-nesting mollymawks) can be noisy with buzzing cries, clattering bills, and wailing screams accompanying a wide repertoire of body displays associated with recognition, threat, and courtship. While there are common components of display throughout the family, the dances and wing displays of the northern Pacific albatrosses have no equivalent in the Southern Hemisphere. The most intense courtship display sequences are seen among adolescent pre-breeders, often in small groups or gams. Some displays are between similar sexes within such groups. Birds that develop a pair-bond remove themselves from the group to a potential nesting site where the displays become shorter, gentler and more mutual without the flamboyance of courtship. Some (e.g. the sooty albatrosses) indulge in courtship flying interspersed with synchronous calling from both sexes both on the ground and in the air. Albatrosses generally defend small spaces associated with the nest site or territory. Fighting is not a regular occurrence, with a reliance on threat displays and charging, but the hooked bill can damage bills and eyes. Chicks at the nest site clapper their bills to discourage intruders (e.g. predatory skuas, *Catharacta*), followed by regurgitation of oily stomach contents if approached too closely. Considerable time is spent in self and mutual

A pair of black-browed albatrosses (*Diomedea melanophris*) at their nest on New Island, Falkland Islands. (Photo by Rod Planck. Photo Researchers, Inc. Reproduced by permission.)

preening of plumage by adults, and of the growing chick by the parents.

Feeding ecology and diet

Various species of squid seem to provide the main component of the albatross diet. Many of these species are bioluminescent, and can be caught during the night. Some localised feeding spots provide a regular annual supply of carrion (e.g. during the annual die-off of *Sepia* cuttlefish on the eastern Australian coast) along established migration routes for some species. The diet also inlcudes a wide range of fish including small flying-fish, lampreys (*Geotrea*), pilchards (*Sardinops*) and crustaceans such as krills (*Euphausia* sp.), amphipods, copepods and crabs. Other recorded prey items include salps, seaweeds, barnacles, and fish spawn. Other small seabirds (prions, diving-petrels, and penguins) have been found in stomach contents as have examples of carrion from dead whales and seals. Some species can feed during the breeding season within a few hundred miles (kilometers) of the breeding place, as is the case with the northern royal albatross and the shy and Chatham mollymawks. Most food is gathered at the surface, but some of the smaller mollymawks may plunge and swim a short distance (up to 16 ft [5 m]) below the surface after prey. Kleptoparisitism has been recorded among waved albatrosses chasing boobies (*Sula* spp.), black-browed albatrosses from *Phalacrocorax*, and among eastern yellow-nosed albatrosses chasing shearwaters. Food is also obtained by some species from human fisheries offal, discards, and stolen baits.

Reproductive biology

Albatrosses usually build bowl-shaped nesting mounds with grasses and small shrubs bound together with soil, peat, or even penguin feathers where no vegetation is available. The waved albatross does not build nests, and the other northern Pacific albatrosses have very rudimentary ones that are rebuilt each season. Many Buller's mollymawks and black-footed albatrosses nest under trees in open forest. Most mollymawks nest in tight colonies just out of pecking range from neighbors, and reuse previous nest mounds.

Albatrosses are generally monogamous and most are annual breeders. Albatrosses lay one large white egg with reddish brown spots at the largest end weighing 7.0–18.2 oz (200–510 g) ranging from 5 to 10% of female body weight. First eggs are narrower and lighter. Incubation lasts 65–85 days with both sexes sharing the incubation stints, which may range from one day to as long as 29 days according to species foraging methods and locations. Hatching takes 2–5 days. Immediately after hatching, during the brooding (guard) stage of chick growth (15–40 days), one parent remains with the chick at the nest. Chicks fledge at 120–180 days for all small

A waved albatross (*Diomedea irrorata*) pair courting in the Galápagos Islands. (Photo by JLM Visuals. Reproduced by permission.)

albatrosses, while *Diomedea* have a range of 220–303 days. Though breeding success can vary according to species and breeding season, fledging may be as high as 80% of eggs laid. Long-term averages can range from 25 to 67%, with the waved albatross being the lowest.

Recruitment of fledglings into the breeding population occurs at 5–15 years of age with 15–65% of those fledged surviving to breed. Biennial breeders take longer to become sexually mature. Annual mortality rates for adults range from 3 to 9%. The oldest known albatross was a northern royal albatross, still breeding at over 62 years old.

Conservation status

Albatrosses are long-lived, with delayed maturity and low reproductive output and adult mortality. This strategy ensures that only a small proportion of the population is breeding at any one time, with the remainder often in other parts of their range as adolescents or resting adult breeders. This mitigates the effects of localized disasters, but may disguise for some years any detrimental effects on populations or age groups which are more widespread. Threats which affect breeding birds have the most immediate impact, and recorded increases in adult mortality of 1–5% have significantly affected some colonies. Of the nearly 2 million breeding pairs of albatrosses worldwide in 24 recognizable taxa, 14 have populations of less than 20,000 breeding pairs. At the most populous level, the black-browed and the black-footed albatrosses have total populations that exceed 600,000 breeding pairs. However, some of these populations are fragmented, with a third of discrete groups having fewer than 100 breeding pairs. Most species have populations where there is not enough data to determine the rate of increase or decline, but have evidence of being exposed to known threats. The most vulnerable populations are those which are confined to one breeding locality. The high degree of philopatry of both juveniles and adults limits any ability to colonize new sites when facing adversity at their natal colony. Most factors adversely affecting populations involve human activities. However, climatic events have been seen to cause changes in habitat, which severely reduced breeding productivity in the northern royal albatross. Changing sea temperatures may also contribute to decline by changing food distribution and availability.

Significance to humans

The Rime of the Ancient Mariner, by S.T. Coleridge (1798), has done much to determine the popular conception of the albatross. The family name is derived from the name of the Greek hero of the Trojan War, Diomedes, whom the gods exiled to an isolated island, turning all of his deceased companions into large, white birds.

The preponderance of albatrosses breeding in locations remote from human habitation may indicate that closer populations were historically extirpated by humans. Certainly harvesting of eggs or chicks continues legally or illegally in a few locations today. During the past 250 years since the first naming of an albatross by Linnaeus, these legendary birds have been directly or indirectly exploited at sea and at their breeding colonies by those on boats—mariners, sealers, and whalers as food and artifacts, passengers as sport, and science as specimens.

1. Light-mantled albatross (*Phoebetria palpebrata*); 2. Northern royal albatross (*Diomedea epomophora sanfordi*); 3. Wandering albatross (*Diomedea exulans*); 4. Black-browed mollymawk (*Diomedea melanophris*); 5. Chatham mollymawk (*Diomedea cauta eremita*); 6. Laysan albatross (*Diomedea immutabilis*). (Illustration by Dan Erickson)

Species accounts

Royal albatross
Diomedea epomophora sanfordi

TAXONOMY
Diomedea epomophora sanfordi Murphy, 1917, Chatham Islands.

OTHER COMMON NAMES
English: Toroa; French: Albatros royal; German: Königsalbatros; Spanish: Albatros Real.

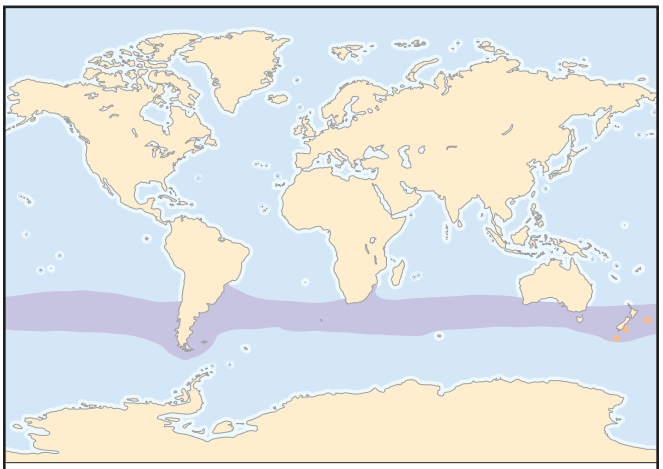
PHYSICAL CHARACTERISTICS
Wingspan 8.85–10.0 ft (270–305 cm); 13.75–18.1 lb (6.25–8.2 kg); length: c. 45 in (115 cm). Large white bodied albatross with upper wing surface black. Eyelids black, spotted white in oldest birds.

DISTRIBUTION
Breeds only on New Zealand South Island (Taiaroa Head), Chatham Islands (Sisters and Forty-Fours Islands), and Enderby Island. The only albatross to have a circumpolar range when not breeding.

HABITAT
Marine, breeding on exposed tops of small islets or headlands.

BEHAVIOR
Extensive repertoire of mutual and group displays at the breeding site, some of which are occasionally performed in the air or on the water. Once pair bond is formed the most extravagantly spread wing displays are not used.

FEEDING ECOLOGY AND DIET
Most food taken by surface seizing. Mainly cephalopods, with some fish, salps, and crustaceans. During the breeding season, feeding occurs over continental shelf breaks within 620 mi (1,000 km) of the colony. Probably an opportunistic feeder when migrating.



REPRODUCTIVE BIOLOGY
Lays one egg 27 October to 8 December with laying time fixed according to parentage. Nest a raised bowl of soil and vegetation rebuilt after each nesting attempt. Will also lay on bare rock with rock chips, but egg failures then are greater than 90%. On average, incubation is 79 days and fledging 240 days. Biennial breeder if successful. Monogamous, pairing usually for life. Breeding starts at 8 years and the average age of the breeding population is 20 years. Adult annual mortality is 4–5%.

CONSERVATION STATUS
Endangered. Total population c. 7,700 pairs, restricted to a tiny breeding range; the habitat supporting 99% of the population in Chatham Islands was severely degraded by storms in the 1980s. The resulting reduced productivity suggests a predicted 50% decline will occur over three generations unless the habitat improves significantly.

SIGNIFICANCE TO HUMANS
At Taiaroa Head the efforts of L.E. Richdale enabled protection of the fledgling colony by 1950. Public viewing started in 1972, and by 2001 more than 100,000 persons annually viewed the nesting colony. ◆

Wandering albatross
Diomedea exulans

TAXONOMY
Diomedea exulans Linnaeus, 1758, Cape of Good Hope. Two subspecies.

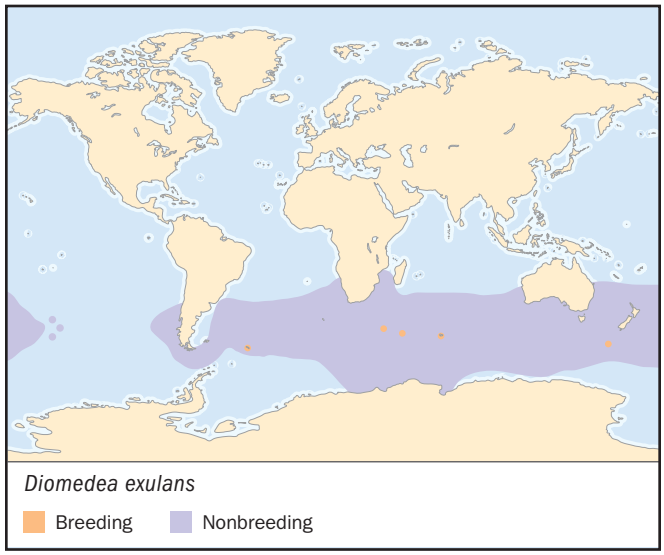
OTHER COMMON NAMES
English: Snowy albatross, white-winged albatross; French: Albatros hurleur; German: Wanderalbatros; Spanish: Albatros Viajero.

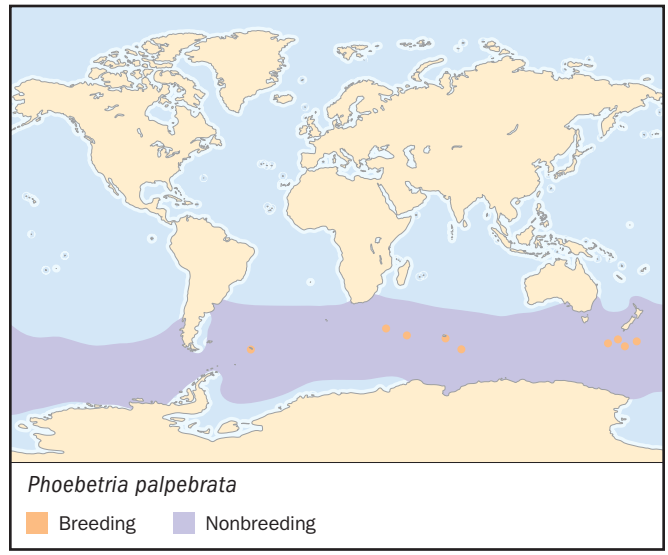
PHYSICAL CHARACTERISTICS
Wingspan 9.2–11.5 ft (280–350 cm); 13.7–25 lb (6.25–11.3 kg). One of largest albatrosses with variable plumage developing from chocolate brown. Back and belly whiten first, followed by head and rump. Wing whitens from center. Oldest males are whitest.

DISTRIBUTION
D. exulans breeds in high latitudes of the southern oceans at South Georgia, Marion and Prince Edward Islands, Crozet Island, Kerguelen Island, Heard and Macquarie Islands. Juveniles are thought to disperse northwards from these locations before developing regular downwind migrations.

HABITAT
Marine and highly pelagic over deep waters away from coastal continental shelves.

BEHAVIOR
Extensive repertoire of group and mutual displays accompanied by a wide range of screams, whistles, moans, grunts, and bill clappering.





FEEDING ECOLOGY AND DIET
Most food taken by surface seizing, but may make shallow plunge dives. Feeds primarily on cephalopods, deepwater and bioluminescent squid at night, but also fish and crustaceans. Feeds on carrion more than other albatrosses and is an extensive follower of ships for galley scraps, and fishing vessels for offal, discards, and baits. During breeding, feeding flights over deep ocean areas may be for as long as 25 days and covering some 13,000 miles (20,800 km).

REPRODUCTIVE BIOLOGY
Lays one egg between 10 December and 5 January. The nest is a raised bowl of soil peat and grassy vegetation rebuilt at each nesting. On average, incubation lasts 79 days, fledging 271 days. Usually a biennial breeder. Monogamous, pairing usually for life. Productivity c. 70%. Adolescents return by 6 years. Breeding starts at 11 years. Only c. 30% of fledglings survive. Adult annual mortality averages 5–7% with females being higher than males.

CONSERVATION STATUS
Vulnerable. The main populations are at South Georgia (2,100 pairs annually), Marion and Prince Edward Island (3,000), Crozet (1,700), and Kerguelen Island (1,400). All colonies have experienced declines in breeding populations which have been attributed to mortality associated with long-line fisheries in different parts of the southern oceans.

SIGNIFICANCE TO HUMANS
None known. ◆

Light-mantled albatross
Phoebetria palpebrata

TAXONOMY
Phoebetria palpebrata J.R. Forster, 1785, south of Cape of Good Hope. Monotypic.

OTHER COMMON NAMES
English: Light-mantled sooty, gray-mantled albatross; French: Albatros fuligineux; German: Graumantel-Rußalbatros; Spanish: Albatros Tiznado.

PHYSICAL CHARACTERISTICS
Wingspan 6.0–7.15 ft (183–218 cm); 6.1–8.1 lb (2.5–3.7 kg). Small, all dark albatross with paler mantle and a partial white eye-ring. Bill black with pale blue sulcus line.

DISTRIBUTION
Widely distributed throughout the southern oceans breeding at South Georgia, Marion, Prince Edward, Crozet, Kerguelen, Heard, Macquarie, Auckland, Campbell, and Antipodes Islands. Distributed at sea generally south of 40° latitude to the edges of Antarctica.

HABITAT
Marine. Generally breeding in isolated nests on sheltered steep slopes or cliff ledges close to a rock face.

BEHAVIOR
Aerial displays and formation flying are a distinctive feature of courtship and pair-bonding behavior. Mutual calling modulated in tone by the position of the head is an essential part of the displays. Does not have open or extended wing displays, but uses the long tail in display more than other albatrosses.

FEEDING ECOLOGY AND DIET
Mainly solitary at sea, feeding by surface seizing or surface plunging, chiefly for cephalopods and krill. Sometimes fish and carrion including remains of birds at sea. Some observed interaction with commercial fishing.

REPRODUCTIVE BIOLOGY
Lays one egg between October and November with the 2 week laying period being shorter than other albatrosses except the dark-mantled sooty albatross. Incubation lasts for 65–72 days. Have the longest incubation shifts of any albatross. Hatching takes 3–5 days. Chicks are guarded by a parent for the first three weeks. Mean fledging varies between 140 days (Macquarie) and 170 days (Marion Island). Productivity variable. Monagamous. Generally classed as a biennial breeder. Starts breeding at 8–15 years. Adult annual mortality probably about 3%.

CONSERVATION STATUS
Data Deficient, not globally threatened. Tentatively estimated to have a world population of 30,000 breeding pairs. Main causes of nesting failure seem to be starvation and desertion by parents, which along with the length of foraging stints suggests

a species with distant and restricted food sources. Incidence of fisheries bycatch not large.

SIGNIFICANCE TO HUMANS
None known. ◆

Chatham mollymawk
Diomedea cauta eremita

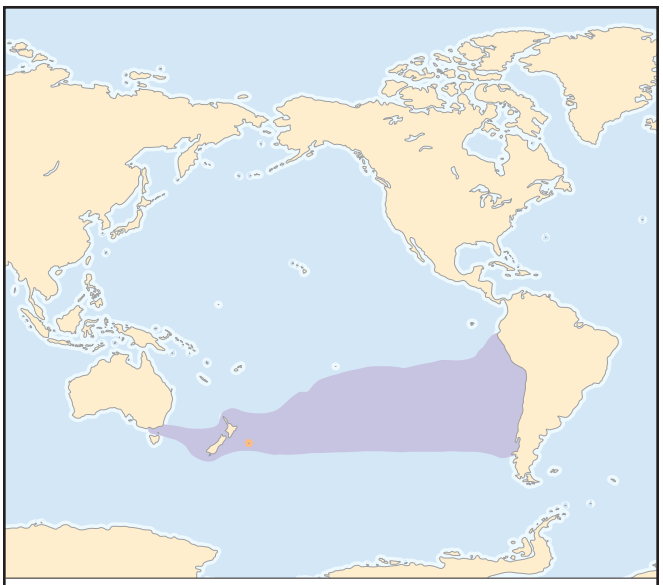
TAXONOMY
Diomedea cauta eremita Murphy, 1930, Pyramid Rock, Chatham Islands.

OTHER COMMON NAMES
English: Chatham Islands albatross; shy albatross; French: Albatros des Chatham; German: Chatham albatros; Spanish: Albatros de Chatham.

PHYSICAL CHARACTERISTICS
The "shy" mollymawks are the largest mollymawks. *D. eremita* is the smallest (6.8–10.4 lb; 3.1–4.7 kg) and darkest of the "shy" mollymawks. White body, dark gray head and mantle, black upper wing and tail, underwing white except for wingtip and small dark patch at base of wing leading edge. Bill chrome yellow with dark spot at tip of lower mandible. Orange cheek stripe.

DISTRIBUTION
Breeds only at The Pyramid, a small rocky cone (650 ft; 200 m high) in the Chatham Islands. Rarely recorded at sea away from breeding location. During the breeding season mainly found within 190 mi (300 km) of the colony on and along the edge of the continental shelf.

HABITAT
Marine. Small pedestal nests of soil and limited vegetation, which may collapse in periods of extended drought, on mainly bare steep rocky slopes, crevices and ledges.



BEHAVIOR
Similar to other mollymawks with harsh buzzing bray with open mouth used in both threat and courtship. A range of displays featuring fanning of the tail, mutual jousting of bills, and tympanic grunting over the back between partly raised wings.

FEEDING ECOLOGY AND DIET
Probably surface seizing of a mix of cephalopods, krill, floating barnacles, and fish. Scavenges behind fishing vessels for baits, discards and offal.

REPRODUCTIVE BIOLOGY
Lays one egg between 20 August and 1 October. Incubation period 68–72 days shared by both parents with short stints rarely longer than 5 days. Fledging estimated at 130–140 days from hatching. Adolescents return from 4 years and first breeding recorded at 7 years. Productivity averages 60% of available nest sites. Crude estimates of annual adult mortality range between 4 and 15%. Breeds annually and seemingly monogamous, pairing for life.

CONSERVATION STATUS
One of two albatrosses classed as Critically Endangered because of tiny single breeding place, and recent evidence of deterioration of habitat. With 5,300 occupied breeding sites, the breeding population is probably c. 4,200 pairs. No evidence of population decline between 1975 and 2001. Now protected, but sporadic small harvests of tens of birds still occur.

SIGNIFICANCE TO HUMANS
None known. ◆

Black-browed mollymawk
Diomedea melanophris

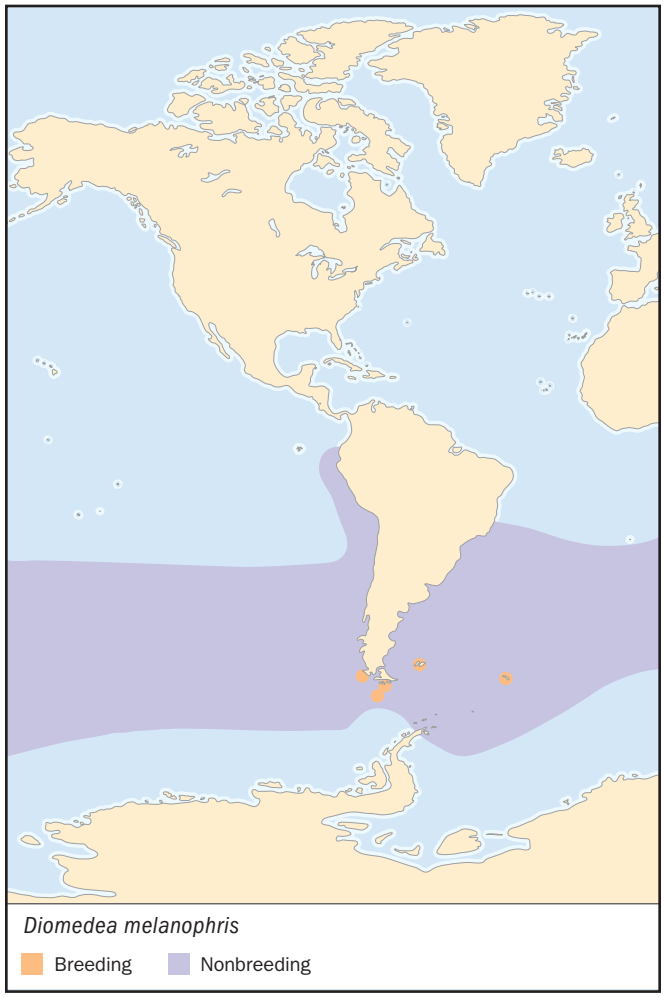
TAXONOMY
Diomedea melanophris Temminck, 1828, Cape of Good Hope. Two subspecies.

OTHER COMMON NAMES
English: Black-browed albatross; French: Albatros à sourcils noirs; German: Schwarzbrauenalbatros; Spanish: Albatros Ojeroso.

PHYSICAL CHARACTERISTICS
Wingspan c. 7.9 ft (240 cm); 6.4–10.3 lb (2.9–4.7 kg). Heavily built mollymawk with mainly all white body and head, black upper wings, mantle and tail, underwing black with variable amounts of central white. Eyebrow black.

DISTRIBUTION
The most plentiful of the albatrosses with 98% of breeding concentrated in the southern Chile at Diego Ramirez, Islas Ildefonso, Diego de Almagra (Chile), south Atlantic at Falkland Islands (12 islands) forming a distinctive genetic grouping; a second genetic grouping comprising South Georgia, small numbers at Crozet, Kerguelen, Heard, and McDonald Islands in the Indian Ocean and very small numbers at Macquarie, Bishop & Clerk, Antipodes, Campbell Islands and The Snares in the southwest Pacific. Most common straggler into North Atlantic.

HABITAT
Marine, not significantly pelagic, being found close to coast more than other albatrosses. Highly colonial breeder, can be in large colonies of thousands of nests. Often on coastal tussock slopes or ledges where nests are built of packed soil and grasses



and used in successive seasons. Largest colonies in the Falkland Islands are on gently sloping rocky terrain without vegetation.

BEHAVIOR
Colonies actively noisy with strident territorial open mouthed bray with flagging of the head, and aggressive harsh cackling. Like other Mollymawks uses fanned tail extensively in display sequences.

FEEDING ECOLOGY AND DIET
Most food taken by surface seizing, with occasional shallow plunging, and swimming below surface. Mainly crustaceans, squid, fish, carrion, and fisheries discards or offal. Feeds extensively on large swarms of krill. Kleptoparisitism (prey theft) observed with stealing from surfacing shags. Sometimes follows whales. Often feeds aggressively among flocks of albatrosses and petrels.

REPRODUCTIVE BIOLOGY
Annual breeder, laying one egg with laying period covering three weeks with a mean of 10 October at South Georgia, but three weeks earlier at Falklands/Crozet and Kerguelen Islands. Incubation is 68–71 days with a guard stage of 1–4 weeks following hatching, before fledging from 120–130 days. Overall productivity averages 27% for chicks fledged from eggs laid. Pairing usually for life. Adolescents return at 2–3 years old and breed at 10 years with c. 28% or less of fledglings surviving to breed. Adults have an annual mortality c. 8–9% with females surviving better than males.

