Grzimek's Animal Life Encyclopedia

Second Edition



Grzimek's Animal Life Encyclopedia

Second Edition



Birds II

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In association with the American Zoo and Aquarium Association







Grzimek's Animal Life Encyclopedia, Second Edition

Volume 9: Birds II

Project Editor

Donna Olendorf

Editorial

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Cover photo of African jacana (*Actophilornis africanus*) by Nigel Dennis, 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.

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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. cn

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.

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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 shortterm 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 longterm 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

Foreword

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 fea-

sible. 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.

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Gruiformes

(Cranes, rails, and relatives)

Class Aves

Order Gruiformes (Cranes, rails, and allies)

Number of families 11

Number of genera, species 82 genera; 210 species

Photo: Red-legged seriema (*Cariama cristata*). (Photo by Doug Wechsler/VIREO. Reproduced by permission.)



Evolution and systematics

The order Gruiformes (parvclass Passerae, superorder Passerimorphae) has often been described as a sort of taxonomic grab-bag consisting of several avian families with questionable evolutionary ties. In *Bustards*, *Hemipodes and Sandgrouse: Birds of Dry Places* (1991), Paul A. Johnsgard wrote, "The traditional order Gruiformes as constituted by Peters (1934) is one that has been rather generally regarded as a collection of seemingly rather disparate and perhaps distantly related forms." W. Meise, the author of the *Grzimek's* (1968) chapter on Gruiformes, wrote, "A parrot can be immediately recognized, so we can readily understand why all parrots are included in one order, with only one family. This is in direct contrast to the order of