CONSERVATION STATUS
Not globally threatened, with a population of c. 600,000 breeding pairs, but with significant declines noted in some areas. But *D. m. impavida* (26,000 pairs) is classed as vulnerable as its breeding is restricted to one island.

SIGNIFICANCE TO HUMANS
None known. ◆

Laysan albatross
Diomedea immutabilis

TAXONOMY
Diomedea immutabilis Rothschild, 1893, Laysan Island. Monotypic.

OTHER COMMON NAMES
French: Albatros de Laysan; German: Laysanalbatros; Spanish: Albatros de Laysan.

PHYSICAL CHARACTERISTICS
Wingspan 6.4–6.7 ft (195–203 cm); 5.3–9.0 lb (2.4–4.1 kg). A slender white albatross, with underwing most similar to *D. melanophris*, but with black patches at wrist and elbow. Distinctive gray patch around eye and cheeks. Bill has yellowish orange broad base, blending to pinker horn and then black at tip.

DISTRIBUTION
The most plentiful of the north Pacific albatrosses. Almost all breed in the Hawaiian chain of islands with largest colonies at Midway and Laysan Island. Tiny new populations at Mukojima in Bonin Islands (west Pacific), and in eastern Pacific off Mexican coast at Islas Guadalupe, Benedicto and Clarion. During the breeding season regularly travels to the seas separating Japan from the western Aleutians.

HABITAT
Marine, combined pelagic and coastal shelves, but rarely approaches land except breeding islands.

BEHAVIOR
Colonies actively noisy during daylight with distinctive brays, whistles, groans, and calls. Along with *P. nigripes*, has a wider range of displays than other albatrosses. There are actively energetic dances with birds circling about each other, walking and standing and prancing on extreme tiptoe, swaying and jousting motions of the head, combining with sideways lifting bent-wing postures similar to all north Pacific albatrosses.

FEEDING ECOLOGY AND DIET
Mainly squid, but also fish and fish eggs, crustaceans and coelenterates. Does not often follow ships. Undertakes a mix of long and short foraging flights when chick rearing, to compensate for far distant feeding locations.

REPRODUCTIVE BIOLOGY
Nest a scrape in ground, built up around rim by debris and sand with one egg. Annual breeder laying between 20 November and 24 December. Incubation lasts an average of 64 days, with longest stints at beginning of incubation lasting more than 3 weeks. Newly hatched chicks are guarded for c. 27 days and are then left alone except for feeding visits until fledging at c. 165 days. Productivity averages 64%, though 4–24% of chicks may die before fledging through dehydration, starvation, or wandering into other territories to beg for food. Only c. 14% of fledglings may survive to breed at 9 years, and adults have annual mortality of 5%.

CONSERVATION STATUS
Not globally threatened with a world population of c. 607,000 breeding pairs, but some colonies may be decreasing. Drift gill-netting in the north Pacific has been a major source of mortality (17,500 in one year) and effects of longline fisheries not yet known. Have recorded high levels of contaminants which may affect breeding, as well as ingestion of plastic rubbish.

SIGNIFICANCE TO HUMANS
Like the oceanic "wanderer" of the Southern Hemisphere which has come to epitomize the albatross, so the "gooney" is the common image of the albatross in the countries surrounding the north Pacific. ◆

Resources

Books

BirdLife International. *Threatened Birds of the World.* Barcelona and Cambridge, UK: Lynx Edicions and BirdLife International, 2000.

Croxall, J.P. ed. *Seabirds: Feeding Ecology and Role in Marine Ecosystems.* New York: Cambridge University Press, 1987.

del Hoyo, J., A. Elliott, and J. Sargatal, eds. *Ostrich to Ducks. Vol. 1 of Handbook of the Birds of the World.* Barcelona: Lynx Edicions, 1992.

Marchant, S., Higgins, P.J., eds. *Ratites to Ducks. Vol. 1A of Handbook of Australian, New Zealand and Antarctic Birds.* Melbourne: Oxford University Press, 1990.

Robertson, G., R. Gales, eds. *Albatross Biology and Conservation.* Chipping Norton, Australia: Surrey Beatty, 1998.

Tickell, W.L.N. *Albatrosses.* Sussex: Pica Press, 2000.

Warham, J. *The Petrels: Their Ecology and Breeding Systems.* New York: Academic Press, 1990.

Warham, J. *The Behaviour, Population Biology and Physiology of the Petrels.* New York: Academic Press, 1996.

Periodicals

Cooper, J. ed. Albatross and Petrel Mortality from Longline Fishing International Workshop, Honolulu, Hawaii, USA. Report and presented papers. *Marine Ornithology* 28 (2000): 153–190.

Flint, E., K, Swift. eds. Second International Conference on the Biology and Conservation of Albatrosses and other Petrels, Honolulu, Hawaii, USA. Abstract of oral and poster presentations. *Marine Ornithology* 28 (2000): 125–152.

Nicholls, D.G., C. J. R. Robertson, P. A. Prince, M. D. Murray, K. J. Walker, G. P. Elliott. Foraging Niches of Three *Diomedea* Albatrosses. *Marine Ecology Progress Series* 231 (2002): 269–77.

Organizations

BirdLife International. Wellbrook Court, Girton Road, Cambridge, Cambridgeshire CB3 0NA United Kingdom. Phone: +44 1 223 277 318. Fax: +44-1-223-277-200. E-mail: birdlife@birdlife.org.uk Web site: <http://www.birdlife.net>

Christopher John Rutherford Robertson

Shearwaters, petrels, and fulmars
(Procellariidae)

Class Aves
Order Procellariiformes
Family Procellariidae

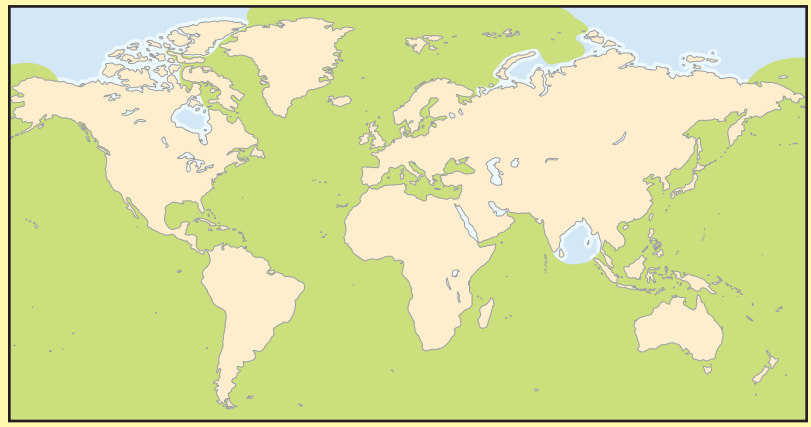
Thumbnail description
Medium-sized tube-nosed seabirds with hooked bill and large wingspan for gliding

Size
9.1–39 in (23–99 cm); 2.8 oz–11 lb (78 g–5 kg); wingspan 20.9–80.7 in (53–205 cm)

Number of genera, species
12 genera; 60–76 species

Habitat
Marine

Conservation status
Critically endangered: 10 species; Endangered: 6 species; Vulnerable: 20 species; Lower Risk/Near Threatened: 9 species



Distribution
Oceans worldwide

Evolution and systematics

The Procellariiformes is one of the most primitive bird orders. In his 1996 book, John Warham proposed that ancestral procellariiforms may have resembled *Bulweria*; that is, they may have been small in size, used natural cavities for nesting, and performed few vocalizations or visual displays. Procellariidae probably diverged from other Procellariiformes in the Eocene, about 40–50 million years ago, coinciding with a wide procellariiform radiation.

Systematics within the family are subject to debate. Because procellariids spend so much time at sea, little is known about them outside of their terrestrial breeding habits. For some species, not even that is known. In addition, the slow rate of speciation makes delineating species difficult. Therefore, debate continues regarding the taxonomy of the family. However, there are four natural groups of Procellariidae. Fulmar-petrels comprise seven species in five genera, ranging from the Arctic to Antarctica. Gadfly-petrels include two genera of 25–36 medium-sized species, some of which are the least known of the family. Prions include seven species in two genera, all of which are found in southern oceans. The shearwaters include 21–26 species in three genera.

Physical characteristics

As Procellariiformes, the procellariids have hooked bills with tubular nostrils. The sharp tip of the bill is an effective implement for handling prey; the tubular nostrils may be related to the well-developed sense of smell used for finding food at great distances and nests in the dark.

Size ranges from 9.1–11 in (23–28 cm) for fairy prions (*Pachyptila turtur*) to 31.9–39 in (81–99 cm) for giant petrels (*Macronectes* spp.), which sport wingspans of about 2.2 yards (2 m). Plumage varies among species and consists of whites, blues, grays, browns, and blacks and does not vary by sex or season; juveniles typically resemble adults.

Most procellariidae are awkward on land because of weak legs set far back on the body. Rather than walking on their legs, they tend to shuffle along on the breast and wings. The giant petrels are the exception; they have strong legs suitable for scavenging beached carcasses.

Prions have a unique upper bill that is fringed with lamellae (thin plates) that act like baleen to filter plankton out of the water.

Distribution

Procellariidae can be found in oceans throughout the world. However, the Southern Hemisphere contains far more species than the Northern. Fulmar-petrels prefer cooler waters and are rarely found in subtropic waters. Prions are found in southern temperate subantarctic and Antarctic zones. Shearwaters, the most diverse in terms of habitats used, are found in both hemispheres, from tropical to arctic waters.

Some procellariids undergo migrations of thousands of miles each year; other species remain closer to their breeding grounds year-round. Short-tailed shearwaters (*Puffinus tenuirostris*) cover 120° of latitude in their annual trek from subantarctic nesting grounds to subarctic feeding grounds. Cory's shearwaters (*Calonectris diomedea*) tend to disperse and wander outside of the breeding season, with less specific feeding grounds.

A northern fulmar (*Fulmaris glacialis*) vomits stomach oils to defend its nest site against an intruder. (Illustration by Bruce Worden)

Habitat

Procellariids are marine; they come to land almost exclusively to breed.

Behavior

Procellariids are excellent flyers, alternating flapping and dynamic soaring. Shearwaters are named for their ability to dip and glide between waves, just above the ocean surface.

Procellariids have an amazing, but not infallible, homing ability. Records of lost procellariids are not uncommon, and in 1999, a great shearwater (*Puffinus gravis*) wandered to inland England when it should have been nesting in the South Atlantic.

Procellariids vomit smelly stomach oils on invaders. Fulmar-petrels vomit on intrusive conspecifics at breeding colonies, but other procellariids reserve this tactic for use against predators or nosy humans.

On land, prions, shearwaters, and most gadfly-petrels are nocturnal, perhaps because they are awkward on land and vulnerable to predation by gulls, raptors, and crows.

Vocal communication is most common at breeding colonies, with sounds ranging from coos to growls to shrill cries. Many species are silent at sea, but fulmar-petrels make a raucous gull-like noise when competing for food in large flocks.

Feeding ecology and diet

Almost all procellariids feed exclusively at sea on squid, fish, plankton, and discards from fishing boats. Procellariids use their keen sense of smell to locate food. Giant petrels focus on seal and penguin carcasses but switch to squid, krill, and fish when carcasses are scarce. Prions eat primarily zooplankton that they strain through their fringed upper bill. Some prions hydroplane: they submerge the bill as they fly low over the water and filter plankton as they go.

Giant petrels (*Macronectes* sp.) treading water in face-to-face feeding competition over the seal carcass floating in the water nearby (South Georgia Island, Falkland Islands). (Photo by Greg Dimijian. Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

Procellarids choose breeding grounds with ready access to the sea. Many species form huge breeding colonies: one sooty shearwater (*Puffinus griseus*) colony on the Snares Islands contains 2.5 million pairs. Other species, such as giant petrels, breed alone or in small, loose colonies.

Procellariid nests vary from mounds of grass or stones built by giant petrels to cliff ledges used by northern fulmars (*Fulmarus glacialis*) to burrows used by shearwaters, prions, and gadfly-petrels. The burrow nesters either excavate their own cavities or find abandoned rabbit dens or natural cavities. Few species are forest nesters.

Breeding is usually annual in the local spring or summer. The age of sexual maturity ranges from three to twelve years, with five to six years as the average age of first breeding. Procellariiformes are typically monogamous, mating for life, with pairs using the same nest year after year. One pair of northern fulmars reportedly has used the same nest for at least 25 years.

One white egg is laid that constitutes an average of 12–16% of the female's body weight. Both parents incubate the egg in alternating shifts of 2–14 days for an incubation period of six to nine weeks, depending on species. After hatching, both parents care for the chick, leaving it alone after 2–20 days (as soon as it can regulate its own body temperature). The parents then visit the chick only for feeding. Food consists of fat-rich stomach oils produced by partial digestion of the adults' normal diet.

Chicks put on large amounts of fat and quickly outweigh their parents, then slim down to an adult weight before fledging. For example, northern fulmar chicks weigh 33.5 oz (950 g) by 40–45 days after hatching. When they fledge at 57 days they weigh 28.2 oz (800 g). The large fat deposits might be insurance against periods of starvation that could occur while parents are away foraging. However, fat stores exceed the amount necessary to survive periods of parental absence and are maintained during fledging—the weight loss prior to fledging is due largely to water loss. Another theory suggests that fat stores are for survival after fledging when chicks must learn to forage for themselves.

A northern fulmar (*Fulmarus glacialis*) and egg at Bass Rock, Scotland. (Photo by J.C. Carton. Bruce Coleman Inc. Reproduced by permission.)

Antarctic petrel (*Thalassoica antarctica*) chick camouflaged in the rocks and snow. (Photo by Joyce Photographics. Photo Researchers, Inc. Reproduced by permission.)

As chicks approach full size, they begin to flap their wings around the nest in preparation for the first flight. A week or two after the parents have abandoned the chick, it fledges, flinging itself out to sea. While most chicks survive fledging, introduced (rats and cats) and natural (gulls and raptors) predators pose a threat.

Life expectancy for procellariids is about 15–20 years, although some individuals are known to have lived much longer. Britain's oldest bird, a northern fulmar aged over 50 years, was missing and presumed dead in November 1997.

Conservation status

While some procellariids are thriving, others are among the most threatened of all birds. The breeding population of Zino's petrel (*Pterodroma madeira*) is estimated to be 20–30 pairs. Estimates put the total Chatham petrel (*Pterodroma axillaris*) population at 800–1,000 birds. It breeds only on tiny South East Island in the Chatham Islands of New Zealand, where broad-billed prions (*Pachyptila vittata*) are the primary threat because they kill chicks, eggs, and sometimes adults.

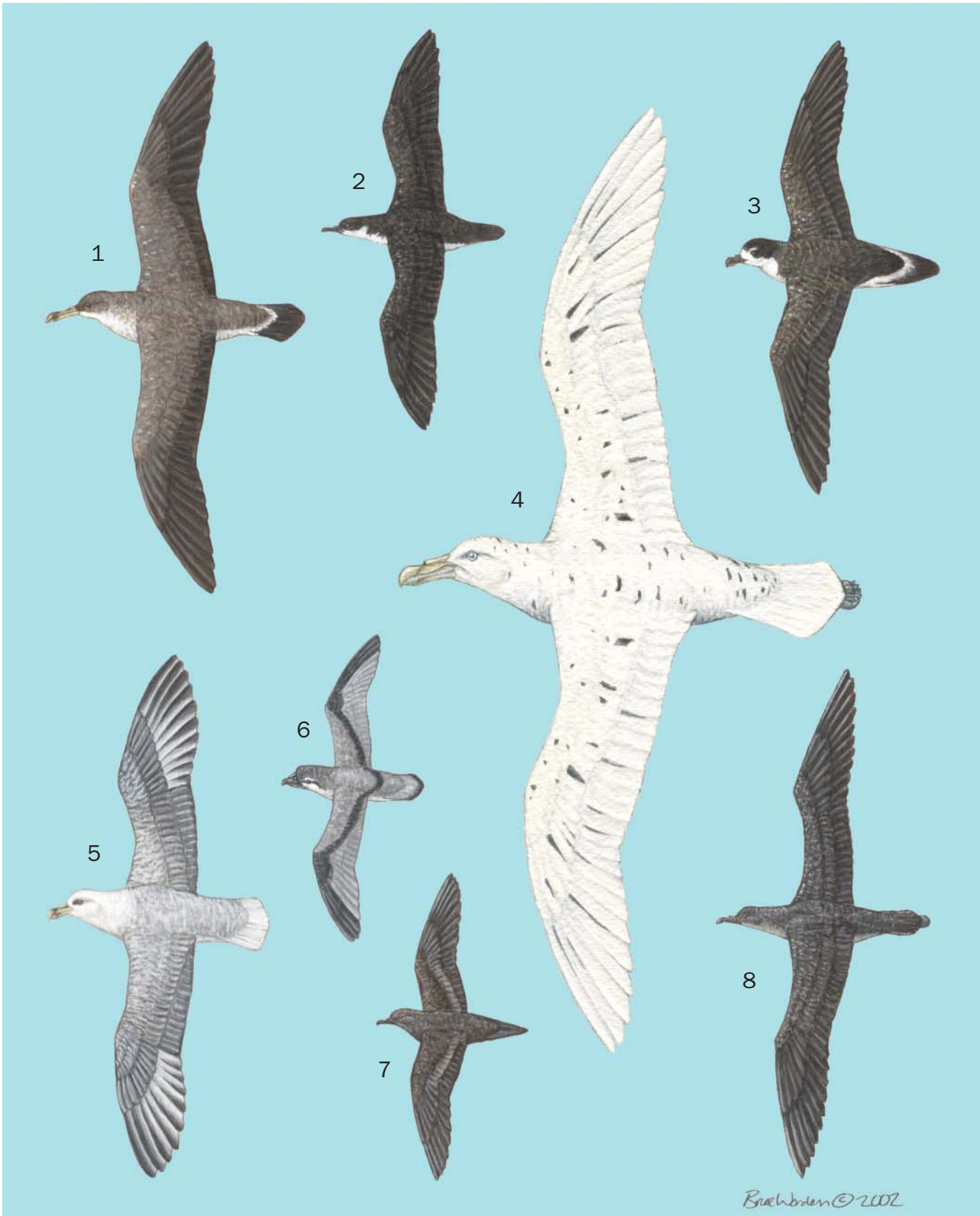
All species face the same challenges: introduced predators, habitat deterioration, and human exploitation. International conservation efforts are protecting breeding grounds. Gough Islands, a South Atlantic breeding ground for great shearwaters and others, was declared a World Heritage Site in 1995 by the United Nations science agency UNESCO. Predator extermination programs show promise. After a 100-year absence, gray (*Procellaria cinerea*) and blue (*Halobaena caerulea*) petrels returned to breed on Macquerie Island in 2001 after the complete removal of feral cats.

Significance to humans

Several cultures including Eskimos, Maoris, and Europeans have traditionally eaten procellariid eggs, chicks, and adults. Natives of New Zealand and Tasmania still harvest several thousand chicks annually for feathers, fat, flesh, oil, and down, earning the short-tailed and sooty shearwaters the local nickname of muttonbirds.

On June 20, 2001, the Agreement on the Conservation of Albatrosses and Petrels was signed by seven major fishing nations. The agreement requires member nations to manage fisheries by-catch, protect breeding sites from disturbance, promote conservation in the fishing industry, and conduct research to understand threatened species. A primary goal is to reduce seabird fatalities by long-line fishing. An estimated 300–350,000 seabirds are killed annually while attempting to get long-line bait. Long-liners present a dilemma for conservationists because this fishing technique is considered environmentally good for fish.

Flesh-footed shearwaters (*Puffinus carneipes*) in their nest in the ground in Mercury Islands, New Zealand. (Photo by Asa C. Thoresen. Photo Researchers, Inc. Reproduced by permission.)



1. Cory's shearwater (*Calonectris diomedea*); 2. Manx shearwater (*Puffinus puffinus*); 3. Bermuda petrel (*Pterodroma cahow*); 4. Southern giant petrel (*Macronectes giganteus*); 5. Northern fulmar (*Fulmarus glacialis*); 6. Broad-billed prion (*Pachyptila vittata*); 7. Bulwer's petrel (*Bulweria bulwerii*); 8. Short-tailed shearwater (*Puffinus tenuirostris*). (Illustration by Bruce Worden)

Species accounts

Cory's shearwater
Calonectris diomedea

TAXONOMY
Procellaria diomedea Scopoli, 1769, no locality: Tremiti Islands, Adriatic Sea.

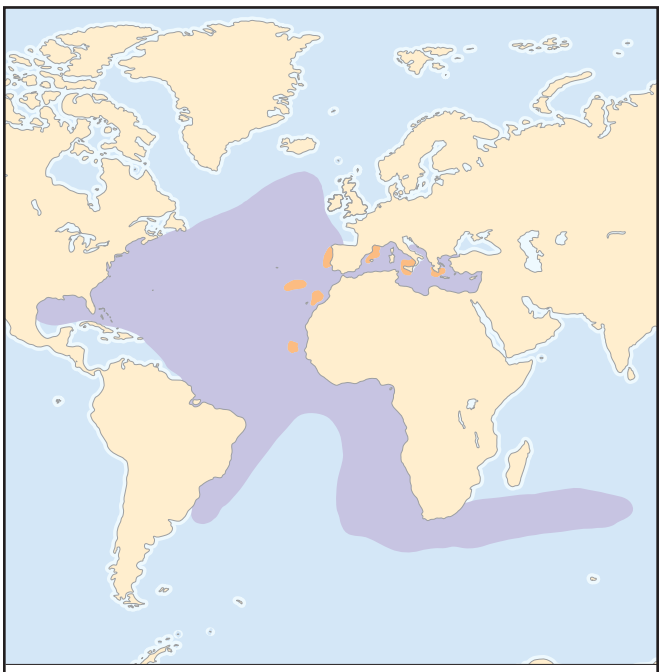
OTHER COMMON NAMES
English: Mediterranean/(North) Atlantic shearwater; French: Puffin cendré; German: Gelbschnabel-Sturmtaucher; Spanish: Pardela Ceniciera.

PHYSICAL CHARACTERISTICS
17.7–18.9 in (45–48 cm); 19.8–33.7 oz (560–956 g); wingspan 39.4–49.2 in (100–125 cm). Heavy bodied. Uniformly pale underneath, with darker gray/brown plumage above; yellow bill. Has lighter cap than the similar greater shearwater.

DISTRIBUTION
Breeds on islands in the eastern North Atlantic and Mediterranean, migrates across the equator to South Atlantic and Indian oceans.

HABITAT
Marine, nesting on barren offshore islands away from mainland. Nests on rocky slopes, on cliffs, or in caves.

BEHAVIOR
Cory's shearwaters fly with a slower, more relaxed wingbeat than do other shearwaters.



FEEDING ECOLOGY AND DIET
Feeds mainly at night on fish, squid, crustaceans, and offal by plunging and surface-seizing. Follows fishing boats.

REPRODUCTIVE BIOLOGY
Breeding season starts in April. Nests in natural nooks such as burrows or rock crevices. The single white egg is incubated for 54 days. The brown chicks are brooded for approximately four days, fledging after 97 days. Sexual maturity at seven to 13 years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Regarding the awesome sight of migrating Cory's shearwaters, the Stuarts wrote in *Birds of Africa*: "Those that breed in the Mediterranean move in from the Atlantic at a rate of some 3,600 birds per hour through the Strait of Gibraltar. At the end of the breeding season when the adults and young birds depart for their overwintering grounds in the open ocean, they stream through the Strait in October to November at an estimated rate of 26,272 each day." ◆

Manx shearwater
Puffinus puffinus

TAXONOMY
Procellaria puffinus Brünnich, 1764, Faeroes and Norway.

OTHER COMMON NAMES
French: Puffin des Anglais; German: Schwarzschnabel-Sturmtaucher; Spanish: Pardela Pichoneta.

PHYSICAL CHARACTERISTICS
11.8–15 in (30–38 cm), 12.3–20.3 oz (350–575 g), wingspan 29.9–35 in (76–89 cm). Blackish upper body with contrasting white underneath. Upper parts are much darker than Cory's shearwater; face has more black than the little shearwater. The white undertail coverts contrast with the dark undertail coverts of the black-vented shearwater, once considered a subspecies of the Manx shearwater.

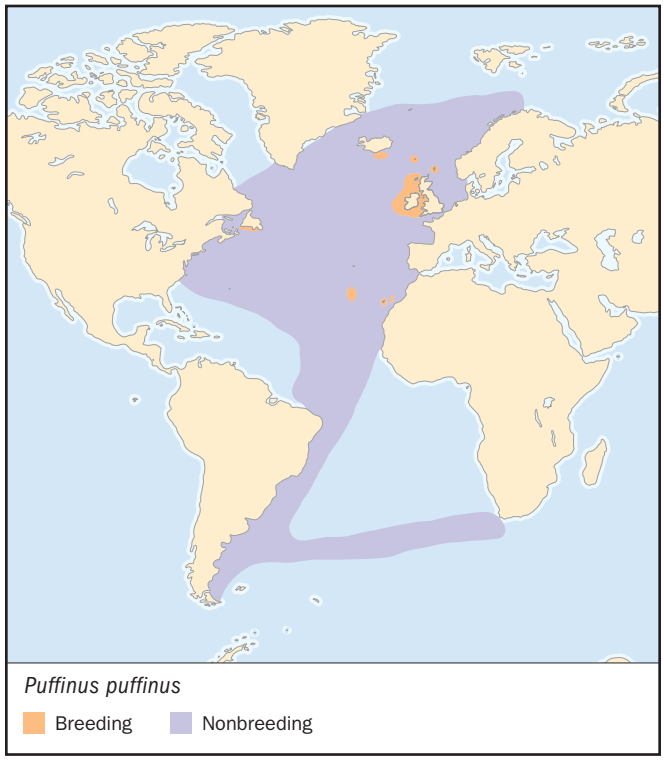
DISTRIBUTION
Breeds on islands on both sides of the North Atlantic, winters in Atlantic off Brazil, Argentina, and South Africa.

HABITAT
Marine, primarily over continental shelf.

BEHAVIOR
Gregarious, swims and dives to feed. Dives can be from the surface or from the air, and do not go deep below the water surface. To start the breeding season, males claim abandoned rabbit burrows, then call from within to attract females.

FEEDING ECOLOGY AND DIET
Feeds on small shoaling fish, squid, crustaceans, and offal. Does not normally feed in large flocks.

REPRODUCTIVE BIOLOGY
Colonial burrow nester. Breeding season begins in March. The egg, laid in mid-May, is incubated 47–55 days and fledging oc-



curs after 62–76 days. Young fledge at night to begin a two to three week journey to wintering sites off Brazil, Argentina, and Uruguay. Sexual maturity at 5–6 years.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Formerly hunted for food. ◆

Short-tailed shearwater
Puffinus tenuirostris

TAXONOMY
Procellaria tenuirostris Temminck, 1835, seas north of Japan and shores of Korea.

OTHER COMMON NAMES
English: Slender-billed shearwater/petrel, Tasmanian mutton-bird; French: Puffin à bec grêle; German: Kurzschwanz-Sturmtaucher; Spanish: Pardela de Tasmania.

PHYSICAL CHARACTERISTICS
15.7–17.7 in (40–45 cm), 16.9–28.2 oz (480–800 g), wingspan 37.4–39.4 in (95–100 cm). Dark brownish-gray above, lighter underneath. Pale chin, dark bill. Dark feet reach beyond short, square tail.

DISTRIBUTION
Breeds in Tasmania and southern Australia, migrates north across the equator to arctic reaches, including Alaska. Stays primarily in the Pacific.

HABITAT
Marine, found near land and in open seas. Typically breeds on grassy coastal islands.

BEHAVIOR
Forms flocks of up to 20,000.

FEEDING ECOLOGY AND DIET
Fish, crustaceans, and cephalopods. Found with whales. Social feeding is common, including flocking at dawn and dusk to feed on swarming euphausids.

REPRODUCTIVE BIOLOGY
Breeding season starts in October, forming crowded colonies of burrow nests. The single white egg is incubated for 52–55 days; the dark gray to brown chick in brooded for two to three days; fledging after 94 days. Sexual maturity at 4–6 years in males, five to seven years for females. Can live at least 30 years.

Parents on Montague Island travel up to 9,600 miles (15,450 km) round-trip on feeding voyages, the longest flights known for birds feeding young. Such long journeys may serve more to replenish the adults' reserves, than to feed the young.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Approximately 300,000 chicks are harvested each year from Tasmania. ◆

Northern fulmar
Fulmarus glacialis

TAXONOMY
Procellaria glacialis Linnaeus, 1761, within the Arctic Circle (Spitsbergen).

OTHER COMMON NAMES
English: Arctic fulmar; French: Fulmar boréal; German: Eissturmvogel; Spanish: Fulmar Boreal.

PHYSICAL CHARACTERISTICS
With a wingspan of 40.2–44.1 in (102–112 cm), white head, and gray upper body, northern fulmars resemble gulls, but their wings are broader and the neck is thicker. Lighter morphs are more common in Atlantic, darker morphs in Pacific.

DISTRIBUTION
Northern Atlantic and Pacific oceans, has spread southward over much of the Atlantic Ocean. Winters farther south.

HABITAT
Marine, especially colder waters of the Northern Hemisphere.

BEHAVIOR
More aggressive in vomiting habits than other procellariids. Stiff wings held out straight from body help to distinguish them from gulls.

FEEDING ECOLOGY AND DIET
Feed on fish, squid, plankton, and fishing refuse. Feeds in flocks, frequently behind fishing boats. Will scavenge on carrion.

REPRODUCTIVE BIOLOGY
Breeding season begins in May. The single white egg is incubated 47–53 days; the white to dark gray chick is brooded for 2 weeks; fledging after 46–53 days. Nests colonially on cliff ledges and on level ground, and has expanded to buildings and rooftops.

CONSERVATION STATUS
Not threatened. One of few seabirds to increase in numbers and range since 1800. Expansion may be due to food from fishing ship discards or to changing oceanographic conditions. The dependence on fishing ships presents an interesting conservation problem. If ships clean up their refuse, then fulmars may be pushed to feed elsewhere, potentially on smaller birds.

SIGNIFICANCE TO HUMANS
Once hunted for food. Now may be anthropophilic, following fishing ships for food. ◆

Broad-billed prion
Pachyptila vittata

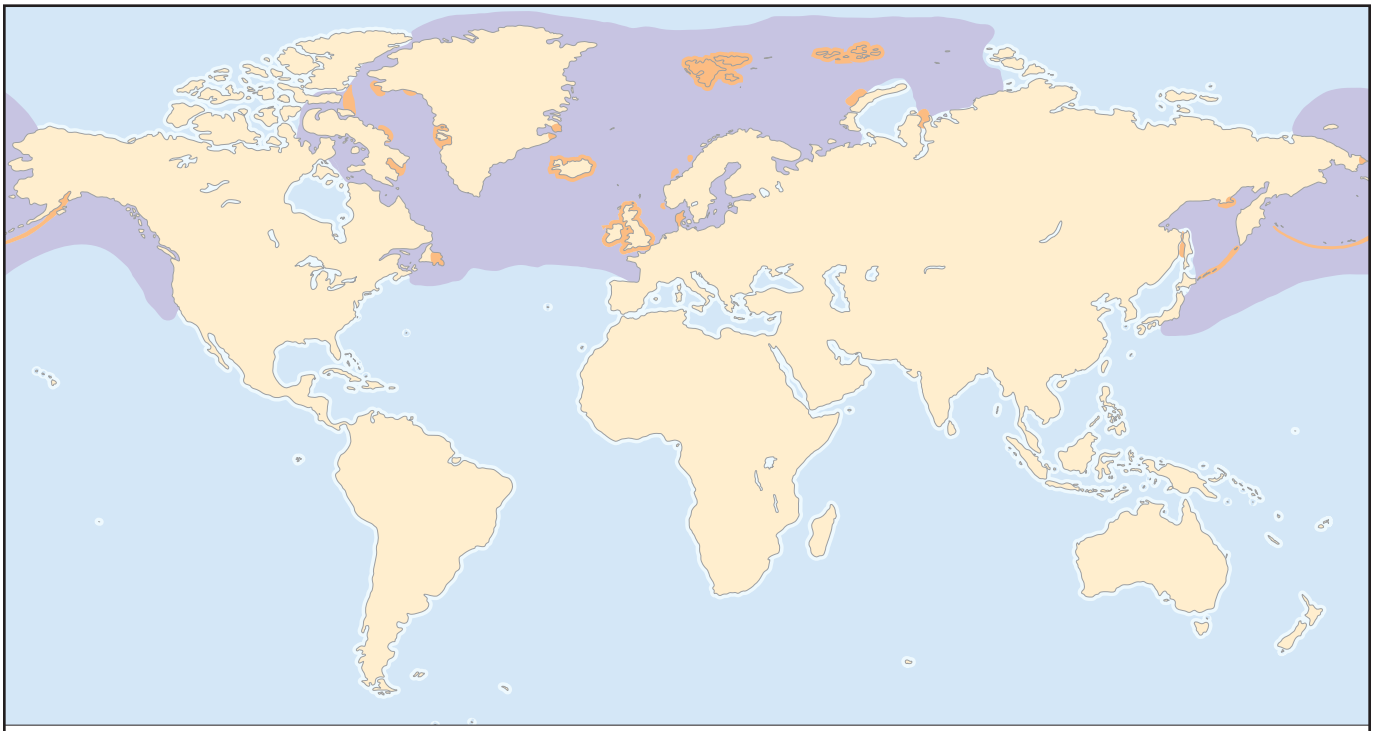
TAXONOMY
Procellaria vittata G. Forster, 1777, lat. 47°.

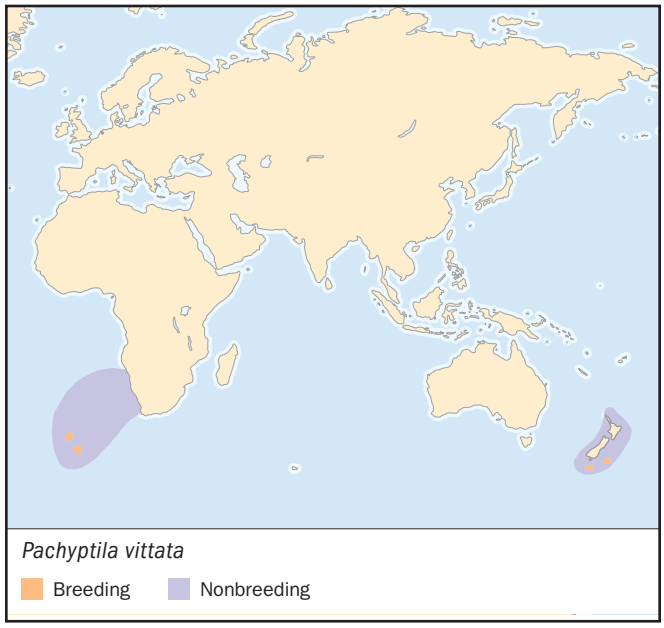
OTHER COMMON NAMES
English: Blue/broad-billed dove-petrel, long-billed/common prion, icebird, whalebird; French: Prion de Forster; German: Großer Entensturmvogel; Spanish: Pato-petrel Piquiancho.

PHYSICAL CHARACTERISTICS
9.8–11.8 in (25–30 cm); 5.6–8.3 oz (160–235 g); wingspan 22.4–26 in (57–66 cm). The largest prion, with a wide bill. Dark patches form an "M" across back of outstretched wings.

DISTRIBUTION
Breeds in South Pacific on New Zealand's South Island and on Chatham Islands, and in the South Atlantic on Gough and Tristan da Cunha Islands.

HABITAT
Marine, stays away from land except to breed. Breeds on barren areas including lava fields, cliffs, and coastal slopes.





BEHAVIOR
Prions are social. Courtship displays are restricted to cover of night or burrows. Pairs defend their burrows aggressively with calls, posturing, or if the threat intensifies, with biting of each other's bill and neck.

FEEDING ECOLOGY AND DIET
Crustaceans (mostly copepods), squid, and fish. Feeds by hydroplaning and by surface-seizing. Does not tend to follow fishing boats. Feeds gregariously.

REPRODUCTIVE BIOLOGY
Breeding season starts in July or August. Forms tight colonies of burrow nests. More than one pair may occupy one nest. The egg is incubated for 50 days and fledging occurs after 50 days.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Bermuda petrel
Pterodroma cahow

TAXONOMY
Aestrelata cahow Nichols and Mowbray, 1916, Castle Island, Bermuda.

OTHER COMMON NAMES
English: Cahow; French: Pétrel des Bermudes; German: Bermudasturmvogel; Spanish: Petrel Cahow.

PHYSICAL CHARACTERISTICS
15.0 in (38 cm); wingspan 35.0 in (89 cm). Brownish-gray upper body, including a cap that covers the eye and a partial brown collar on the nape. Black bill. White underneath, except for black edges of wings. Easily confused with the larger black-capped petrel.

DISTRIBUTION
Islets in Castle Harbour, Bermuda.

HABITAT
Marine. Formerly excavated burrows in sand or soft soils, but now nests on small, rocky offshore islands and in artificial burrows.

BEHAVIOR
Little is known about the natural behavior of these birds. Their normal night-time aerial courtship has been disrupted by lights from human facilities.

FEEDING ECOLOGY AND DIET
Very little known; not known to follow ships.

REPRODUCTIVE BIOLOGY
Breeding season January to June. The single white egg is incubated for 51–54 days; the chick is brooded for one or two days; fledging after 90–100 days. Historically it bred inland in soil burrows, but rats have driven colonies to suboptimal, rocky offshore islets.

CONSERVATION STATUS
Endangered. Had been thought extinct since 1621 after colonists hunted it for food. In 1921, it was found living, and in 1951, 18 breeding pairs were found. Intensive conservation efforts began in 1961; 45 pairs were found breeding in 1994. Current threats include native species (white-tailed tropicbirds [*Phaethon lepturus*] compete for nesting sites), human disturbance (light pollution disrupts nocturnal courtship), natural disasters (flooding of nests became a problem in the 1990s, with rising sea levels), and atmospheric pollution. In 1997, the population was estimated at 180 birds.

SIGNIFICANCE TO HUMANS
Formerly hunted for food. ◆

Bulwer's petrel

Bulweria bulwerii

TAXONOMY
Procellaria bulwerii Jardine and Selby, 1828, Madeira.

OTHER COMMON NAMES
French: Petrel de Bulwer; German: Bulwersturmvogel; Spanish: Petrel de Bulwer.

PHYSICAL CHARACTERISTICS
10.2–11.0 in (26–28 cm); 2.8–4.6 oz (78–130 g); wingspan 26.8–28.7 in (68–73 cm). One of the smallest procellarids. Dark brown plumage, long wings, flies with tail narrowed to a point.

DISTRIBUTION
Throughout the tropics in eastern Atlantic and Pacific oceans. One study suggests that Bulwer's petrel prefers warm waters of intermediate salinity, while Joaquin's petrel (*Bulweria fallax*) prefers slightly higher salinity levels.

HABITAT
Marine, strongly pelaqic. Breeds on barren, remote islands.

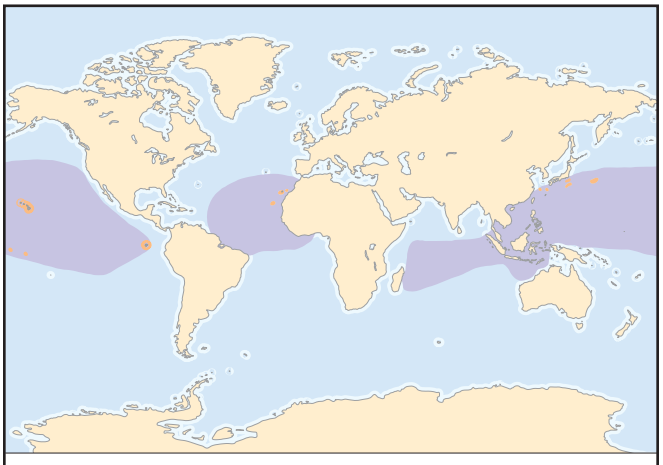
BEHAVIOR
Nocturnal. Both sexes make a barking call known as a "woof." They do not call while flying.

FEEDING ECOLOGY AND DIET
Feeds primarily at night on fish, squid, some crustaceans and sea-striders, by seizing prey from the surface.

REPRODUCTIVE BIOLOGY
Breeding season starts in April or May. Nest in burrows, crevices, cracks, caves, or under other cover. The single white egg is incubated for 44 days; the chick is blackish when it hatches; fledging after 62 days.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Collected for food and fish bait on Atlantic islands. ◆



Southern giant petrel

Macronectes giganteus

TAXONOMY
Procellaria gigantea Gmelin, 1789, Staten Island, off Tierra del Fuego.

OTHER COMMON NAMES
English: Antarctic giant petrel, giant fulmar, stinker, stinkpot; French: Fulmar géant; German: Riesensturmvogel; Spanish: Abanto-marino Antártico.

PHYSICAL CHARACTERISTICS
Largest procellariid; 33.9–39 in (86–99 cm); male 11 lb (5 kg), female 6.6–17.6 lb (3–8 kg); wingspan 72.8–80.7 in (185–205 cm). Enormous yellow bill. Head, neck, and upper breast are pale; the rest of the body is mottled brown on the dark morph, with the underside lighter than the upper parts. Dark legs. The dark color morph resembles the northern giant petrel, but the less common all-white morph is distinctive.

DISTRIBUTION
Found throughout the Southern Hemisphere from Antarctica to the subtropics of Chile, Africa, and Australia.

HABITAT
Marine, feeding in coastal and pelagic southern hemisphere waters. Nests on bare or grassy, exposed ground throughout Antarctica, on the coasts of Chile and Argentina, and on subantarctic and Antarctic islands.

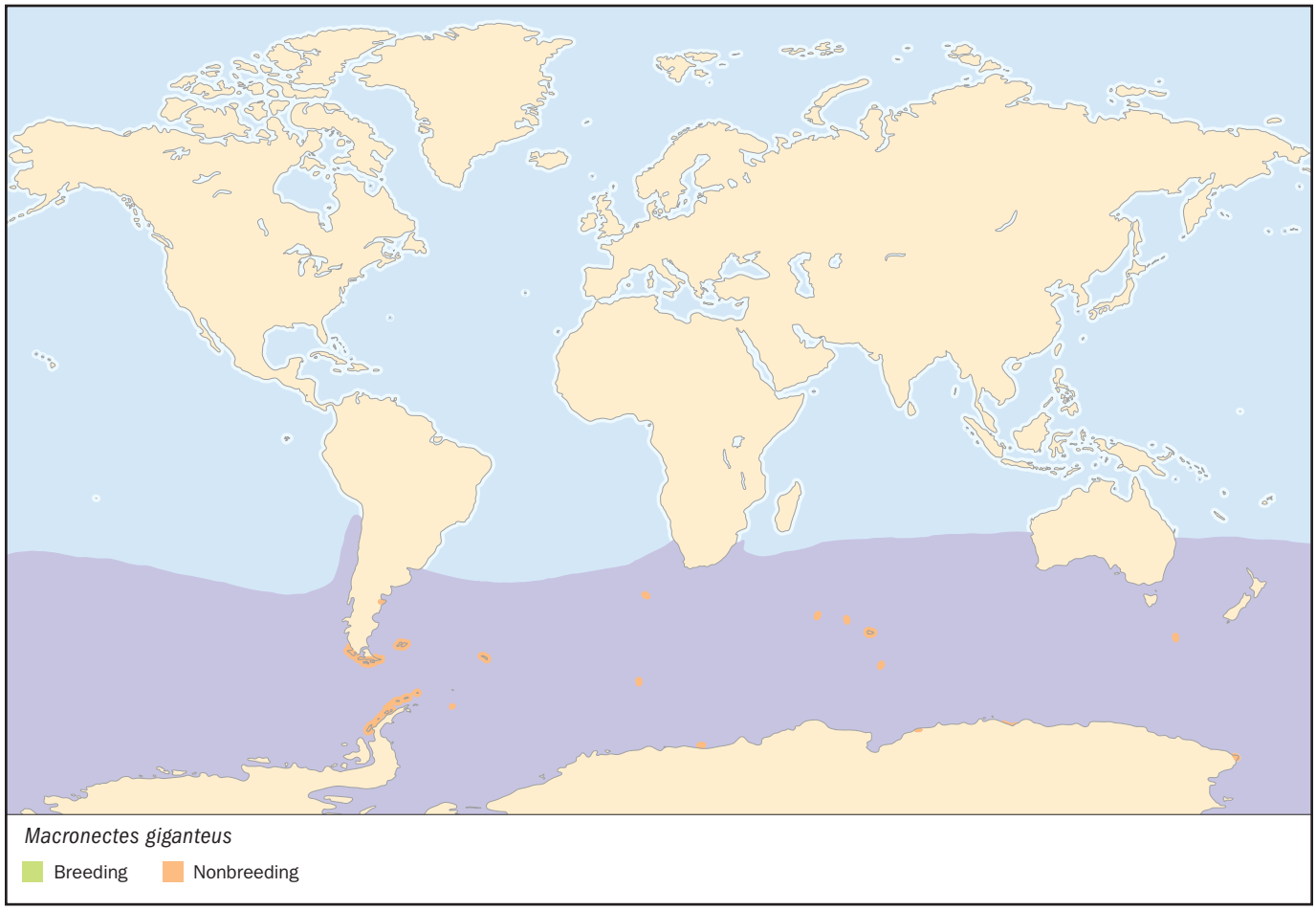
BEHAVIOR
The birds are so tame that researchers can walk up to brooding females and remove chicks from underneath them for study. Their strong legs, unusual for a procellariid, allow the giant petrels to scavenge beached carcasses. The larger males exclude females from carcasses, forcing the females to depend more heavily on live prey taken at sea. Both sexes visit the colony year-round, even outside of the breeding season.

FEEDING ECOLOGY AND DIET
Shunned, even by avid birders, for feeding on rotting carcasses. Parents travel up to 3,000 miles (4,830 km) to ice packs to feed on krill and squid brought to the surface by ocean upwellings. Gather in the thousands at long-line fishing boats.

REPRODUCTIVE BIOLOGY
Sexual maturity at six to seven years of age. Breeding season starts in October. Nest is made by gathering grass and moss, or small stones, into a mound, with a depression in the middle. The single white egg is incubated 55–66 days; the whitish chick is brooded for two or three weeks; fledging at 104–132 days.

CONSERVATION STATUS
Vulnerable. Total population about 36,000 breeding pairs. Many populations have inexplicably decreased by 30–35% since 1981.

SIGNIFICANCE TO HUMANS
Their long lives (the oldest known lived 50 years) make them a valuable indicator species to judge the health of the Antarctic ecosystem. ◆



Resources

Books

BirdLife International. *Threatened Birds of the World.* Cambridge: BirdLife International, 2000.

del Hoyo, J., A. Elliot, and J. Sargatal, eds. "Ostrich to Ducks." In *Handbook of the Birds of the World.* Vol. 1. Barcelona: Lynx Edicions, 1992.

Stuart, Chris, and Tilde Stuart. "Birds of the Oceans." In *Birds of Africa from Seabirds to Seed-Eaters.* Cambridge, Massachusetts: The MIT Press, 1999.

Warham, John. *The Behavior, Population Biology and Physiology of the Petrels.* San Diego, CA: Academic Press, 1996.

Periodicals

Braasch, Gary. "Antarctic Mystery." *International Wildlife* 31 (2001): 52–57.

Phillips, R.A., and K.C. Hamer. "Postnatal Development of Northern Fulmar Chicks, *Fulmarus glacialis*." *Physiological and Biochemical Zoology* 73 (2000): 597–604.

Schultz, Mark A., and Nicholas I. Klomp. "Does the Foraging Strategy of Adult Short-Tailed Shearwaters Cause Obesity in Their Chicks?" *Journal of Avian Biology* 31 (2000): 287–294.

Thompson, Paul M., and Janet C. Ollason. "Lagged Effects of Ocean Climate Change on Fulmar Population Dynamics." *Nature* 413 (2001): 417–420.

Other

Earth-Life Web Productions."Shearwaters (Procellariidae)." 21 Oct. 2001 (21 Feb. 2002). <http://www.earthlife.net/birds/shearwaters.html>.

Gough, G.A., J.R. Sauer, and M. Iliff. *Patuxent Bird Identification Infocenter.* 1998. Version 97.1. Patuxent Wildlife Research Center, Laurel, MD. 28 Dec. 2000 (21 Feb. 2002). <http://www.mbr-pwrc.usgs.gov/Infocenter/infocenter.html>.

Barbara Jean Maynard, PhD

Storm-petrels
(Hydrobatidae)

Class Aves
Order Procellariiformes
Family Hydrobatidae

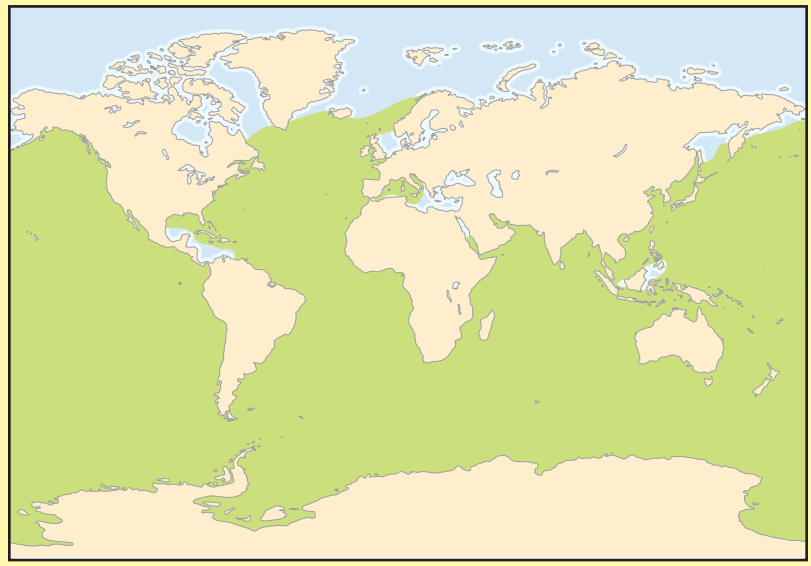
Thumbnail description
Small seabirds with prominent upturned nostrils and dancing flight over the waves

Size
5.5–10 in (13–26 cm)

Number of genera, species
8 genera; 21 species

Habitat
Open sea

Conservation status
Several species, whose status is unknown, are possibly rare



Distribution
Worldwide

Evolution and systematics

The fossil record is poor, represented only by *Oceanodroma hubbsi* from the Upper Miocene of California, *Oceanites zalascarthmus* from the South African Pliocene, and *Primodroma bournei* from the English Eocene.

A number of studies based on comparative anatomy and DNA analyses suggest that the order evolved close to the base of procellariiform radiation.

The family Hydrobatidae is divided into two subfamilies: the Oceanitinae contains seven very long-legged species found in southern seas, and the Hydrobatinae contains 14 rather shorter-legged species mainly found in northern waters.

Physical characteristics

Storm-petrels are small, delicate seabirds whose long legs are used to fend off from the water as the birds snap up food items. The wings are rounded at their tips because the tenth and outermost functional primary is shorter than that of the ninth (primaries are main flight feathers). The fused tubular nostrils are prominent and span nearly half the length of the bill. The smallest species, least storm-petrels (*Oceanodroma microsoma*), weigh only 0.7 oz (20 g) and have a wing span of about 12.6 in (32 cm); the largest, Tristram's storm-petrels (*Oceanodroma tristrami*), weigh about 2.9 oz (83 g) and have a wingspan of 22.4 in (57 cm).

Storm-petrels tend to have dark blackish or brownish plumage, but many are paler ventrally and have white rumps. The tail may be square cut or forked. The feet of birds of the genera *Fregetta* and *Nesofregetta* bear strange spade-like claws. Female storm-petrels tend to be larger than males. Most (perhaps all) storm-petrels carry the musty body odor characteristic of tubenoses. The olfactory lobes of the brain are large and a functional sense of smell has been demonstrated in field experiments at sea and over land.

Distribution

Storm-petrels are found worldwide, but they are particularly numerous in the vast Southern Ocean. Many breed around Australasia but five species are concentrated around islands from Mexico to California. At sea they occur in all oceans but fail to penetrate Arctic seas.

Habitat

Marine distributions of storm-petrels are poorly known; being small, storm-petrels are hard to see and identify as they dart along hugging the waves. Some species prefer warm or cool waters. For example, Leach's storm-petrels (*Oceanodroma leucorhoa*) inhabit cooler water well offshore of the western United States, and wedge-rumped storm-petrels (*Oceanodroma tethys*) and Elliot's storm-petrels (*Oceanites gracilis*) seem confined to cool waters of the Humboldt Current. Some species congregate along areas of upwellings, as does the band-rumped storm-petrel, (*Oceanodroma castro*), which prefers warm water and aggregates off Florida and South Carolina along Gulf Stream eddies. Storm-petrels breed on islands that are free of mammalian predators.

Wedge-rumped storm-petrels (*Oceanodroma tethys*) feed together at the ocean's surface. (Photo by R.L. Pitman/VIREO. Reproduced by permission.)

Behavior

Most nests are in burrows, and the nest sites are retained from season to season and form the focus for the maintenance of the same pair bonds from year to year. Most visit their nests only after dark and appear to have little by way of display except for mutual preening. Aerial flight displays and chasing in species like the wedge-rumped storm-petrel and Wilson's storm-petrel (*Oceanites oceanicus*) have been described. The spectacular performances of the first species take place by day, and this species is evidently adapted to nighttime feeding.

In all species studied the sexes call differently. A variety of churring or whirring sounds is heard from burrows of northern species such as the European storm-petrel (*Hydrobates pelagicus*). On the Norwegian island of Rost, European storm-petrels flutter around the exhaust of the lighthouse engine, and the birds' calls match the rhythm of the engine. Calls may vary from bird to bird, which suggests a role in individual recognition—important for communication after dark. The voices of the southern Oceanitinae tend to be a higher pitch than those of the Hydrobatinae, and their whistles may have a ventriloqual quality.

Most storm-petrels tend to be solitary at sea but flocking also occurs. Some species, like Wilson's storm-petrels, are highly migratory. White-faced storm-petrels (*Pelagodroma marina*) from Western Australia migrate north to winter along the convergences of the northern Indian Ocean. Other species, such as Leach's and European storm-petrels, shift south after breeding, the former to the tropical Atlantic and Pacific oceans and the latter mainly to the Benguela Current off Africa. Other North Pacific species also shift south; for example, Matsudaira's and Swinhoe's storm-petrels (*Oceanodroma matsudairae* and *O. monorhis*) from Japanese seas reach the Indian Ocean via the Straits of Malacca and the Timor Sea. Most storm-petrels breeding off California just disperse into local seas, although the black storm-petrel (*Oceanodroma melania*) moves south to the Humbolt current.

Feeding ecology and diet

Crustaceans are important foods for storm-petrels. For example, euphausids are the most frequent prey item for Wilson's storm-petrels nesting around Antarctica; the euphausid species and its relative importance varies with locale and season. Farther north around the Crozet Islands, the same bird still eats crustaceans, but copepods and cirripedes are relatively more abundant in the diet. The gray-backed storm-petrel (*Garrodia nereis*) seems to specialize on barnacles that evidently are picked off floating rafts of seaweed.

Storm-petrels have a penchant for oily foods. They snip up oil droplets from the sea but seem to avoid man-made oil slicks, perhaps by using their sense of smell. Stomachs usually contain the stomach oil found in most tubenoses, and this oil, being digestible and full of energy, forms an important food for adults and chicks. It is derived directly from prey items, many of which contain heavy loads of oil droplets (especially when breeding).

Storm-petrels usually feed solitarily but will congregate around a suitable food source such as a dead seal or squid. Some species associate with pods of whales, and Wilson's storm-petrels ingest whale feces. Ship following is common; the birds eat small prey churned up by propellers. Wake followers tend to attract others, and up to 50 black storm-petrels have been seen combing the wake at one time.

Storm-petrels feed from the top few inches of the sea. They seem to have the ability to stay within bill range of a heaving sea. This ability is aided by their low wing loadings, which means that as the wave heaves, the air above moves with it and so does the bird. Both Wilson's and black storm-petrels will dive to retrieve food. The precise mode of feeding varies with the species, the length of the legs, and other factors. Some species, like Wilson's storm-petrels, hold their wings high while fending off from the surface with both feet, whereas black-bellied storm-petrels (*Fregetta tropica*) hold their wings out and skip from side to side. Feeding birds face the wind, and if a gale shifts abruptly through 90 degrees to blow straight down the wave furrows, the tiny birds may be unable to feed and be forced far down wind.

A white-vented storm-petrel (*Oceanites gracilis*) feeds by plucking tiny debris from the sea surface near Fernandina Island, in the Galápagos. (Photo by Tui De Roy. Bruce Coleman Inc. Reproduced by permission.)

Reproductive biology

Typically monogamous, storm-petrels first visit their natal colonies as prebreeders, and they breed at 4–5 years old. Nesting occurs when surrounding seas provide plenty of food; that is in the spring or summer in middle and high latitudes. Tropical breeders often have an extended laying season.

With few exceptions (e.g., the wedge-rumped storm-petrel in the Galápagos), all activity on land occurs after dark, and for many species the behaviors culminating in mating are unclear. European storm-petrels often crash into one other, apparently deliberately, and then fall to the ground before disentangling themselves. In Alaska, fork-tailed storm-petrels (*Oceanodroma furcata*) circling overhead call in response to cries from burrows below, suggesting pair bonding. High-speed zigzagging chases have been seen among other species, but, in general, the significance of these maneuvers is obscure. Not much more is known of their behavior on the ground, but using night vision equipment, copulation of fork-tailed storm-petrels has been seen in the nest chamber and on the ground outside. There was little precopulation ceremony other than mutual preening.

Some female storm-petrels feed at sea while producing the single egg; this trek is called the prelaying exodus. In a study of Wilson's storm-petrels, the females of 31 pairs stayed away for 16–18 days, leaving their partners to visit the nests from time to time, perhaps to keep them clear of snow. In other species there seems to be no clear exodus. In Leach's storm-petrels, semen is stored in special glands in the vaginal folds of the cloaca. This arrangement allows fertilization to be delayed while the bird travels to the best feeding area while producing her egg and returning to her nest.

The single egg is ovoid, whitish, and often sprinkled with pinkish dots. It is laid within 24 hours of the female's return and is very large compared to her body size. That of the least storm-petrel is 29% of her body weight—probably the heaviest egg relative to body size of any bird. Highly migratory species lay over a relatively short period, whereas sedentary birds like the ashy storm-petrel (*Oceanodroma homochroa*) breeding off California lay over a period of about 100 days.

The nest is a chamber at the end of a tunnel bored into soft ground or in a crevice among rocks. Males seem to be the tunnel diggers and the chambers are often sparsely lined with bits of local vegetation. Gray-backed storm-petrels and white-bellied storm-petrels (*Fregetta grallaria*) burrow into the fibrous debris at the bases of tussock clumps and so are, in effect, above ground. The microclimate in a burrow is milder than the climate outside, being more humid and warmer in cold climates and cooler than ambient temperatures in tropical regions. The egg is tucked snugly into a bare, well-vascularized incubation patch. Incubation shifts vary from two to three days in cold water species but average 4.5 days in warm water species like the white-faced storm-petrel.

The female usually leaves for the sea within 24 hours of laying. The male takes the first incubation shift and the sexes take turns thereafter. The total time between laying and hatching in continuously covered eggs varies from 38 to 42 days. When eggs are temporarily abandoned, this interval is longer. Eggs are resistant to chilling, can be abandoned for several days, and yet will still produce a chick. In one extreme case, a fork-tailed storm-petrel egg left uncovered for 31 days still hatched. The embryo's resistance to chilling while still remaining viable is a valuable adaptation for a small seabird having to cope with variable weather and sea conditions which may prevent parent's return.

The chick is hatched covered in down, its eyes closed, and with incomplete control of its body temperature. It is brooded by one or other of the parents for three or more days—known as the guard stage. In their thick down the chicks look like powder puffs. They are grayish or whitish, often paler on the belly. In most, the initial down (protoptile) is replaced by a second (mesoptile) down that grows attached to the protoptile, which, in turn, is pushed out by the feathers proper (the teleoptiles). At least two of the southern birds, Wilson's storm-petrels and white-faced storm-petrels, have only one down.

Initially the chick gets small meals, perhaps mostly of stomach oil, but meal sizes increase when the guard stage is over. With the milder climate in the burrow and a layer of subdermal fat, the chick can then thermoregulate with the milder climate in the burrow. Both parents feed the chick and a fairly even division of labor seems to be the norm. Some meals can be huge, e.g., as much as the chick's own body weight (usually after both adults have fed it on the same night). Parental feeding visits are frequent at first but decline in older chicks. For instance, European storm-petrel chicks 11–20 days old received visits on 93% of the nights, those aged 31–40 days on 85% of the nights, and 51–60 day-olds on 66% of nights. Chicks can withstand fasting for 6–7 days. Starved chicks may become torpid to reduce energy needs, but their body weight falls and death may result.

A chick's growth follows a typical logistical curve, climbing steeply for about the first half of the nestling stage then stabilizing above adult weight and finally falling in the last 10–20 days before first flight. This is preceded during its last week or so by its leaving the burrow to exercise its wings and to explore the vicinity of the nest. A chick's first flight usually takes place from some nearby eminence. Parents take no part in this; the chick leaves alone and, as far as is known, once at sea is really on its own. Average nestling periods (the days between hatching and the first flight) range from 57 to 84 days. Nestling periods are much more variable than incubation periods, partly due to erratic provisioning. Breeding success (percent of eggs laid that produce flying young) varies from year to year.

Conservation status

Some species are abundant with many colonies scattered widely. These include Leach's, European, Wilson's, gray-backed, white-faced, and band-rumped storm-petrels. There are also a number of very localized species such as Matsudaira's storm-petrel, which breeds only at the Volcano Islands, and the ashy, least, and black storm-petrels, which nest off southern California and Mexico.

For some species, breeding places are virtually unknown. For example, Markham's storm-petrel (*Oceanodroma markhami*) has been found nesting on the Paracas Peninsula, Peru, but more undiscovered colonies must exist to account for the numbers of birds encountered at sea. None of these seems to be endangered, but Elliot's storm-petrel may well be as only one pair of the subspecies *Oceanites gracilis gracilis* has been found nesting off Chile. Breeding places of *O. g. galapagoensis* remain undetected.

Colonies of storm-petrels have been wiped out by predators, which are usually mammals like rats and mustelids (even mice can damage these small birds by eating their eggs). The extinction of the Guadalupe storm-petrel (*Oceanodroma macrodactyla*) has been attributed to a combination of predation by cats and erosion from grazing by goats. A particularly noteworthy conservation effort is the extermination of foxes from colonies of Leach's and forked-tailed storm-petrels in Alaska, which resulted in the reestablishment of many colonies. Another success story concerns the use of tape playbacks of Leach's storm-petrel calls plus the provision of artificial burrows on islands in Muscongus Bay, Maine. Attracted by the amplified calls, birds investigated the burrows and eventually bred there. A colony was established (on Ross Island) where there had been no previous evidence of breeding.

No storm-petrel species is threatened, although birds like Hornby's (*Oceanodroma hornbyi*) and Markham's, being quite unknown, badly need investigation. The populations of Tristram's storm-petrel on Midway Island, formerly decimated by rats, seem to be recovering since the rats were wiped out.

Significance to humans

Storm-petrels were well known to early sailors and very familiar to sealers and whalers because their hunting activities attracted birds like the cosmopolitan Wilson's storm-petrel. They lumped several species together as Mother Carey's Chickens, *Mater cara* referring to the Virgin Mary under whose protection seafarers were supposed to come. Although killing of these birds was sometimes considered fraught with danger, they were often caught for use as bait. Wilson's storm-petrels were killed at night from the stern of the ship, and many are attracted to lights. Sealers threaded wicks through the alimentary tracts of adults or fat chicks to draw out the stomach oil, which could be used as a candle.

Small though they are, several species have been eaten regularly by primitive societies: Aleuts, American Indians, and the inhabitants of the Izu Islands, Japan, all ate Leach's storm-petrels, while the Morioris of the Chatham Islands, New Zealand and aborigines of eastern Australia ate white-faced storm-petrels when available.

Species accounts

Wilson's storm-petrel
Oceanites oceanicus

SUBFAMILY
Oceanitinae

TAXONOMY
Oceanites oceanicus Kuhl, 1840, no locality. *O. o. oceanicus*: Islands off Tierra del Fuego and subantarctic islands of Atlantic and Indian Oceans, including South Georgia; *O. o. exasperatus*: South Shetland, South Sandwich, South Orkney Islands, Elephant Island, coasts and offshore islands of Antarctica.

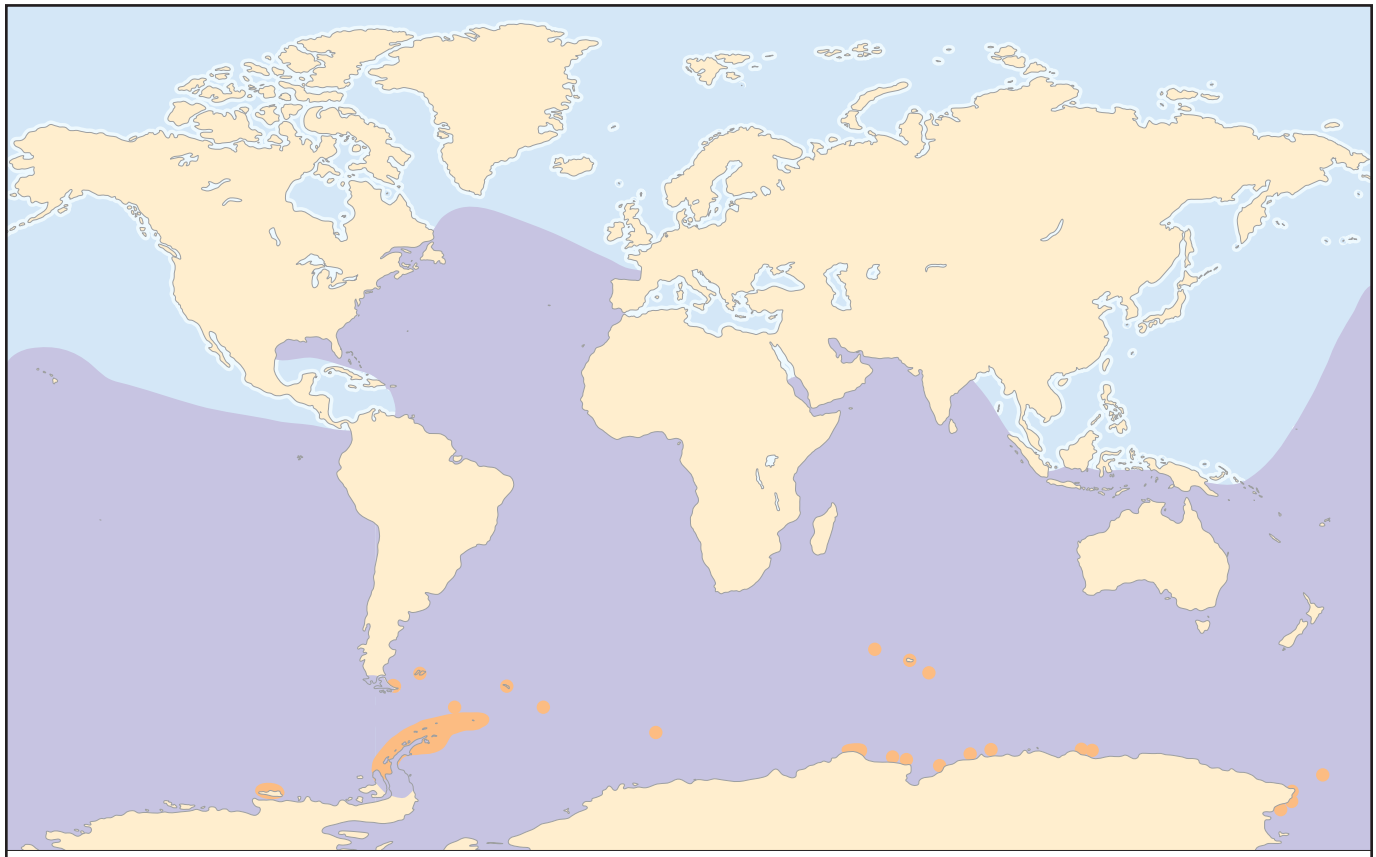
OTHER COMMON NAMES
English: Mother Carey's chicken; French: Pétrel océanite; German: Buntfüssige Sturmschwalbe; Spanish: Paiño de Wilson.

PHYSICAL CHARACTERISTICS
7 in (18 cm); 1.3 oz (35 g). Wholly black above and below except for white rump merging into the white lower flanks and thighs and a pale band across the center of each wing. Tail square cut and black. Legs black, very long, and projecting beyond the tail when flying; webs between toes yellow. Juvenile like adult. Bill black with prominent nasal tubes reaching about halfway along the ridge of the bill. Sexes alike.

DISTRIBUTION
Wholly marine except when nesting, found in all oceans particularly along coastal upwellings and fronts. It tends to be more often seen offshore compared to other storm-petrels such as Leach's and white-faced storm-petrels, which prefer deeper water.

Oceanites oceanicus

Highly migratory, moving from April to June from the southern breeding stations to northern reaches of the oceans, but avoids Arctic seas. In the Atlantic the journey from the south is 7,000 miles (11,000 km) for some birds.



HABITAT
These birds are concentrated along the ocean shelves during the northern summer. Although most move back to southern waters to breed during the northern winter, some remain: these are probably juveniles or birds that are taking a season off-duty—a so-called sabbatical year.

BEHAVIOR
The feeding behavior is distinctive with a flight characterized by alternate glides and wing flutterings while the long legs are drooped and often break the surface. Most food is snipped from the surface without alighting, and this is the most common ship's follower. Calls used on the breeding grounds include a grating sound used by both sexes and a chatter call used by the males to attract females.

FEEDING ECOLOGY AND DIET
Crustaceans, but fish are also eaten (these are more energy rich than crustacea) with mycophids up to 3.3 in (8.5 cm) long being fed to the chicks (quite a meal for a bird with a bill only 0.5 in [1.2 cm] long).

REPRODUCTIVE BIOLOGY
The pair-bond is held over several seasons and most pairs tend to breed annually. The nest forms their focus. There is little to suggest that they stay together during migration. Because of the short polar summers, Wilson's storm-petrels breeding around Antarctica have accelerated the development of the egg and chick: the time from laying to fledging is 91 days (the shortest period for any tubenose). Birds farther north, though slightly smaller, take longer, perhaps because the food supply is less concentrated than it is off the southern continent.

Most nests are hidden in crevices among rocks or coarse scree. The egg is laid on the bare earth in a shallow scrape, and those on the southern islands are often lined with scraps of local vegetation.

The eggs take about 40 days to hatch if continually incubated. The chick flies at 48–78 days old. A major cause of mortality is unseasonal weather that stops birds entering their nests or freezes chicks within them. Predation by skuas is not usually significant.

CONSERVATION STATUS
Not threatened. One of the most abundant seabirds. Its isolation is its major safeguard.

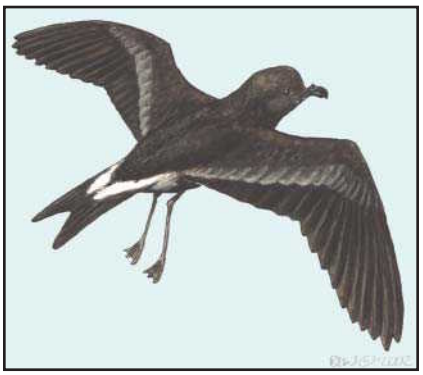
SIGNIFICANCE TO HUMANS
None known. ◆

Leach's storm-petrel
Oceanodroma leucorhoa

SUBFAMILY
Hydrobatinae

TAXONOMY
Oceanodroma leucorhoa Vieillot, 1818, maritime parts of Picardy. *O. l. leucorhoa*: all North Atlantic and North Pacific populations south to California. Populations in eastern Pacific vary in size and degree of white on rump; *O. l. chapmani*: breeds on San Benitos and Los Coronados islands, Mexico. *O. l. socorrensis*: breeds in summer on islets off Guadalupe Island, Mexico. *O. l. cheimomnestes*: breeds in winter on islets off Guadalupe Island, Mexico.

OTHER COMMON NAMES
French: Pétrel culblanc; German: Wellenlaüfer; Spanish: Paiño de Leach.

PHYSICAL CHARACTERISTICS

Oceanodroma leucorhoa

7.0–8.5 in (180–220 mm); 1.3–1.9 oz (38–54 g). Medium-sized storm-petrel with white rump patch and distinctly forked tail, blackish brown above and below with paler diagonal upperwing bar from carpal joint back to trailing edge near body. Strongly downhooked bill and prominent nostrils. Legs and feet black. Sexes alike. Flight less fluttering than that of Wilson's storm-petrel and wings tend to be held more horizontally than those of Wilson's storm-petrel (which raises its wings into a V). Feet not visible beyond tail and much less prone to pattering.

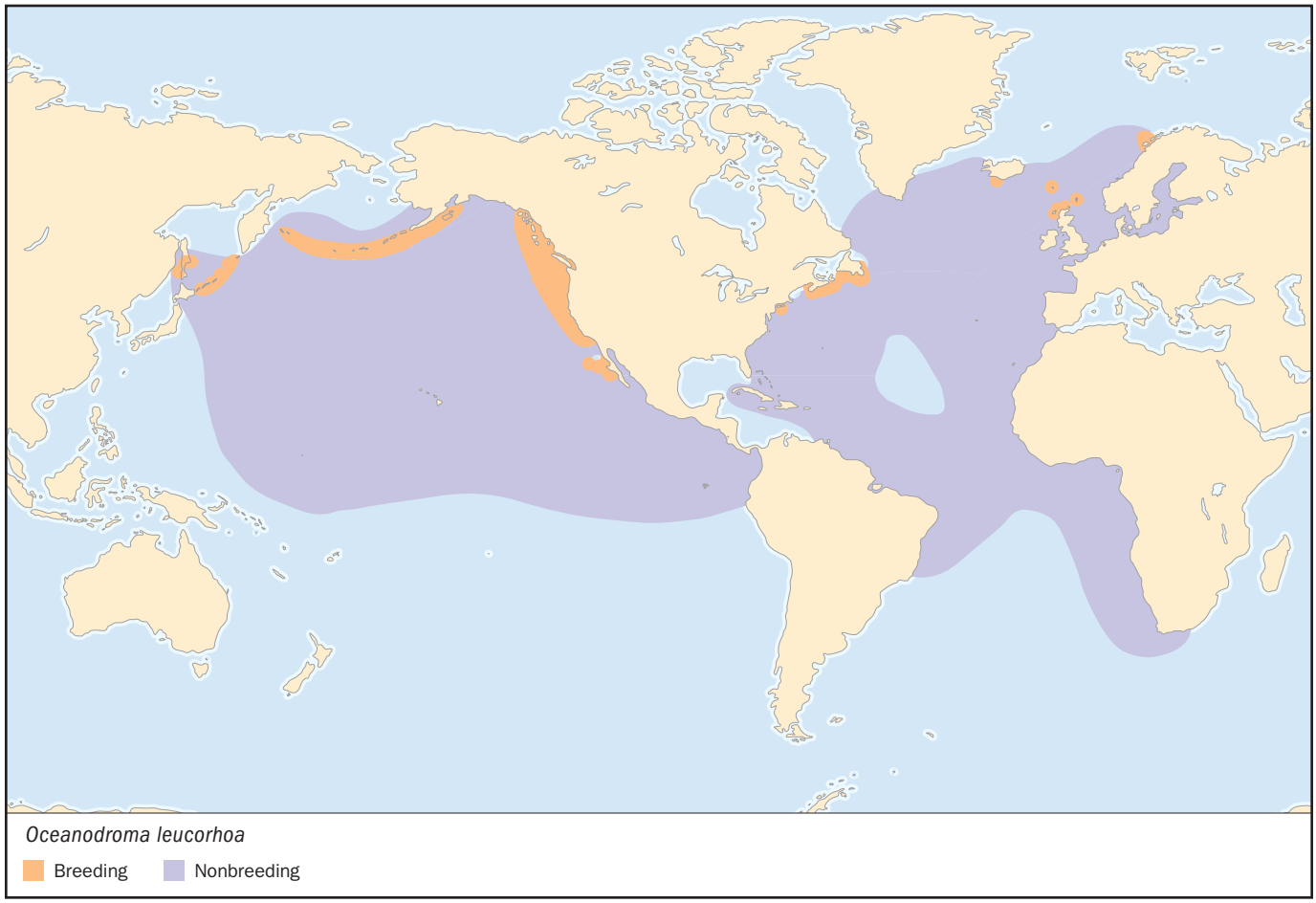
DISTRIBUTION
Breeds on islands in the North Atlantic and North Pacific that lack mammalian predators. Found at sea throughout these seas, migrates south into the tropics after breeding. Pairs have even been found in burrows on the Chatham Islands, New Zealand. One bird was found on St. Croix Island, South Africa, which suggests the possibility of extending the breeding range southwards. The eastern North American populations shift south to Brazilian waters but many cross to European seas like the Bay of Biscay. British breeders appear to winter mainly off tropical Africa. Japanese and Alaskan birds also winter in tropical seas.

HABITAT
Ranges widely in the open sea. California birds feed farther out in warmer, less productive seas than do ashy and fork-tailed storm-petrels with which they often share nesting islands.

BEHAVIOR
On land, overflying birds that emit calls are mainly prebreeders; nesting birds call mostly from their burrows. Little display occurs between breeding birds except persistent calling using two main types of rhythmic purrings and chatterings. Chatter calls are given from the air and the burrow, and research in Japan suggests that variation in the pitch of calls among birds of the same sex may be used for individual recognition.

FEEDING ECOLOGY AND DIET
Nekton and planktonic organisms are taken from the surface while the bird hovers facing the wind, sometimes alighting momentarily. Otherwise the flight is a mixture of gliding and rather wild dashes, with many changes of direction. Seldom follows ships but is prone to be wrecked on beaches during gales.

Diet includes a great range of fish, crustaceans, and squid as available. The birds tend to seek areas where upcurrents bring organisms to the surface. Their stomachs often contain deep-sea animals that only approach the surface at night, evidently taken after dark. They appear to find some prey using their good sense of smell.



REPRODUCTIVE BIOLOGY

Most breed at around five years old. Having gained a nest site, a pair remains intact as long as they reproduce satisfactorily. Most dig burrows, but some occupy crevices among rocks or stone walls. The single egg is occasionally replaced if it is lost soon after laying. Both sexes incubate in 2–3 day shifts for about 43 days. Chick is fed almost nightly in the first few days after the brief brooding period, then less often as it grows. Unfed chicks become torpid but can recover. Growth follows the normal curve: weight climbs steadily at a constant rate, levels out at above parental weight, then falls in the last 10 or so days before fledging.

Fledging occurs when the chick is between 56 and 79 days. The number of chicks fledged per egg laid differs between seasons and places and ranges from 48 to 73%. Losses have often been due to introduced mammals like mink, cats, and others, but natural predators also include owls, eagles, corvids, and gulls.

CONSERVATION STATUS

Not threatened, but existing colonies need protection against the introduction of placental mammals and trampling of burrows.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

Ainley, D.G., and R.J. Boekelheide, eds. *Seabirds of the Farallon Islands.* Stanford, CA: Stanford University Press, 1990.

Huntington, C.E., R.G. Butler, and R.A. Mauck. "Leach's Storm-petrel." In *The Birds of North America,* No. 223, edited by A. Poole and F. Gill. Philadelphia: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union, 1996.

Lockley, R.M. *Flight of the Storm-petrel.* London: David and Charles, 1983.

Warham, J. *The Behaviour, Population Biology and Physiology of the Petrels.* San Diego: Academic Press, 1996.

Warham, J. *The Petrels: Their Ecology and Breeding Systems.* San Diego: Academic Press, 1990.

Resources

Periodicals

Croxall, J.P., H.J. Hill, R. Lidstone-Scott, M.J. O'Connell, and P.A. Prince. "Food and Feeding Ecology of Wilson's Storm-petrel *Oceanites oceanicus* at South Georgia." *Journal of Zoology, London* 216 (1988): 83–102.

Taoka, M., T. Sato, T. Kamada, and H. Okumura. "Sexual Dimorphism of Chatter-Calls and Vocal Sex Recognition in Leach's Storm-Petrels (*Oceanodroma leucorhoa*)." *Auk* 106 (1989): 498–501.

Other

Warham, J. *A Bibliography of the Procellariiformes or Petrels.* February 1999. (January 31 2001). <http://www.zool.canterbury.ac.nz/jwjw.htm>

John Warham, DSc

Diving-petrels
(Pelecanoididae)

Class Aves
Order Procellariiformes
Family Pelecanoididae

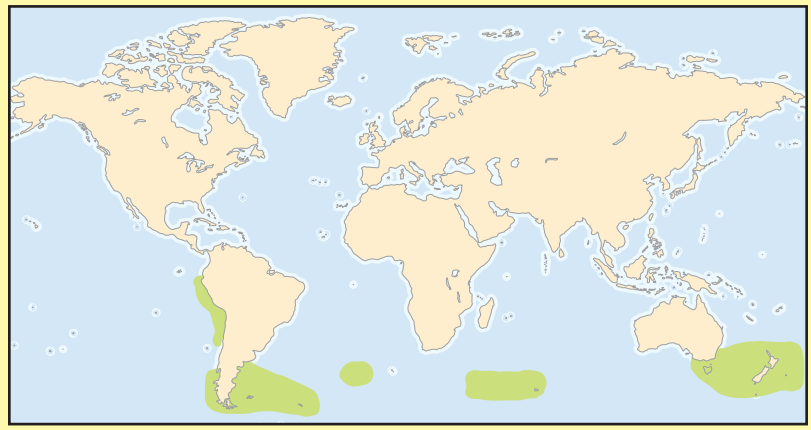
Thumbnail description
Small-sized, black-and-white colored, stocky, short-winged, tube-nosed seabirds with nostrils pointing upwards. Diving-petrels dive and swim for their food

Size
7–10 in (18–25 cm); 4–8 oz (120–220 g)

Number of genera, species
1 genus; 4 species

Habitat
Cool and cold oceans

Conservation status
One species is Endangered



Distribution
Occurs in cool and cold oceans of the Southern Hemisphere, usually close to breeding sites

Evolution and systematics

Diving-petrels (family Pelecanoididae) are in a group of seabirds known as tubenoses (order Procellariiformes), all of which have a distinctive pair of tube-like, salt-excreting, external nostrils on the top or sides of the upper mandible. Other families in this group are the albatrosses (Diomedeidae), storm-petrels (Oceanitidae), and fulmars, petrels, shearwaters, and prions (Procellariidae).

With their rapid wing beats and stocky, short-necked appearance, diving-petrels resemble the little auks of the Northern Hemisphere (family Alcidae). This resemblance represents an example of convergent evolution between unrelated species occupying similar ecological niches in widely separated parts of the world.

Physical characteristics

Diving-petrels are small, stocky-bodied, short-winged, tube-nosed seabirds that dive and swim to catch their food. Their body length is 7–10 in (18–25 cm) and they weigh 4–8 oz (120–220 g). Their bill is small, short, broad, and slightly hooked at the tip. The nostril tubes on the upper bill are parallel, short, have a thin partition between them, and are directed upward. Diving-petrels are the only tubenoses in which the nostrils project upward rather than forward, which may be an adaptation to diving. The wings are relatively short and wide and the flight is consequently swift, direct, fluttering, and whirring. When diving and swimming, the wings are used as flippers to achieve forward propulsion. The plumage is gray, blue-gray, or black on top and whitish on the underside. The primary feathers all molt simultaneously, rendering the birds temporarily flightless.

Distribution

Diving-petrels are restricted to waters of the Southern Hemisphere, generally between latitudes 35° south and 60° south. They usually occur in coastal waters but may sometimes be found well offshore.

Peruvian and Magellan diving-petrels (*Pelecanoides garnotii* and *P. magellani*) inhabit South American waters. Common and South Georgian diving-petrels (*P. urinatrix* and *P. georgicus*) are circumpolar species.

Habitat

Diving-petrels breed on remote oceanic islands. They feed in cool and cold oceans, usually rather close to their breeding sites.

Behavior

Diving-petrels characteristically fly low, direct, and fast over water, occasionally diving and swimming to catch their prey. In rough weather, they may fly right through the crests of waves rather than around or over them. Diving-petrels are the only tubenoses that swim underwater using their wings for propulsion. Diving-petrels only come to land to breed, and they will do so only at night. This wariness is an adaptive response to predation by larger seabirds, such as skuas. Diving-petrels are not migratory, but they may wander during the nonbreeding season.

Feeding ecology and diet

Diving-petrels catch their prey of small fishes and crustaceans by flying directly into the water and then using their wings to swim underwater to pursue their food. They emerge

A common diving-petrel (*Pelecanoides urinatrix*) on Karewa Island, New Zealand. (Photo by K. Westerkov/Animals Animals. Reproduced by permission.)

from the water in a similar manner, by flying directly out into the air. Diving-petrels usually feed in flocks.

Reproductive biology

Diving-petrels breed in colonies. They nest in burrows excavated in organic turf and also in cavities among rocks and tufts of grass. Each female lays only one relatively large white egg that weighs 10–15% of the female's body weight. The incubation period is about eight weeks, and both parents tend the egg during one-day-long watches. Egg laying generally occurs between July and December. The newly hatched chick is brooded closely for its first two weeks of life. After about eight weeks the chick fledges and begins to fend for itself. After the breeding season ends, adults molt all flight feathers and are flightless until this plumage has regrown. Diving-petrels reach sexual maturity in two or three years, which is considerably faster than other tubenoses.

Conservation status

The Peruvian diving-petrel is listed as Endangered. This rare species has an extremely small breeding range on only four islands off the west coast of South America, and all of its subpopulations are declining, some quite rapidly. The declines in abundance have been caused by excessive hunting of these birds for food, disturbance of their habitat during guano collection, predation on eggs, nestlings, and adults by introduced mammals, and diminishment of their food supply by commercial overfishing of the waters around their breeding colonies.

Significance to humans

Diving-petrels are not of much importance to humans, except for the economic benefits of marine ecotourism related to birdwatching.

Species accounts

Common diving-petrel
Pelecanoides urinatrix

TAXONOMY
Pelecanoides urinatrix Gmelin, 1789, New Zealand. Six subspecies.

OTHER COMMON NAMES
English: Subantarctic diving-petrel; French: Puffinure plongeur; German: Lummensturmvolgel; Spanish: Potoyunco Común.

PHYSICAL CHARACTERISTICS
8–10 in (20–25 cm); wingspan 13–15 in (33–38 cm). Coloring similar to other *Pelecanoides* species; differentiated by configuration of its bill and nostrils.

Pelecanoides urinatrix

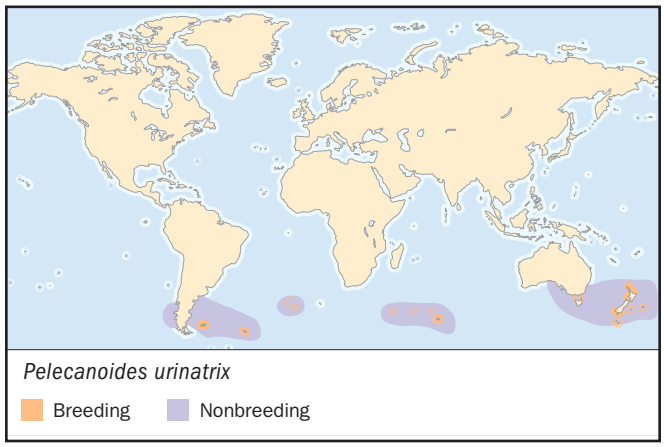
DISTRIBUTION
This is the most widespread of the diving-petrels, occurring in the Southern Ocean between about latitudes 35° south and 55° south. It breeds on islands off Australia, New Zealand, Chile, Argentina, and in the south Atlantic Ocean and south Indian Ocean.

HABITAT
Breeds on oceanic islands and feeds in cool and cold oceans, usually close to breeding sites.

BEHAVIOR
Flies low, direct, and fast, both through the air and in the water.

FEEDING ECOLOGY AND DIET
Dives and swims to feed on small fish and crustaceans.

REPRODUCTIVE BIOLOGY
Lays a single egg in a burrow or crevice. The egg is incubated by both parents.



Pelecanoides urinatrix
Breeding Nonbreeding

CONSERVATION STATUS
Not threatened. Locally widespread and abundant.

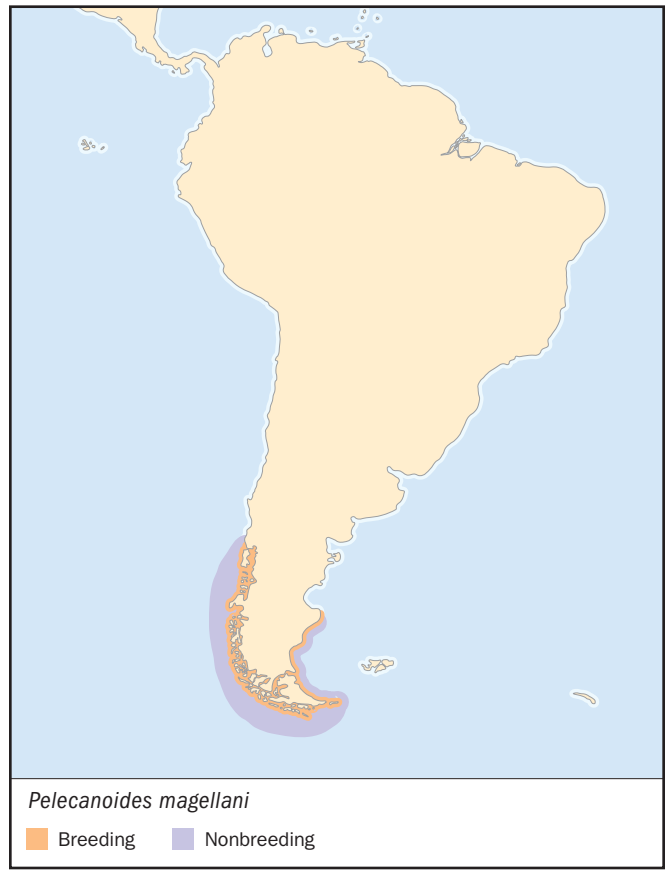
SIGNIFICANCE TO HUMANS
None other than through economic benefits of birdwatching and ecotourism. ◆

Magellan diving-petrel
Pelecanoides magellani

TAXONOMY
Pelecanoides magellani Gray, 1871, Strait of Magellan. Monotypic.

OTHER COMMON NAMES
English: Magellanic diving-petrel; French: Puffinure de Magellan; German: Magellan-Lummensturmvogel; Spanish: Potoyunco Magallánico.

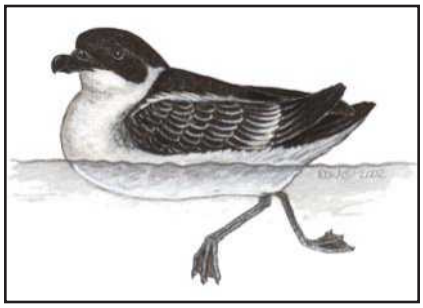
PHYSICAL CHARACTERISTICS
7.5–8 in (19–20 cm), side of neck bears a crescent-shaped half collar.



Pelecanoides magellani
Breeding Nonbreeding

DISTRIBUTION
Occurs only in extreme southern South America, off southernmost Argentina and Chile.

HABITAT
Breeds on oceanic islands and feeds in cold oceans, usually close to breeding sites.



Pelecanoides magellani

BEHAVIOR
Flies low, direct, and fast, both through the air and in the water.

FEEDING ECOLOGY AND DIET
Dives and swims to feed on small fish and crustaceans.

REPRODUCTIVE BIOLOGY
Lays a single egg in a burrow or crevice. The egg is incubated by both parents.

CONSERVATION STATUS
A locally abundant species.

SIGNIFICANCE TO HUMANS
None other than through economic benefits of birdwatching and ecotourism. ◆

Resources

Books

BirdLife International. *Threatened Birds of the World.* Barcelona: Lynx Edicions and BirdLife International, 2000.

Carboneras, C. "Family Pelecanoididae (Diving-petrels)." *Handbook of the Birds of the World.* Vol. 1, edited by J. del Hoyo, A. Elliott, and J. Sargatal. Barcelona: Lynx Edicions, 1992.

Harrison, P. *Seabirds. An Identification Guide.* Beckenham, U.K.: Croom Helm Ltd., 1983.

Warham, J. *The Behaviour, Population Biology and Physiology of the Petrels.* San Diego: Academic Press, 1996.

Organizations

BirdLife International. Wellbrook Court, Girton Road, Cambridge, Cambridgeshire CB3 0NA United Kingdom. Phone: +44 1 223 277 318. Fax: +44-1-223-277-200. E-mail: birdlife@birdlife.org.uk Web site: <http://www.birdlife.net>

IUCN–The World Conservation Union. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41-22-999-0001. Fax: +41-22-999-0025. E-mail: mail@hq.iucn.org Web site: <http://www.iucn.org>

Bill Freedman, PhD

Sphenisciformes
Penguins
(Spheniscidae)

Class Aves
Order Sphenisciformes
Family Spheniscidae
Number of families 1

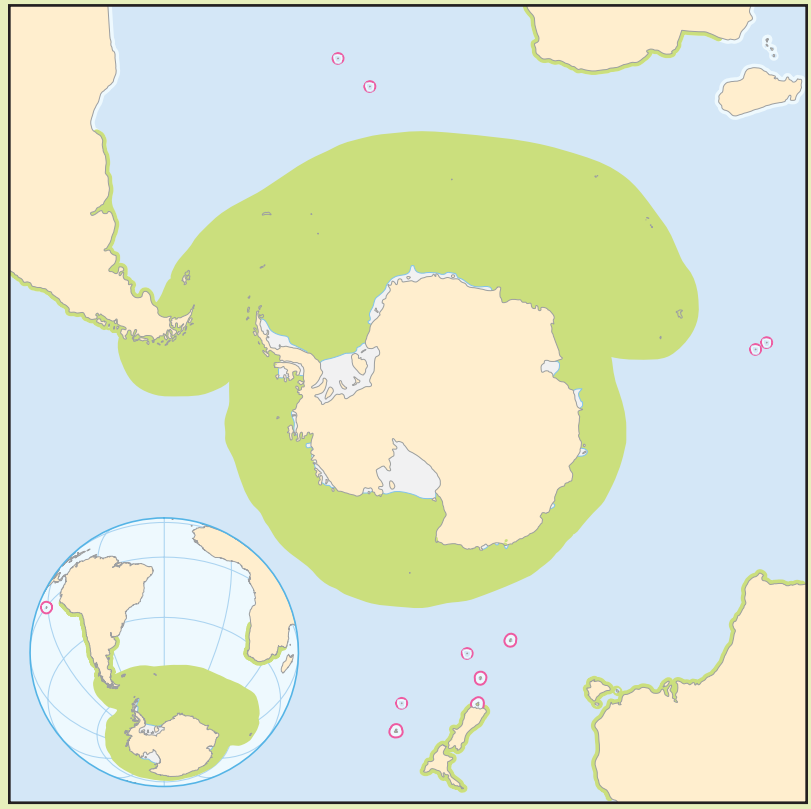
Thumbnail description
Medium to large flightless seabirds with streamlined bodies adapted for swimming and diving underwater

Size
17.7–51.2 in (45–130 cm); 1.8–88 lb (842 g–40 kg)

Number of genera, species
6 genera; 17 species

Habitat
Marine coastal areas of the southern hemisphere; one species found at the equator

Conservation status
Endangered: 3 species; Vulnerable: 7 species; Lower Risk: 2 species



Distribution
Cool waters of the southern hemisphere, including coastal Antarctica, New Zealand, Australia, South Africa, and South America and the Falkland Islands; one species occurs at the equator, on the Galápagos Islands

Evolution and systematics

Ninteenth-century French explorer Dumont d'Urville described penguins as "fish-birds" when he first spotted them in Antarctic waters. Like fish, penguins have streamlined, torpedo-shaped bodies and swim easily underwater; however, they are indisputably birds, members of the order Sphenisciformes, which consists of a single family, the Spheniscidae. Their closest living relatives are thought to be petrels and albatrosses (Procellariidae) and loons and grebes (Gaviidae).

Taxonomists concur that penguins probably evolved during the Cretaceous period (140–65 million years ago) from an ancestor that could fly but also swam underwater to catch food. The ancestor might have resembled an auk (Alcidae) or a diving-petrel (Procellariidae).

More than 40 fossil penguin species have been described; a distinctive fused foot bone, the tarsometatarsus, is diagnostic. In a report published in 1990, Ewan Fordyce and C. M. Jones suggested that mass extinctions of marine reptiles during the late Cretaceous left open ecological niches that penguins evolved to fill. In the period from 40 to 10 million years ago, penguins flourished; species diversity was higher than it is in the twenty-first century, and the penguin fauna included many species even bigger than the largest living species, the emperor penguin (*Aptenodytes forsteri*). By the Miocene period (about 15 million years ago) most of the large species were extinct, perhaps because seals and small whales had evolved and were outcompeting penguins for food.

As of 2001, scientists recognize 17 species of penguins in 6 genera. The genus *Aptenodytes* includes the two largest penguins, emperor penguins and three-foot-tall king penguins (*A. patavonicus*). The genus *Pygoscelis* includes Adelie (*P. adeliae*), chinstrap (*P. antarctica*), and gentoo (*P. papua*) penguins. Adelie penguins, with their black-and-white plumage that suggests a formal tuxedo, are what most people think of when they hear the word penguin. The genus *Eudyptes* consists of

Gentoo penguins (*Pygoscelis papua*) leave the water in the Falkland Islands. (Photo by Tim Davis. Photo Researchers, Inc. Reproduced by permission.)

macaroni (*E. chrysolophus*), rockhopper (*E. chrysocome*), Snares (*E. robustus*), erect-crested (*E. sclateri*), royal (*E. schlegeli*), and Fiordland (*E. pachyrhynchus*) penguins; these are also known as crested penguins because of the wispy yellow feathers that sprout above their eyes. African (*Spheniscus demersus*), Humboldt (*S. humboldti*), Magellanic (*S. magellanicus*), and Galapagos (*S. mendiculus*) penguins make up the genus *Spheniscus*, also referred to as black-footed penguins. Members of this group have curving white stripes on either side of their black heads and a black stripe that forms a horseshoe shape on their white chests. *Spheniscus* penguins are also nicknamed jackass penguins because of their braying calls. The final two penguin genera each consist of a single species: *Eudyptula minor*, little penguins (as its name suggests, the smallest of the penguins), and *Megadyptes antipodes*, yellow-eyed penguins.

Physical characteristics

With their large heads, elongate bodies, and upright stance, penguins look somewhat human as they waddle around on land. The most common plumage, a black back and white chest, evokes a comparison with tuxedoed waiters. All penguins share a set of anatomical features that make them uniquely adapted for life in a marine environment. They are able to dive and maneuver with agility underwater. They have solid, heavy bones; wings that are modified into stiff, flat flippers; webbed feet set well back on the body; and short, stiff feathers that repel water and provide excellent insulation.

Species vary in size. Little penguins generally weigh less than 3 lb (1100 g) and stand less than 18 in (45 cm) tall; the emperor penguin can be nearly four ft (115 cm) tall, and a male at the beginning of the breeding season may weigh as much as 88 lb (40 kg). The weight of each penguin may vary dramatically over the course of the breeding season; male emperor penguins go without eating for as long as 115 days during courtship and egg incubation and may lose 41% of their initial body weight during this period. Male penguins are slightly larger than females, especially with regard to the length of their flippers and the size of the bill, but except among the eudyptid penguins (in particular the macaroni) this difference can be hard to detect on casual observation.

All penguins have black, blue-gray, or gray feathers on the back and white feathers on the chest and belly. Many species have distinct orange or yellow plumes sprouting from the head or patches of bright yellow or orange on the face. Males and females look similar; chicks are covered with a layer of fluffy down.

Even though penguins are flightless, they have a keeled breastbone like that of flying birds (the keel anchors the pec-

toral muscles usually used for flight). Penguin bones differ from those of most birds in being solid and heavy instead of light and filled with air spaces; heavy bones are an adaptation for diving underwater. Penguin wings have been modified into flippers for "flying" underwater; the joints at elbow and wrist are almost fused so that the flippers do not fold up the way wings do. Penguin legs are short and stout with webbed feet; underwater, the feet trail behind, pressed against the stiff tail where they serve as a rudder.

In most birds, feathers grow only from certain sections of the skin called feather tracts, while large areas of skin between the tracts are bare. Penguins, on the other hand, have feathers over almost the entire body surface; the exception is the bare brood patch on the belly. Tropical penguins have the largest areas of bare skin to facilitate cooling. The tips of feathers overlap like scales to form a waterproof outer covering, while fluffy down at the base of each feather traps a layer of air that holds in body heat. Most species experience a complete molt annually; they stay on land and fast during the molting period of 13–34 days.

A layer of blubber provides additional insulation, and a heat-exchange system in blood vessels of the flippers and legs helps maintain body temperature while swimming in cold water. One other adaptation to life in the water is the ability to reduce blood flow to the muscles while submerged. How penguins such as emperors dive repeatedly to great depths without developing decompression sickness and nitrogen narcosis is not known.

An Adelie penguin (*Pygoscelis adeliae*) toboggans at Petermann Island, Antarctica. (Photo by Renee Lynn. Photo Researchers, Inc. Reproduced by permission.)

Distribution

Penguins live almost exclusively in the southern half of the world. A single species, the Galapagos penguin, occurs just north of the equator. Popularly thought to be birds of the Antarctic, penguins are actually widely distributed, and more than half of the 17 species are never found in Antarctica. Most species live between 45 and 60° south. Seven penguin species breed on the mainland and islands of southern New Zealand; other species breed along the subtropical coasts of South America and South Africa. Only four species breed in Antarctica—the emperor, Adelie, gentoo, and chinstrap—and only the emperor and Adelie stay in the Antarctic year-round.

Habitat

Penguins spend much of their time at sea, diving underwater to catch fish, crustaceans, and squid. Like marine mammals, however, they must go ashore to rest and to breed and rear their young. Most breeding colonies are within a few hundred yards of shore, although gentoo and king penguin colonies can be almost 2 mi (3 km) inland. Breeding habitats range from the snowfields and ice sheets of Antarctica (where male emperors cradle their eggs on their feet rather than in a nest) to the famous equatorial islands off the coast of Ecuador, where Galapagos penguins breed in lava fields. Most species establish colonies in open, level terrain, often beneath coastal cliffs, although macaroni and chinstrap penguins nest on rocky slopes. Gentoo penguins nest amid mounds of tussock grass, and all of the *Spheniscus* penguins nest in protected places, either in underground burrows or beneath bushes. In Southern Chile, Magellanic penguins go ashore to lay their eggs in coastal beech forests.

Behavior

Penguins are highly social birds. They gather to breed in small groups or in large, noisy colonies, and they take to the water in flocks. Penguins interact constantly with their neighbors and they have evolved a large repertoire of complex behaviors that allow them to appease aggression, court a mate, and recognize the mate and offspring amid the throngs of birds.

To avoid aggression when entering or leaving the colony, a penguin adopts the "slender walk" behavior, lowering its head and holding its flippers forward as it threads its way past other birds. Many species use a sideways stare to signal "Keep away." Fights break out despite such submissive and defensive behaviors, and penguins will peck, bite, and hit opponents with their flippers. Some species engage in ritualized bill-jousting, using the bill like a sword to attack and parry.

A male penguin claiming a nest site puts on an "ecstatic display," standing erect with his bill pointed skyward while waving his flippers and calling loudly. When a female joins her mate, they cement the pair bond with a mutual ecstatic display and by bowing to one another. Among the smaller penguin species, courting pairs also engage in mutual preening.

Mutual displays and bowing continue after the pair have mated and one or two eggs are laid; these behaviors constitute a "nest relief ceremony" conducted when the male and female change places on the nest. Adult birds recognize one another

An adult rockhopper penguin (*Eudyptes chrysocome*) grooms a chick in the Falkland Islands. (Photo by Rod Planck. Photo Researchers, Inc. Reproduced by permission.)

by these behaviors and also by voice. Species that form the largest colonies (pygoscelids and some eudyptids) have the most elaborate mate-recognition displays. Experiments with recorded calls have shown that king penguins respond to their mate's calls but not to those of neighbors or other colony members, and chicks recognize their parents by a distinct vocal signature based on frequency modulation.

When penguins head to sea to forage, they typically stay in groups rather than hunt alone. This way each individual reduces its risk of being eaten. Foraging flocks may also be more efficient at finding food than are solitary birds.

Swimming penguins sometimes progress by porpoising, or shooting out of the water to skim above the surface for a few feet before splashing back down. While porpoising, the birds grab a breath in mid-air. On land, penguins walk upright with a waddling gait; some also progress by two-footed jumps (this method of locomotion gives the rockhopper penguin its name). Penguins can also travel by tobogganing, or sliding on their bellies over ice and snow. Some species travel hundreds of miles to inland nesting sites this way.

Feeding ecology and diet

Penguins feed at sea by diving after prey, which may be small fish, crustaceans, or squid. A bird can swallow a large number of prey items before it has to return to the surface to breathe. Different species take different prey; crested penguins (eudyptid species) eat mostly krill and other small crustaceans that occur in dense swarms. *Spheniscus* penguins and the little penguin eat small fish such as anchovies and sprats. Pygoscelid penguins eat almost nothing but krill.

Because penguins pursue their prey underwater, often in very cold water, few humans have seen a penguin capture prey. Nonetheless, using radio and satellite telemetry and miniaturized instruments that record depth, swimming speed, and duration of dives, scientists have learned much in the past decade about penguin foraging behavior. Penguins make shallow dives as they move from the shore to a foraging area, resting on the surface between dives. When they are pursuing prey, they dive deeper and stay underwater longer. The longest documented penguin dive was 18 minutes for an emperor penguin. Emperors are also the deepest divers; one researcher documented a bird that reached a depth of 1755 feet (535 meters). Diving ability seems to be positively correlated with body size: king penguins can dive for seven to 10 minutes, most medium-sized penguins dive for three to six minutes, and little penguins rarely dive for more than a minute or deeper than 98 ft (30 m). Penguins dive deepest at midday; they rely on excellent vision to spot prey, so low light conditions at dawn and dusk probably limit them to shallower dives at these times.

Reproductive biology

Penguins do not breed until they are at least two to five years old. For example, gentoo, little, and yellow-eyed penguins attempt to breed at age two; king and emperor penguins delay breeding until they are at least three years old; and macaroni and royal penguins wait at least five years. Females are ready to breed at a younger age than males. Penguins are usually monogamous and may take the same mate year after year; however, extra-pair copulations do occur among Humboldt penguins and others.

Emperor and king penguins build no nest and simply hold the egg on their feet. Gentoo penguins build nests of stones, and the spheniscids and little penguins dig burrows and nest underground.

The two largest penguin species lay a single egg. Other species usually have a two-egg clutch but occasionally lay one or three eggs. Crested penguins lay two eggs but rarely raise two offspring; the first egg laid is usually smaller than the second and is often lost or destroyed before it hatches.

Incubation period varies among species from 33 to 64 days. Chicks in the same clutch hatch at the same time or within a

A pair of chinstrap penguins (*Pygoscelis antarctica*) in courtship at their nest made of pebbles. (Photo by George Holton. Photo Researchers, Inc. Reproduced by permission.)

day of each other. One parent broods the down-covered chicks while the other goes on a foraging trip; upon return, the parent regurgitates food for the chicks. When the chicks no longer require brooding to maintain body temperature, the parents continue to guard them from predators.

Parental care can be quite extended; for example, king penguins care for chicks for more than 12 months. Young birds are ready to leave the nest when their down is replaced by feathers. Juveniles look much like adults, though the species-specific crests or cheek patches are less bright in young birds. After young birds leave the nest, they jump in the water and pursue prey without having had any obvious training from their parents in how to forage.

Conservation status

The exact impact of human actions on penguin populations is hard to measure because these birds naturally experience dramatic population fluctuations when changing ocean conditions affect food availability. From the eighteenth century to the early twentieth century, crews of whaling and sealing ships took millions of penguins and their eggs for food and also used the birds as bait. In places, penguins were rendered to produce oil; king penguins are thought to have been eradicated on Heard Island for this reason. Human enterprise has caused other problems for penguins; for example, Humboldt penguins in South America prefer to dig breeding burrows in centuries-old mounds of accumulated guano, but most of these breeding sites have been mined for fertilizer. Among the modern problems penguins face are oil pollution from tanker spills and bilge flushing and entanglement in discarded fishing nets. Commercial fishing may also reduce food supplies for some populations. Where human populations concentrate near penguin habitat, domestic animals can be a problem: cattle and sheep trample burrows and nests; rabbits browse away the concealing vegetation around nests; and introduced species including dogs, feral cats, ferrets, and stoats prey on nestlings.

Twelve of 17 penguin species are included on the 2000 IUCN Red List of Threatened Species. Erect-crested, Galapagos, and yellow-eyed penguins are listed as Endangered. The yellow-eyed penguin, found in New Zealand, has the smallest population of any species; much of its habitat has been lost to logging and farming, and introduced predators are also a problem. Rockhopper, macaroni, Fiordland, Snares, royal, African, and Humboldt penguins are listed as Vulnerable. Two species are classified as Lower Risk: gentoo penguins and Magellanic penguins.

Significance to humans

During the era of sailing ships, penguins were taken by the hundreds of thousands, for food and for the extraction of oil. Eggs were also collected in large numbers, and penguin guano was mined for fertilizer. Though penguins are now protected in most countries, they are sometimes taken illegally for food and bait. Since the 1960s, penguin colonies in the Antarctic, Argentina, and the Galapagos have become tourist attractions, drawing thousands to tens of thousands of visitors. Penguins are also popular as advertising logos (most notably for books, coffee, and cigarettes), as hockey team mascots, and as characters in cartoons and children's books.

1. Emperor penguin (*Aptenodytes forsteri*); 2. Yellow-eyed penguin (*Megadyptes antipodes*); 3. Macaroni penguin (*Eudyptes chrysolophus*); 4. Little penguin (*Eudyptula minor*); 5. Adelie penguin (*Pygoscelis adeliae*); 6. Magellanic penguin (*Spheniscus magellanicus*). (Illustration by Patricia Ferrer)

Species accounts

Emperor penguin
Aptenodytes forsteri

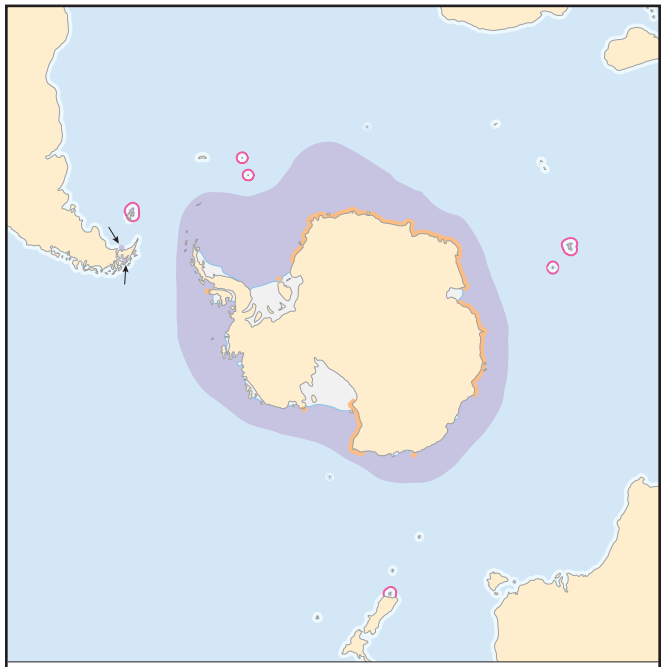
TAXONOMY
Aptenodytes forsteri G. R. Gray, 1844, Antarctic Seas.

OTHER COMMON NAMES
French: Manchot empereur; German: Kaiserpinguin; Spanish: Pingüino Emperador.

PHYSICAL CHARACTERISTICS
39.4–51.2 in (100–130 cm); female weight 44.5–70.5 lb (20.2–32 kg); male 48.3–88 lb (21.9–40 kg). The largest penguin is about the same size as the smallest diving marine mammal, the Galapagos fur seal (*Arctocephalus galapagoensis*). Bright yellow ear patches contrast sharply with black head, chin, and throat. Back is dark blue-gray, underparts are white shading to pale yellow on upper breast. Bill is slender and down-curving. Eyes are brown. Upper bill is black and lower bill is pink, orange, or lilac. Feet and legs are black. Juvenile is similar to adult but smaller and duller, with white ear-patches and black bill.

DISTRIBUTION
Breed on the coast of the Antarctic continent and adjacent islands, from 66° to 78° south latitude. Rarely seen outside of the Antarctic, although migrating birds are occasionally spotted near the Falkland Islands, southern New Zealand, and southern South America.

HABITAT
Cold waters of the Antarctic zone, where pack ice forms. Usually breed on sea ice, often on level sites sheltered by ice cliffs.



BEHAVIOR
Less aggressive than some penguins and behavioral repertoire is less varied, perhaps because incubating males do not defend territories but instead huddle together for warmth. Nest colonially and forage in groups. Loud vocalizations characterized as trumpeting. Horizontal head-circling signals aggression but is also common during pair formation, copulation, egg-laying, and as part of nest-relief ceremony.

FEEDING ECOLOGY AND DIET
Birds appear to coordinate their foraging at sea, diving and surfacing as a group. Main prey type varies with location; in a 1998 study, small fish made up more than 90% of the diet in three locations. Antarctic silverfish (*Pleuragramma antarcticum*) were the main prey item, and small cephalopods and crustaceans were also taken. About a third of all dives are deeper than 330 ft (100 m); birds sometimes dive as deep as 1,480 ft (450 m), and may feed near the sea bottom. Birds also feed near the surface along underside of ice where crustaceans gather to graze on algae. May travel 90–620 mi (150–1,000 km) in a single foraging trip.

REPRODUCTIVE BIOLOGY
Less mate-faithful than smaller penguins. After laying a single, large, greenish-white egg, females return to sea to feed. Males incubate alone, fasting for up to 115 days (from arrival at breeding colony to end of incubation, which lasts for 64 days). Chick has comical appearance, with black-and-white head emerging from what looks like a brown fur coat enveloping the body (actually, a layer of insulating down). Females return soon after chicks hatch and parents alternate feeding and brooding duties for 45–50 days. Chicks then form crèches (large numbers of young birds huddle together for warmth, standing close enough to touch one another). They are independent at 150 days. Adults molt after chicks leave colony.

CONSERVATION STATUS
Not threatened. Population stable or increasing; total breeding population was estimated in 1993 to be 314,000 pairs. Susceptible to human disturbance but at present face no major threats.

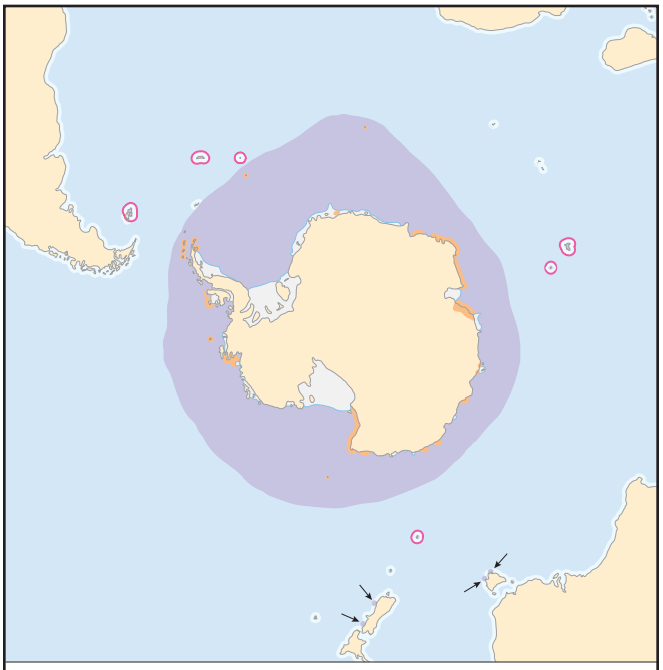
SIGNIFICANCE TO HUMANS
Emperor penguins are a key attraction on Antarctic ecotours, and also at Sea World in San Diego, where the Penguin Encounter exhibit is the world's only successful emperor penguin breeding colony outside of Antarctica. ◆

Adelie penguin
Pygoscelis adeliae

TAXONOMY
Catarrhactes adeliae Hombron and Jacquinot, 1841, Adelie Land.

OTHER COMMON NAMES
French: Manchot d'Adélie; German: Adeliepinguin; Spanish: Pingüino Adelia.

PHYSICAL CHARACTERISTICS
Female weight 8.6–10.5 lb (3,890–4,740 g); male 9.6–11.8 lb (4,340–5,350 g). Back, tail, and head (including face) are



blue-black; underparts are white. Distinctive white eye ring. Feathers cover half of bill, which is black with orange base. Eyes are brown. Legs and feet are dull white to pink with black soles.

DISTRIBUTION
Circumpolar, associated with pack ice of Antarctic Zone. Breeds on coasts of the Antarctic continent and surrounding islands; non-breeding distribution is not well known.

HABITAT
Within home range, they breed wherever land is ice-free and access from the sea is feasible.

BEHAVIOR
Male and female defend territory vigorously; often fight with neighbors. Birds signal apprehension by raising head feathers. Common threat display is a sideways stare with crest raised and eyes rolled downward.

FEEDING ECOLOGY AND DIET
Take mostly krill but also fish and cephalopods. During incubation, the bird not tending the nest may make a very long foraging trip, traveling more than 93 mi (150 km) from the colony over the course of 9–25 days. One study of birds at Hope Bay documented a maximum dive of 558 ft (170 m); estimated prey capture rate was 1,150 krill per foraging trip (7.2 krill per minute).

REPRODUCTIVE BIOLOGY
Well studied. Monogamous, often return repeatedly to same nest site. Nest in large colonies of up to 200,000 pairs. Build nests of small stones. Considerable energy devoted to stone searching, stone stealing, and rearranging stones in nest. Two eggs laid; parents alternate incubation duties (sometimes with egg on feet) for 32–24 days. Young brooded for 22 days, then join small crèches; fed by parents until they leave colony at 50–60 days.

CONSERVATION STATUS
Not threatened. Stable or increasing; population estimated in 1993 at 2,610,000 breeding pairs. Susceptible to disturbance from human activity.

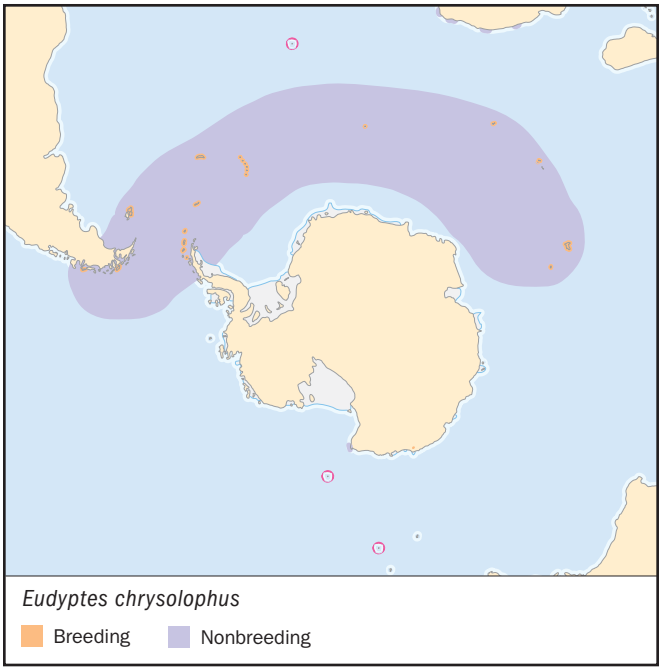
SIGNIFICANCE TO HUMANS
Ornithologist Robert Cushman Murphy called Adelies "the type and epitome of the penguin family." Adelies are responsible for the habitual comparison of penguins to little men in evening clothes. ◆

Macaroni penguin
Eudyptes chrysolophus

TAXONOMY
Catarrhactes chrysolophus Brandt, 1837, Falkland Islands.

OTHER COMMON NAMES
English: Crested penguin, royal penguin; French: Gorfou doré; German: Goldschopfpinguin, Haubenpinguin; Spanish: Pengüino Macarrones.

PHYSICAL CHARACTERISTICS
27.9 in (71 cm); male weight 8.2–14.1 lb (3,720–6,410 g); female weight 7.0–12.6 lb (3,180–5,700 g). Comical appearance, with long, yellow and orange plumes like shaggy eyebrows growing from a patch in the center of the forehead. Males noticeably larger than females but plumage similar. Head and cheeks are black or dark gray; back is slate black with blue sheen; breast, belly, and rump patch are white. Bill is stout and dark orange-brown, often ridged in older birds. Eyes are garnet red. Juveniles are smaller than adults and have lighter plumage, smaller and more scattered crest feathers, and a more slender bill.



DISTRIBUTION
Breeds farther south than other eudyptids, on Antarctic Peninsula and on Antarctic and subantarctic islands. In non-breeding season, probably remains in subantarctic waters.

HABITAT
Often nests on steep, rough terrain with little or no vegetation, including lava flows and scree slopes.

BEHAVIOR
Forms colonies of 100 to more than 100,000 birds. Birds on neighboring nests often fight by bill-jousting. A courting male collects pebbles and places them at female's feet. Mated pairs engage in mutual preening of feathers. Very noisy and aggressive in breeding colonies; after females begin incubating, males go to sea and females may then be attacked by unmated males. When birds return from foraging, harsh braying calls are essential for recognition between mates and between parent and chick. Parents take turns incubating and brooding young.

FEEDING ECOLOGY AND DIET
Typically dives to 66–330 ft (20–100 m) in pursuit of prey; mean dive duration 1.48 minutes. In one study, estimated prey capture rates were 4.0–16.0 krill per dive and up to 50 amphipods per dive. At first, young are fed krill exclusively; gradually, small fish and squid are added to the diet. In the last week before the chick becomes independent, parents feed it only fish and squid.

REPRODUCTIVE BIOLOGY
Female alone scrapes out depression to serve as nest; both members of the pair line nest with pebbles. Eggs rough-textured with faint blue tinge. Egg laying tightly synchronized within colonies; first-laid egg is small, weighing 61–64% of second egg, which is laid 3.2 days later. First egg almost always lost or destroyed; if second egg is destroyed, normal, healthy chick may hatch from first egg. Incubation period is 35–37 days from laying of second egg. Males guard chicks for about 20 days after hatching, when young birds form crèches. Both parents continue to feed their offspring until independence at 60–70 days.

CONSERVATION STATUS
Listed as Vulnerable because the world population appears to have decreased by at least 20% over a 36-year period. Designation was based on extrapolation from a small amount of data, so large-scale surveys will be needed to confirm this penguin's status.

SIGNIFICANCE TO HUMANS
Communities in the Falkland Islands formerly observed November 9 as a holiday on which children were excused from school to collect the eggs of macaroni and other penguins. ◆

Magellanic penguin
Spheniscus magellanicus

TAXONOMY
Aptenodytes magellanicus J. R. Forster, 1781, Strait of Magellan.

OTHER COMMON NAMES
French: Manchot de Magellan; German: Magellanpinguin; Spanish: Pingüino de Magallanes.

PHYSICAL CHARACTERISTICS
28 in (71 cm); female weight 5.9–9.0 lb (2.7–4.1 kg), male 6.4–10.6 lb (2.9–4.8 kg). Boldly striped penguin with two black bands across chest. Sexes similar but female smaller than male. Cheeks and cap brownish black, divided by wide white ring. Black back and white underparts lightly splotched with black. Stubby black bill with gray band near tip. Eyes are brown. Feet are pink blotched with black. Juveniles smaller than adults and breast bands are not distinct.

DISTRIBUTION
Breeds in coastal areas and on offshore islands along the southern part of South America, occasionally in southern coastal Australia and New Zealand. Breeding distribution seems to be moving northward. Migratory outside of breeding season; birds from colonies at the tip of south America may travel as far north as Peru and southern Brazil.

HABITAT
Breeds on bare or vegetated islands, in flat areas and on cliff faces. Colonies located in areas where offshore winds cause upwelling of deep, cold, nutrient-rich waters so that primary productivity is high. Birds have best nesting success in protected sites under bushes or other vegetation. Feed inshore during breeding season and in pelagic waters during migration.

BEHAVIOR
Foraging birds may be seen porpoising in long lines, one after the other. Breed in large colonies; often return to the same nest site from year to year. Voice described as a mournful, donkey-like braying; often call in chorus at night.

FEEDING ECOLOGY AND DIET
Eat mostly small, schooling fish such as anchovies, sardines, and sprats but diet varies depending on prey availability. Most dives descend 66–164 ft (20–50 m). Underwater swimming speed measured at about 4.7 mi/hr (7.6 km/hr).

REPRODUCTIVE BIOLOGY
Where soil allows digging, they nest in burrows; otherwise they build nests on the ground. Both members of pair build nest. Two-egg clutch is laid and eggs are of similar size. Parents share incubation, brooding, and guarding duties. Chick hatched from second-laid egg less likely to survive to fledging. Chicks independent at 60–70 days.

CONSERVATION STATUS
Listed as Near Threatened. A 1994 study estimated that oil pollution kills 40,000 penguins a year on the southern coast of Argentina.

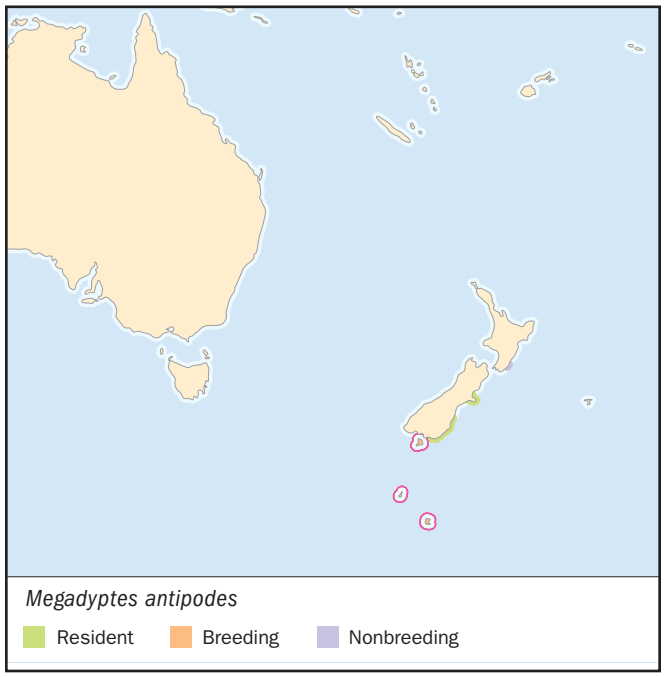
SIGNIFICANCE TO HUMANS
In the past, native peoples killed penguins for meat and for their skins. Today, Magellanic penguin rookeries at Punta Tombo in Argentina are a major ecotourism destination, attracting 50,000 visitors a year. ◆

Yellow-eyed penguin
Megadyptes antipodes

TAXONOMY
Catarrhactes antipodes Hombron and Jacquinot, 1841, Auckland Islands.

OTHER COMMON NAMES
French: Manchot antipode; German: Gelbaugenpinguin; Spanish: Pingüino de Ojos Amarillos.

PHYSICAL CHARACTERISTICS
22.0–30.7 in (56–78 cm); female weight 9.3–15.5 lb (4,200–7,500 g); male 9.70–18.7 lb (4,400–8,500 g). The only penguin with yellow eyes; band of yellow feathers extends from one edge of mouth to the other, passing through the eyes and around the nape of the head. Head feathers are yellow with a central black streak; back and tail are slate blue; flippers are darker blue; and breast and belly are white. Long slender bill is red-brown above cream shading to red-brown below. Pale pink feet turn magenta with exertion. Juveniles lack yellow band of feathers around nape.



DISTRIBUTION
Endemic to New Zealand and nearby smaller islands. Most birds winter on or near the breeding grounds.

HABITAT
Breed in coastal areas of southern New Zealand and neighboring subantarctic islands. Birds stay near breeding sites year round, except for juveniles that move north to feeding grounds for a few months after fledging. Nest from sea level to elevation of 820 ft (250 m) on sea-facing, forested slopes and cliff tops, usually amid dense forest vegetation. Probably choose cool, shady forests to avoid overheating.

BEHAVIOR
Gregarious in winter (non-breeding season); roost communally on flat, open ground and gather in groups of 50–100 on beaches before departing for foraging areas. They forage alone at sea. Secretive and especially wary of humans. During breeding season they come ashore at night and negotiate difficult terrain to reach cliff-top breeding areas. The least colonial of penguins when breeding; nests are clustered together only because appropriate habitat is limited. Calls are less harsh than those of other penguins; Maori name, hoiho, means “noise shouter.”

FEEDING ECOLOGY AND DIET
Eat mostly fish, some squid, and rarely crustaceans. While one parent guards chick, off-duty bird heads to sea to forage in afternoon and returns at dusk. Outside of the breeding season, most birds head to sea at dawn and return before dark.

REPRODUCTIVE BIOLOGY
Nest out of sight of nearest neighbors amid dense vegetation. Prefer hardwood (*Podocarpus*) forests (where nest sites are at the base of trees or alongside fallen longs) but also nest in fields of tussock grass. Nesting territory may be defended year-round. Nest is a shallow bowl of twigs and other plant matter constructed by both parents. Two eggs laid, three to five days apart. Parents alternate incubation shifts of one to seven days during 39–51 day incubation period and also take turns brooding chicks for four to six weeks.

CONSERVATION STATUS
A 1990 study indicated the population had declined at least 75% over 40 years. Changed from Vulnerable to Endangered; total breeding population estimated to be fewer than 2,000 pairs. Breeding range is very small, and habitat has been degraded, especially by clearing of hardwood forests for farming. In addition, cattle trample nests and introduced ferrets, stoats, and feral cats are significant predators. Adults also caught and killed accidentally in fishing nets. Ongoing conservation efforts may be starting to reverse population decline.

SIGNIFICANCE TO HUMANS
Yellow-eyed penguins have become a figurehead species of the New Zealand environmental movement. ◆

Little penguin
Eudyptula minor

TAXONOMY
Eudyptula minor J. R. Forster, 1781, Dusky Sound, South Island, New Zealand.

OTHER COMMON NAMES
English: Fairy penguin, little blue penguin, white-flippered penguin; French: Manchot pygmée; German: Weissflügelpinguin, Zwergpinguin; Spanish: Pingüino Pequeño.

PHYSICAL CHARACTERISTICS
15.7–17.7 in (40–45 cm); weight 2.2 lb (1 kg). The smallest penguin; male larger than female. Indigo-blue above, white below. Eyes are gray to hazel. Stout black bill is slightly hooked. Feet are white above with black soles. Juveniles similar to adult but smaller and with slimmer bill; plumage brighter than that of adults.

DISTRIBUTION
Southern coast of Australia; coastal New Zealand; offshore islands.

HABITAT
Temperate inshore waters; often seen in bays and estuaries. Often breeds in secluded bays, promontories, or islands, often at the base of cliffs. Prefers flat areas with protective vegetation. Nests in burrows but also under rocks, in caves, and under mounds of tussock-grass. Has adapted to nest around humans, including under houses and in culverts, and will also use artificial burrows. Require the shelter of burrows or rocks or bushes during molt.

BEHAVIOR
Colonial; adults reside at breeding sites year-round. Typically forage within 0.6 mi (1 km) of shore but may travel farther. Mated pairs stay together year-round. Roost alone or in pairs, often in burrows. The most nocturnal of all penguins. Calls include short yaps, grunts, trilling, and braying.

FEEDING ECOLOGY AND DIET
Prefer small fish or cephalopods. When swimming underwater, a bird will circle a school several times and then plunge through its middle.

REPRODUCTIVE BIOLOGY
Both parents dig the burrow and build the nest; they also share incubation and feeding duties. Nest built of grass and other plant material. Two eggs laid over three to five days. Parents accept eggs other than their own and have been seen to incubate stones, golf balls, and teacups. Chicks are brooded for 10 days and are guarded for another 10–21 days.

CONSERVATION STATUS
Not threatened; however, populations described as stable or decreasing. Housing developments and farmland have replaced many breeding areas. Face predation from introduced foxes and dogs; also, livestock trample nesting sites and rabbits eat protective vegetation around nests. Erosion and run-off from agriculture affects marine water quality, which can reduce food supply and also increase rates of disease.

SIGNIFICANCE TO HUMANS
Little penguins returning from a night's fishing form a parade that is a popular tourist attraction on resort beaches. ◆

Resources

Books
Davis, L. S., and J. T. Darby, eds. *Penguin Biology.* New York: Academic Press, 1990.

Marchant, S., and P. J. Higgins, eds. *Handbook of Australian, New Zealand, and Antarctic Birds.* Vol. 1, *Ratites to Ducks.* New York: Oxford University Press, 1990.

Marion, R. *Penguins: A Worldwide Guide.* New York: Sterling Publishing Co.,1999.

Reilly, P. *Penguins of the World.* New York: Oxford University Press, 1994.

Williams, Tony D. *The Penguins: Spheniscidae.* New York: Oxford University Press, 1995.

Periodicals
Bried, J., F. Jiguet, and P. Jouventin. "Why do *Aptenodytes* Penguins Have High Divorce Rates?" *Auk* 116 (1999): 504–512.

Cherel, Y., and G. L. Kooyman. "Food of Emperor Penguins (*Aptenodytes forsteri*) in the Western Ross Sea, Antarctica." *Marine Biology Berlin* 130 (1998): 335–344.

Gandini, P., P. D. Boersma, E. Frere, M. Gandini, T. Holik, and V. Lichtschein. "Magellanic Penguins (*Spheniscus magellanicus*) Are Affected by Chronic Petroleum Pollution Along the Coast of Chubut, Argentina." *Auk* 111 (1994): 20–27.

Green, K., R. Williams, and M. G. Green. "Foraging Ecology and Diving Behavior of Macaroni Penguins *Eudyptes*

Resources

chrysolophus at Heard Island." *Marine Ornithology* 25 (1998): 27–34.

Jouventin, P., T. Aubin, and T. Lengagne. "Finding a Parent in a King Penguin Colony: The Acoustic System of Individual Recognition." *Animal Behavior* 57 (1999): 1175–1183.

Kent, S., J. Seddon, G. Robertson, and B. Wienecke. "Diet of Adelie Penguins *Pygoscelis adeliae* at Shirley Siland, East Antarctica, January 1992." *Marine Ornithology* 26 (1998): 7–10.

Lengagne, T., T. Aubin, P. Jouventin, J. Lauga. "Perceptual Salience of Individually Distinctive Features in the Calls of Adult King Penguins." *Journal of the Acoustical Society of America* 107 (2000):508–516.

Schwartz, M. K., D. J. Doness, C. M. Schaeff, P. Majluf, E. A. Perry, and R. C. Fleischer. "Female-Solicited Extra-Pair Matings in Humboldt Penguins Fail to Produce Extra-Pair Fertilizations." *Behavioral Ecology* 10 (1999): 242–250.

Scolaro, J. A., R. P. Wilson, S. Laurenti, and M. Kierspel. "Feeding Preferences of the Magellanic Penguin over its Breeding Range in Argentina." *Waterbirds* 22 (1999): 104–110.

Stokes, D. L., and P. D. Boersma. "Nest Site Characteristics and Reproductive Success in Magellanic Penguins (*Spheniscus magellanicus*)." *Auk* (1998) 115: 34–49.

Cynthia Ann Berger, MS

Gaviiformes
Loons
(Gaviidae)

Class Aves
Order Gaviiformes
Family Gaviidae
Number of families 1

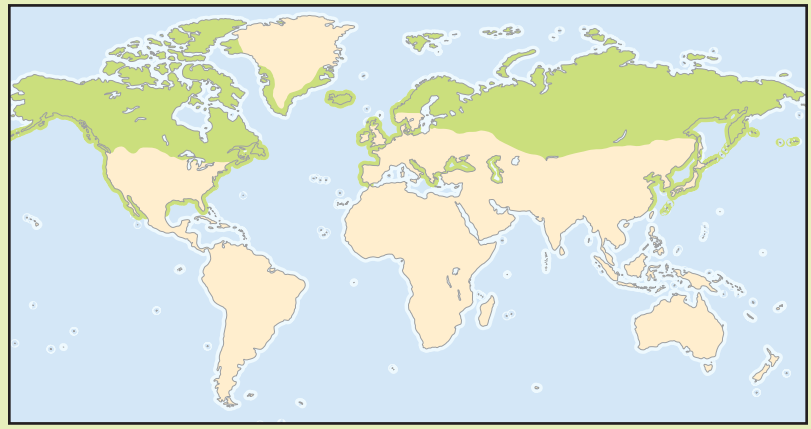
Thumbnail description
Medium to large-sized, foot-propelled diving waterbirds that feed mainly on fish. Foot placement is far posterior, making walking on land difficult. Bills are sharp and dagger-like. Alternate (breeding) plumage is boldly patterned primarily with black, white, and gray; nonbreeding plumages are drab gray-brown and white. All have brilliant red iris in alternate plumage, and distinctive eerie vocalizations

Size
20.8–35.8 in (53–91 cm); 2.2–14.1 lb (1.0–6.4 kg); males slightly larger than females in all species

Number of genera, species
1 genus; 5 species

Habitat
Breed in forested and tundra lakes and ponds, winter at sea and large reservoirs

Conservation status
No species considered Endangered or Threatened



Distribution
Holarctic

Evolution and systematics

The five extant species currently recognized are descendants of an ancient bird lineage. The extinct genus *Colymboides* arose in the late Eocene to early Miocene. *Gavia* appeared in the Miocene, and radiated into three size classes by the early Pliocene. Biochemical analyses suggest that loons are most closely related to penguins (Sphenisciformes), tubenoses (Procellariiformes), frigatebirds (Fregatidae), and possibly auks and gulls (Charadriiformes). Traditionally loons have been grouped with grebes (Podicipediformes) because the two orders are convergent. Within the family, common (*Gavia immer*) and yellow-billed (*G. adamsii*) loons are very closely related, as are Arctic (*G. arctica*) and Pacific (*G. pacifica*) loons. Red-throated loons (*G. stellata*) are considered less closely related to the other four species, but phylogenetic relationships are uncertain and controversial.

Physical characteristics

Loons are medium to large, foot-propelled diving waterbirds, with anatomy specialized for pursuit and capture of fish. Overall shape is very distinctive with a short neck, pointed wings, and legs set far back on the body. Loon tarsi are flattened and knife-like, cutting through the water efficiently. The feet are large and palmate with the front three toes webbed, and a free hallux. Loon feet, legs, and nails are uniquely countershaded such that when swimming white surfaces, the tops of their feet are oriented down, helping the bird blend in against light sky. Bills are medium-sized and dagger-like. All species have a distinct blood red iris in alternate plumage. Sexes are similar, with the male larger than the female in all species. Each species has four plumages after they are fully grown: juvenal, second alternate (second summer), basic (nonbreeding), and alternate (breeding). Molt times are slightly different for all species.

In alternate plumage all species have striking patterns composed of black, white, and gray. Upperparts are dark gray or black, with faint white speckling to bold white checkering. Underparts are completely white. Each species has a series of bold, thin, black-and-white parallel stripes on the neck. Head patterns are similar in Arctic/Pacific loons and common/yellow-billed loons. The head pattern of red-throated loon is unique: it is the only loon to have brick red in its plumage.

All loons have similar juvenal, second alternate, and basic plumages. Upperparts are gray-brown and underparts are

Red-throated loon (*Gavia stellata*) turning eggs during incubation in Yukon Delta National Wildlife Refuge, Alaska. (Photo by Stephen J. Krasemann. Photo Researchers, Inc. Reproduced by permission.)

white as a rule; head pattern is slightly different for all species. Juvenal and second alternate birds appear more scaly than adults due to the presence of pale fringes on many contour feathers. Identification of non-breeding birds can be difficult, and general body shape, bill shape and size, and posture can be more helpful than plumage differences for identification.

Molt is complicated and not yet fully understood. Loons have one complete pre-basic molt in fall and one partial pre-alternate molt in spring. The complete molt in fall is prolonged, and individuals may appear to be molting much of the year. Due to the high wing loading in loons, flight is impossible with the loss of a few primaries. Instead of a gradual molt, which would leave them flightless for months, loons have evolved to molt all of their primaries simultaneously, which only leaves them flightless for a couple of weeks. This molt occurs during winter, from about January to April in all species but the red-throated loon, which is small enough that it can fly during a gradual molt of flight feathers. First-year birds also molt primaries simultaneously in their first summer on salt water.

Distribution

Holarctic in distribution, loons breed from north temperate areas to the high arctic. All species migrate up and down coasts and across land to winter primarily at sea, south to coastal Baja California, Gulf of Mexico, Mediterranean Sea, and coastal China. Loons may stage on inland lakes and rivers during migration. Nonbreeding birds will often spend summer in their species' winter range.

Habitat

Loons breed in freshwater inland lakes and tundra ponds. Where sympatric, different species occupy different-sized lakes. Larger species exclude smaller species from breeding ponds, but are limited to larger ponds by minimum take-off distances. Smaller species can occupy ponds too small for larger species. Individuals usually spend winter near shore in oceans and seas, less than 62 mi (100 km) offshore. They are occasionally found in large freshwater lakes and rivers during winter.

Behavior

Loons are extremely territorial on their breeding grounds. Pairs have been observed attacking their own species, as well as other species of loons, ducks, and geese. In one study, 50% of common loons had healed fractures believed to have been caused by the bill of other common loons. Loon pairs have a series of territorial threat postures and calls to prevent fighting, which can be fatal. In winter and during migration loons may be found singly or in loose flocks.

Loons are known for their unusual vocalizations, described as yodels, wails, and tremolos. Most vocalizations are given on the breeding grounds, occasionally during winter, or on migration. Territorial yodels, most often given at night or early morning, can be heard from great distances (reports have been made of calls heard up to 16 mi [25.8 km] by humans). These male yodels are individually recognizable throughout the birds' lifetime.

Flight is powerful and direct, with wings beating constantly. Most species require running on the surface of water to gain speed for take-off. The red-throated loon is the only species that can take off from land. All species are awkward on land; the posterior positioning of the feet often forces them to push themselves along breast first on their bellies. Occasionally loons accidentally land on wet pavement after mistaking it for water, or are forced to land during storms. In this case, they are stranded and will most likely die, although adults in this situation have traveled over a kilometer to seek water at the expense of broken toes and wrists.

The agility of loons on water compensates for their inadequacies on land. Posterior placement of the feet allows for powerful swimming and diving capabilities. Adults can stay submerged for several minutes and can travel hundreds of meters underwater. Loons dive with a forward thrust using both feet simultaneously to propel them through water. Occasionally, wings are also used to supplement the feet underwater, and they can use one foot as a rudder when turning.

Feeding ecology and diet

Loons take a variety of vertebrate and invertebrate foods, but small to medium-sized fish up to about 7–8 in (18–20 cm) are the primary items. Young are also fed crustaceans, mol-

lusks, and worms. Prey is located by sight from the surface of the water. Loons peer downward, often with their bill in the water, and dive with a thrust from both feet. Most prey is eaten underwater; fish that are too large to be handled underwater are taken to the surface. Most foraging is done close to the surface, but loons may forage as deep as 230 ft (70 m) if the water is clear enough. Very small serrations on the bill help loons hold onto prey. Adults and young consume large quantities of prey; an adult common loon consumes 1,214 kilocalories a day, and a pair may eat 2,000 lb (910 kg) of fish in a breeding season. Loons have large salt glands that remove excess salt consumed from marine environments.

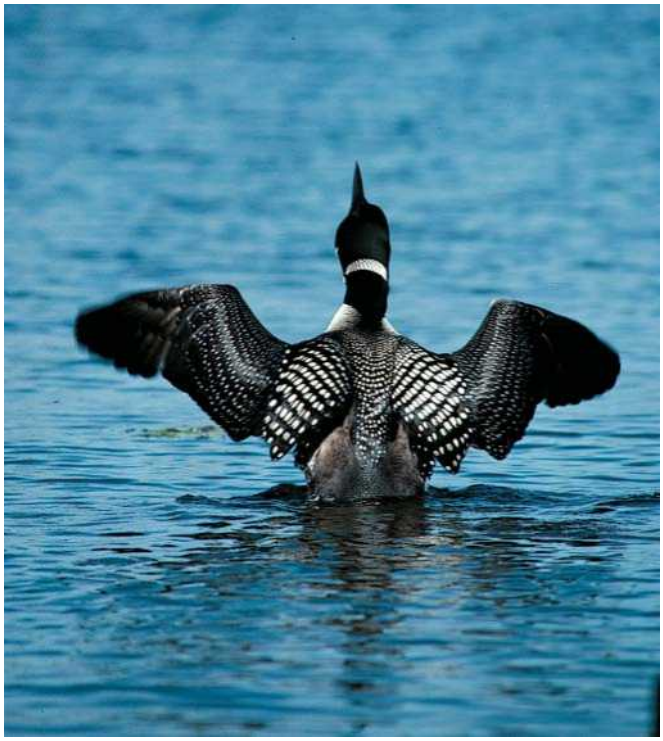
Stomach contents have shown that loons consume a wide variety of fish, including sticklebacks (*Gasterosteus*), trout (*Salvelinus*), sculpin (*Leptocottus*), cods (*Gadus*), herrings (Clupeiidae), haddock (*Melanogrammus*), whitefish (*Coregonus*), capelins (*Mallotus*), minnows (Cyprinidae), and many other species. At sea, menhaden (*Brevoortia*) are extremely important. Little is known about prey selection.

Reproductive biology

Loons are monogamous, although they will quickly replace a lost mate. Extra-pair copulation has been noted with marked birds, but has not been studied extensively to determine frequency. Pair bonds, which may last for life, are first formed on breeding grounds. Pair formation is not well understood, although it includes bill-dipping and paired-swimming displays where both adults rise out of the water in various postures. Both sexes quickly build the nest, sometimes in as little as half a day to a week; returning pairs may reuse old nests. Nests are constructed of wet vegetation on land or as a floating mat, with a 15–32 in (38–82 cm) diameter. Two eggs are usually laid (rarely one or three) from May to July, depending on latitude and weather; in northernmost areas there may be only two to three months to breed. Eggs are long, subelliptical in shape, from 2.9 by 1.8 in (72.7 by 44.8 mm) to 3.5 by 2.2 in (89.4 by 55.15 mm) in size, and are olive green with brown markings. Pairs will re-lay if the first clutch is lost. Both sexes incubate, beginning with the laying of the first egg. Incubation period is 24–30 days; larger species have longer incubation periods. Chicks hatch asynchronously, are semiprecocial, and covered with dark gray natal down. Chicks leave the nest soon after they dry, but may return for brooding. Young rely on both parents for food but will begin to dive on their own in three days. Chicks will occasionally ride on a parent's back when small. Young can fly in six to eight weeks. Predators of eggs and chicks include many mammals and other birds. To avoid predators, chicks dive to the bottom of the water to stir up sediments, resurfacing in emergent vegetation for cover. Adults have few predators, and band recoveries suggest loons have a life span of 25–30 years.

Conservation status

No loons are listed on the IUCN Red List of Threatened Species of Birds. Isolation of breeding habitat protects their numbers from human disturbance in many areas, but where overlap does occur loons have declined due to habitat encroachment and acid precipitation, which can lower pH levels enough to kill all the fish in many lakes. Loon conservation groups have formed to protect them in many areas. At sea, fishnets kill many adults, and are responsible for one-third of red-throated loon banding recoveries. Oil spills kill many loons, which are especially susceptible when adults are flightless while molting primaries. The *Exxon Valdez* spill in Alaska resulted in hundreds of loons being washed ashore. Botulism, a bacterial disease, has killed thousands of loons staging on the Great Lakes. Common loon populations, in particular, have declined in parts of northeastern United States and in Ontario, Canada, due to increase in human activities—boating, use of jet skis, and canoeing—lake acidification, and mercury poisoning.



Common loons (*Gavia immer*) stretch, remove water, and signal with this motion. (Photo by Gregory K. Scott. Photo Researchers, Inc. Reproduced by permission.)

Significance to humans

The Inuit legally hunt loons in arctic North America for subsistence purposes. Roughly 4,600 may be taken each year. They are not considered to be the best-tasting food, and may be fed to dogs. Native Americans honor loons with many stories and parables. Loons are a symbol of the north, and a symbol of tranquility. The common loon is featured in Canadian currency on the $1 coin (commonly called "loonies") and the $20 bill.

1. Red-throated loon (*Gavia stellata*); 2. Arctic loon (*Gavia arctica*); 3. Pacific loon (*Gavia pacifica*); 4. Common loon (*Gavia immer*); 5. Yellow-billed loon (*Gavia adamsii*). (Illustration by Marguette Dongvillo)

Species accounts

Red-throated loon
Gavia stellata

TAXONOMY
Colymbus stellatus Pontoppidan, 1763, Tame River, Warwickshire, England. Monotypic.

OTHER COMMON NAMES
English: Red-throated diver; French: Plongeon catmarin; German: Sterntaucher; Spanish: Colimbo Chico.

PHYSICAL CHARACTERISTICS
20.8–27.19 in (53–69 cm); 2.2–5.9 lb (1.0–2.7 kg). The smallest and least robust in the family, with proportionally smaller, upturned bill and smaller feet than other loons. Smaller size allows red-throated loons to take off directly from water and even from land. In alternate plumage, has grayish upperparts, white underparts, gray face, and brick red throat patch. In basic plumage, has grayish upperparts with white speckling, gray cap and nape, white underparts, throat, and face. Juvenal and second alternate plumages similar to basic plumage, with gray-brown wash on head and neck.

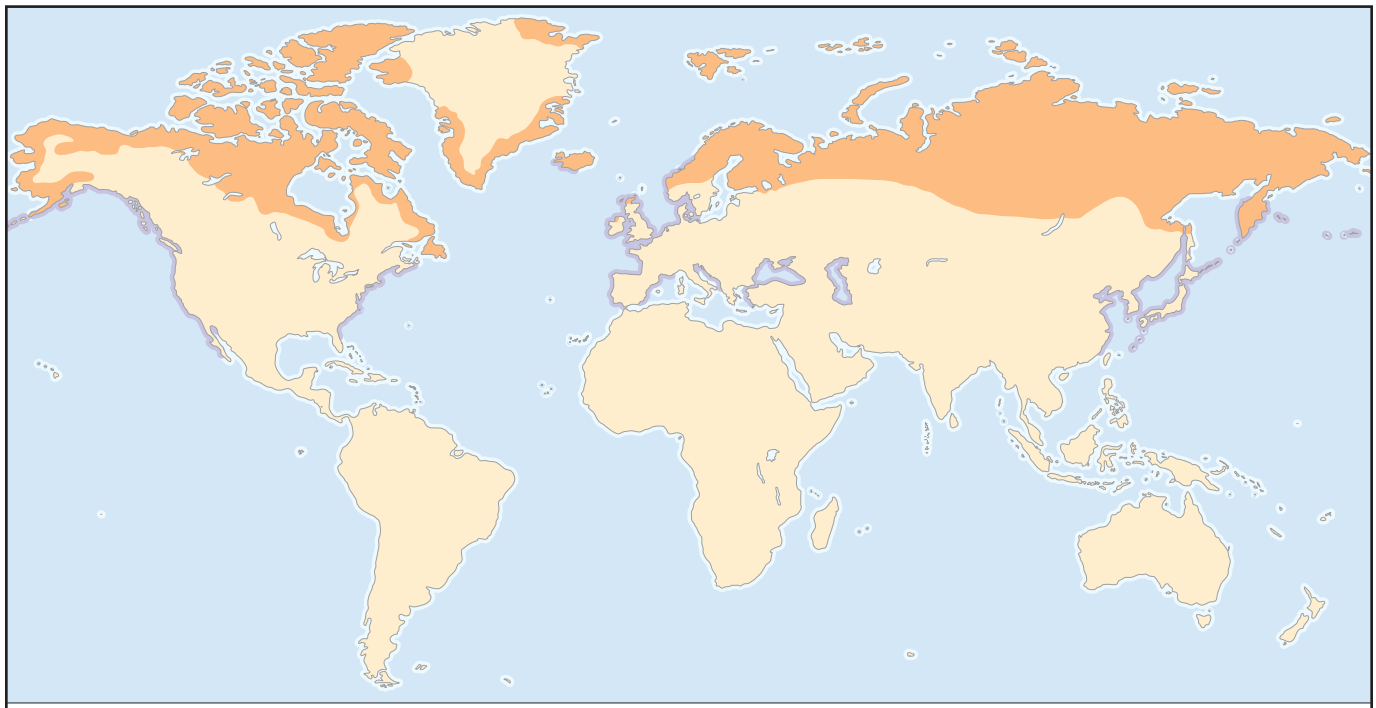
DISTRIBUTION
Breeding range is circumpolar, ranging farther north than other loons. Occupies coastal plain in Alaska, northern Canada, Greenland, Iceland, northern British Isles, Norway, Sweden, Finland, and across Russia. Winters on coasts on Atlantic and Pacific Oceans north of the tropic of Cancer, occasionally found inland. Migrates mostly along coast, occasionally over land.

HABITAT
Breeds mainly on ponds in coastal tundra, occasionally inland up to 3,511 ft (1,070 m) in elevation. Where it competes with other loons, occupies smaller (sometimes fishless) ponds too small for larger loons. In the far north where it is the only loon present, will breed on larger ponds and lakes. Winters on coasts, usually within 3 mi (5 km) of shore in areas with a soft, sandy substrate. Occasionally found inland on large lakes and rivers.

BEHAVIOR
The only loon to have duet vocalizations, given by pairs on breeding ponds. May migrate singly or in loose flocks. Does not require running start from water during take-off like other loons, and is the only loon that can take off from land.

FEEDING ECOLOGY AND DIET
Feeds on variety of small freshwater and marine fish. Will feed invertebrates to small chicks, and will feed on invertebrates as adults when fish are scarce. When breeding in fishless ponds, will fly to the coast and other ponds to catch prey to bring back to the young.

REPRODUCTIVE BIOLOGY
Breeds from May to September, depending on latitude and climate. Incubation 24–27 days. Occasionally moves from breeding



pond to a larger pond or the ocean. Chicks are more agile on land than are adults, and have been seen traveling over a kilometer over land. Young can fly after 38 days. Predators include Arctic fox (*Aloplex lagopus*) and other mammals, jaegers (*Stercorarius*), and gulls (*Larus*).

CONSERVATION STATUS
Declining over much of its range, although the cause is unknown. Not listed on IUCN Red List of Threatened Birds.

SIGNIFICANCE TO HUMANS
Inuit legally hunt around 4,600 loons (of all species) each year for subsistence; the proportion that are red-throated is unknown. ◆

Pacific loon
Gavia pacifica

TAXONOMY
Gavia pacifica Lawrence, 1858. Monotypic.

OTHER COMMON NAMES
English: Pacific diver; French: Plongeon du Pacifique; German: Weissnackentaucher; Spanish: Colimbo del Pacifico.

PHYSICAL CHARACTERISTICS
20–27 in (50–68 cm); 3.7 lb (1.7 kg). Very similar to the larger Arctic loon in all plumages. Bill medium-sized, straight. Black upperparts with white patches, white underparts, black throat, and gray head and neck (darker near bill). Differentiated from the Arctic loon by black flanks, paler nape, and thinner white stripes on neck. In hand, throat shows faint purple iridescence. Basic, juvenal, and second alternate plumages similar, with gray upperparts, crown, and nape and white underparts.

DISTRIBUTION
Breeds on tundra ponds from eastern Siberia to Hudson Bay; winters on Pacific Ocean from southern Japan to Siberia, Alaska to southern California. Migration chiefly occurs coastally.

HABITAT
Breeds on medium-sized lakes and ponds in northern forests and tundra. Excluded from large lakes by yellow-billed and common loons; excludes red-throated loons from medium-sized lakes. Winters in coastal areas, often farther offshore than other species.

BEHAVIOR
Males give territorial yodel call that is individually recognizable, and can be heard from miles away. Pacific loons are unafraid of humans, and allow close approach on breeding grounds. A pair was observed adopting a brood of spectacled eiders; this is the only reported case of adoption in Gaviidae.

FEEDING EC OLOGY AND DIET
Consumes a wide variety of fish; feeding and diet similar to other species.

REPRODUCTIVE BIOLOGY
Breeds on medium-sized ponds, sympatric with the Arctic loon where ranges overlap; pairs of both species have been found on the same lake. Breeds from May to September. Incubation 28–30 days, fly at 60 days. Predators include gulls (*Larus*), foxes (*Aloplex* and *Vulpes*), jaegers (*Stercorarius*), and ravens (*Corvus*).

CONSERVATION STATUS
Most populations stable. Not listed on IUCN Red List of Threatened Birds.

SIGNIFICANCE TO HUMANS
Inuit legally hunt loons for subsistence on breeding grounds; 4,600 loons (of all species) are taken yearly. ◆

Arctic loon
Gavia arctica

TAXONOMY
Colymbus arcticus Linnaeus, 1758, Sweden. Two subspecies recognized.

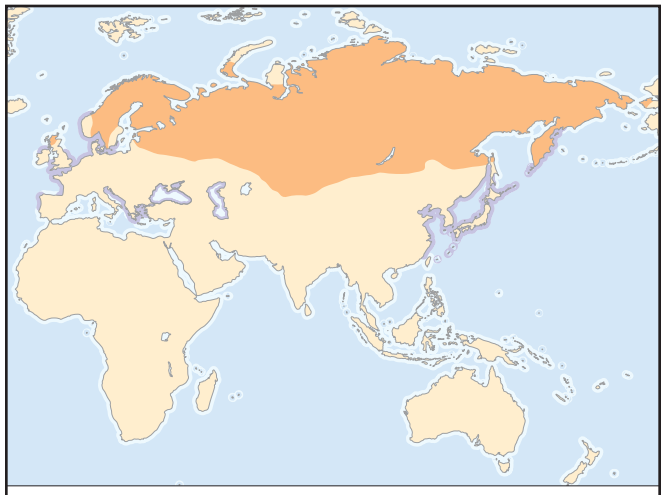
OTHER COMMON NAMES
English: Black-throated diver; French: Plongeon Arctique; German: Prachttaucher; Spanish; Colimbo Arctico.

PHYSICAL CHARACTERISTICS
23.6–29.6 in (60–75 cm); 5.7 lb (2.6 kg). Very similar to the smaller Pacific loon. Black upperparts with white patches, white underparts, black throat, and gray head and neck (darker near bill). Differentiated from the Pacific loon by white flanks, darker nape, more distinct white stripes on neck. In hand, throat shows faint greenish iridescence. Basic, juvenal, and second alternate plumages similar, with gray upperparts, crown, and nape and white underparts.

DISTRIBUTION
Breeds from extreme western Alaska across northern Eurasia to northern Scotland. Winters coastally from Japan to China and Europe.

HABITAT
Breeds on medium-to-large lakes and ponds in northern forests and tundra; winters on coasts.

BEHAVIOR
Similar to the Pacific loon.



FEEDING ECOLOGY AND DIET
Consumes a wide variety of fish, similar to other loons. Has been observed catching frogs.

REPRODUCTIVE BIOLOGY
Incubation 28–29 days, flight 60 days. In Scotland, artificial breeding platforms have been used to increase chick production by an estimated 44%.

CONSERVATION STATUS
Most populations stable, not listed on IUCN Red List of Threatened Birds.

SIGNIFICANCE TO HUMANS
A species of interest for many people. Nest platform programs have been started in Scotland, where populations have declined. ◆

Common loon
Gavia immer

TAXONOMY
Colymbus immer Brünnich, 1764, Faeroes. Monotypic.

OTHER COMMON NAMES
English: Great northern diver; French: Plongeon huard, Plongeon Imbrin; German: Eistaucher; Spanish: Colimbo grande, Colimbo Comun.

PHYSICAL CHARACTERISTICS
26.0–35.8 in (66–91cm); 5.5–13.4 lb (2.5–6.1 kg). Very similar to the yellow-billed loon in all plumages. In alternate plumage, black upperparts with white checkering and spotting, black neck with white stripping, and black head. Underparts are white. Juvenal, second alternate, and winter plumages similar, dark gray brown upperparts, head, and nape; white underparts and throat. Bill is straight and black in alternate and dark gray with a black culmen in other plumages.

DISTRIBUTION
Breeds throughout Alaska, Canada, northern New England, northern Midwest, and parts of Greenland and Iceland. Winters in Pacific Ocean from southern Alaska to Baja California, on Atlantic Ocean from Newfoundland to Mexico, also Europe and Iceland. Migrates over land and down coasts; stages on larger lakes. Many non-breeders summer in winter range.

HABITAT
Breeds in clear, oligotrophic, forested lakes and large tundra ponds. Winters mainly on coast within 62 mi (100 km) of shore, occasionally on large inland lakes and rivers.

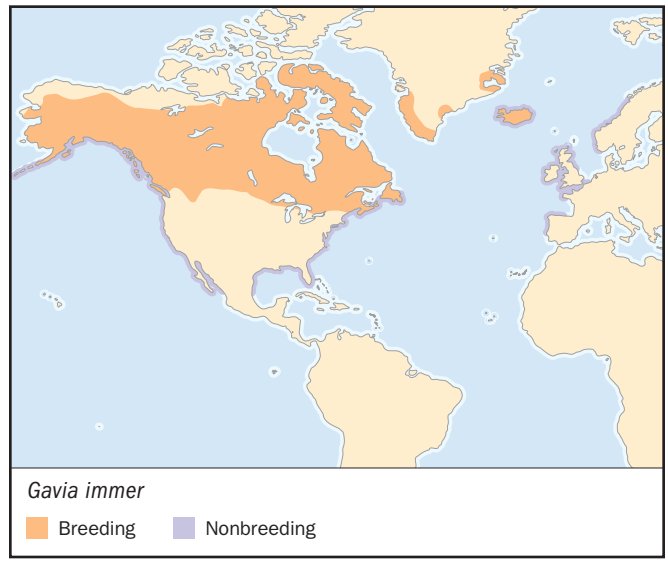
BEHAVIOR
Found in pairs on breeding grounds, singly or in loose flocks during migration and winter. Requires 100–650 ft (30–200 m) to take off, limiting common loons to large lakes. Extremely territorial on breeding grounds—other loons and waterbirds are chased off. Yodel call, a series of repeated two-note phrases, is recognizable to individuals and used to defend territories.

FEEDING ECOLOGY AND DIET
Feed mainly on fish and invertebrates; vegetation occasionally taken. Crayfish are a common food when fish are scarce.

REPRODUCTIVE BIOLOGY
Nests farther south than other loons, from May to October. Little is known about pair formation. Nest is made of vegetation in about a week, on land at the edge of a lake. Incubation 27–30 days. Young leave nest in one day, but may return for brooding. Young able to fly in 11 weeks. Predators include gulls (*Larus*), ravens and crows (*Corvus*), pike (*Esox*), and raccoons, weasels, and skunks (Carnivora).

CONSERVATION STATUS
Populations are stable. Not listed on IUCN Red List of Threatened Birds, but is listed as threatened or of special concern in several northeast states. Acidification of lakes, heavy metal contamination, and human encroachment threaten populations in southern range.

SIGNIFICANCE TO HUMANS
Inuit hunt 4,600 loons (of all species) per year for subsistence. Many Native American tribes have stories about common



loons. Many loon conservation groups have also been formed to protect common loons in their southern range. ◆

Yellow-billed loon
Gavia adamsii

TAXONOMY
Colymbus adamsii Gray, 1859, Alaska. Monotypic.

OTHER COMMON NAMES
English: White-billed diver; French: Plongeon a Bec Blanc; German: Gelbschnabel-Eistaucher; Spanish: Colimbo de Adams.

PHYSICAL CHARACTERISTICS
30–36 in (76–91cm); 9.0–14.1 lb (4.1–6.4 kg). Largest loon, with the largest bill. Very similar to the common loon in all plumages. In alternate plumage, black upperparts, neck, and head; white striping on the neck and white checkering on the back. Underparts white. Juvenal, second alternate, and winter plumages similar, dark gray brown upperparts, head, and nape; white underparts and throat. Bill is large and upturned, yellow to ivory.

DISTRIBUTION
Replaces common loon in high arctic, breeds in Canada and Alaska, also across Siberia. Winters along coasts in northern Pacific, and along the coast of Norway. Winters farther north than other loons.

HABITAT
Breeds in large tundra lakes; winters along coasts.

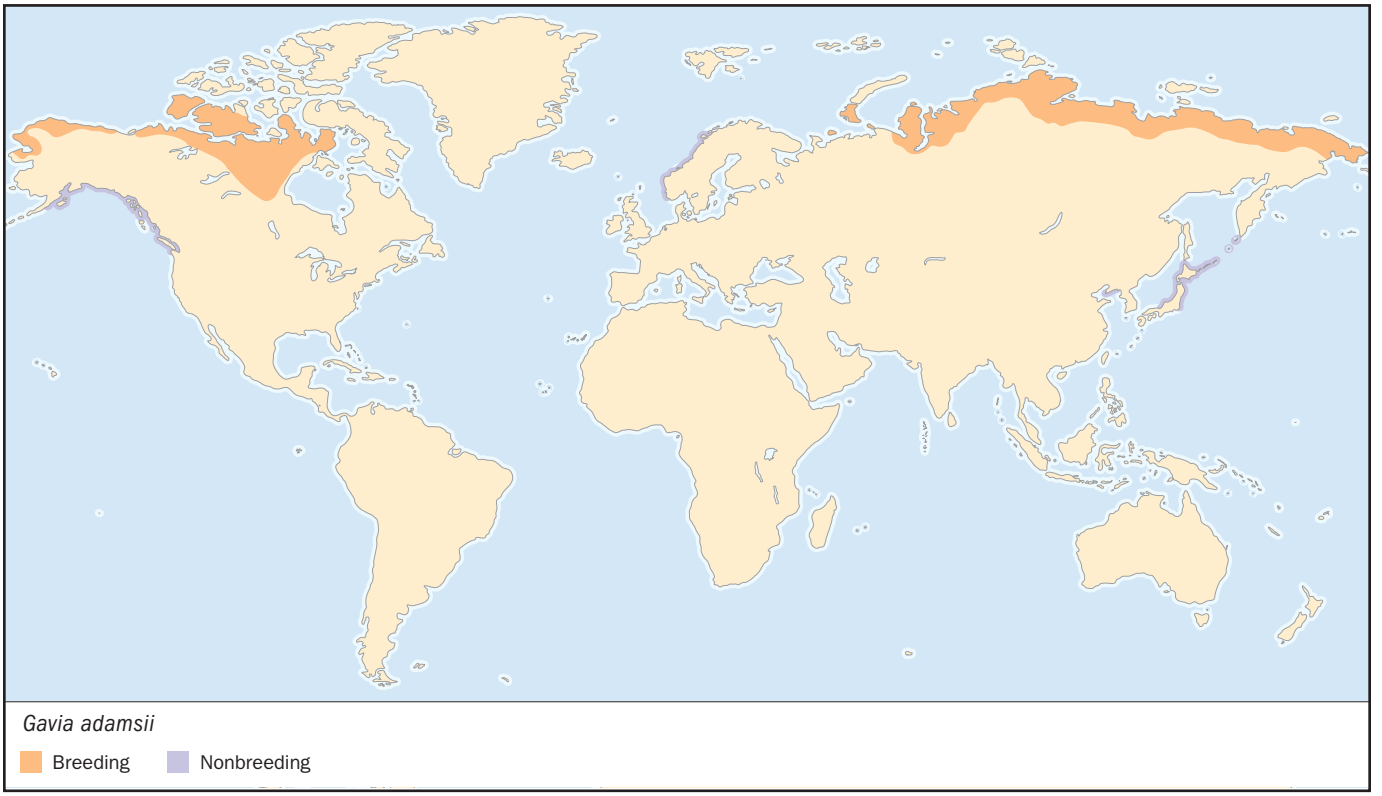
BEHAVIOR
Similar to the common loon.

FEEDING ECOLOGY AND DIET
Up-turned bill has been suggested as an adaptation for feeding along water bottom; very little data on diet, probably similar to other loons.

REPRODUCTIVE BIOLOGY
Nests from June to September on hummocks near breeding ponds. Incubation around 28 days; young leave nest within one day of hatching. Young can fly at about 11 weeks. Predators include foxes (*Aloplex*), ravens (*Corvus*), and gulls (*Larus*).

CONSERVATION STATUS
Rarest of the loons, but not threatened. Populations stable.

SIGNIFICANCE TO HUMANS
Taken occasionally for subsistence by Inuit. ◆



Resources

Books

Harrison, C. J. O., and P. Castel. *Bird Nests, Eggs, and Nestlings of Britain and Europe.* Milan: New Interlew Spa, 1998.

Josson, Lars. *Birds of Europe with North Africa and the Middle East.* Princeton: Princeton University Press, 1993.

Wild Bird Society of Japan. *A Field Guide to the Birds of Japan.* Tokyo: Wild Bird Society of Japan, 1985.

Periodicals

Abraham, Kenneth F. "Adoption of Spectacled Eider Ducklings by Arctic Loons." *Condor* 80, no. 3 (1978): 339–340.

Barr, Jack F., Christine Eberl, and Judith W. McIntyre. "Red-Throated Loon (*Gavia stellata*)." *Birds of North America* no. 513 (2000): 1–28.

Hancock, Mark. "Artificial Floating Islands for Nesting Black-Throated Divers (*Gavia arctica*) in Scotland: Construction, Use and Effect on Breeding Success." *Bird Study* 47, no. 2 (2000): 165–175.

McIntyre, Judith W., and Jack F. Barr. "Common Loon (*Gavia immer*)." *Birds of North America* no. 313 (1997): 1–32.

North, Michael R. "Yellow-Billed Loon (*Gavia Adamsii*)." *Birds of North America* no. 121 (1994): 1–24.

Vallianatos, Mary, and Jon McCracken. "Loons and Type E Botulism." *Birdwatch Canada* 15 (2001): 9.

Woolfenden, Glen E. "Selection for a Delayed Simultaneous Wing Molt in Loons (Gaviidae)." *Wilson Bulletin* 79, no.4 (1967): 416–420.

Peter Andrew Hosner

Podicipediformes
Grebes
(Podicipedidae)

Class Aves
Order Podicipediformes
Family Podicipedidae
Number of families 1

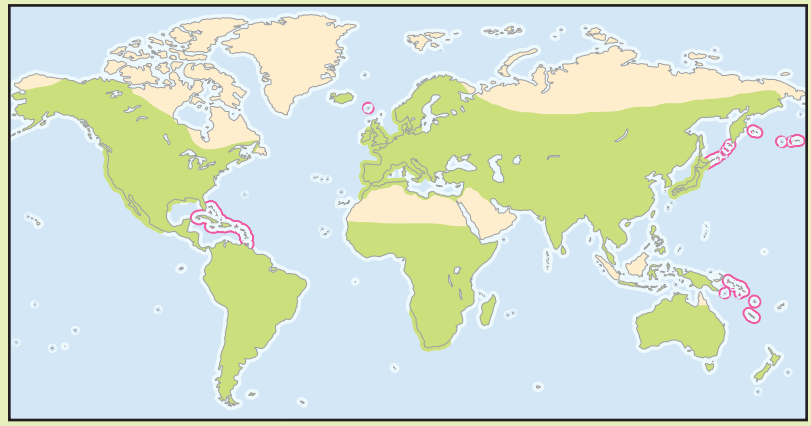
Thumbnail description
Medium-sized, swimming and diving birds, recalling ducks, gallinules, or finfoots. Head small, bill pointed, neck medium to long. Rear end of body fluffy and appearing tail-less. Wings not used during diving. Most species dull-colored, a few with golden head plumes

Size
7.9–31 in (20–78 cm); 0.25–4.0 lb (112–1,826 g)

Number of genera, species
7 genera; 22 species

Habitat
Freshwater lakes, in winter also on coast

Conservation status
Two species recently Extinct, two Endangered, one Near Threatened; two with restricted range, one of them seriously declining



Distribution
Worldwide except for Antarctic and high Arctic regions

Evolution and systematics

For a long time grebes were thought to be related to loons, but it is now known that the similarity is merely owing to convergence. Despite their fairly similar lifestyle and shape, the two have very different tongues, knees, toe webbing, tail, and wing structure. DNA comparisons show that grebes have evolved independently since the early Tertiary, whereas loons branched off from the penguin-tubenose lineage much later, in mid Tertiary. The details of neck musculature, shape of sternum, and some special muscles that pull the skin of the nape forwards to raise the cheeks and crown, might link the grebes to coots (Rallidae) and finfoots (Heliornithidae). Seven genera with 22 species are currently recognized. Three species, Atitlán (*Podilymbus gigas*), Colombian (*Podiceps andinus*), and Alaotra grebes (*Tachybaptus rufolavatus*) are fairly poorly differentiated and have at some time been treated as subspecies of pied-billed (*Podilymbus podiceps*), eared (*Podiceps nigricollis*), and little grebes (*Tachybaptus ruficollis*), whereas others currently treated as subspecies might deserve status of full species. These latter include the large and nearly flightless Malvinas race of the white-tufted grebe (*Rollandia roland*), two or even three populations of silvery grebe (*Podiceps occipitalis*), and perhaps the yellow-eyed forms of the little grebe.

Physical characteristics

Grebes have rather flattened, round bodies, long necks that are nearly twice the length of the body and composed of 17–21 vertebrae, pointed bills, vestigial tails, and fluffy rear ends. Their feet are flattened, lessening resistance, and are the birds' only means of propulsion during swimming and diving. The feet are placed far back on the body, beat parallel to the water surface, and function as a rudder. The feet have become so adapted for swimming and diving that grebes are barely able to walk, doing so only for short distances and with a labored waddle and the body held upright. During relaxed swimming grebes only use one leg at a time, but during dives they move them simultaneously. Each toe has a large, unilateral swimming lobe and the three large front toes are only slightly webbed. The hind toe is small, but also lobed. The rear edge of the tarsus is serrated in adults. Serration is most pronounced in the genera *Tachybaptus* and *Rollandia*, and might serve to cut through entangling submergent vegetation. Some species have very long necks and long bills used for darting during rapid pursuit of fish, a characteristic that has evolved independently three times in the family. Most species have moderately long necks and shorter bills that also serve for feeding on small arthropods and other invertebrates. To handle fish grebes have evolved a strong bite,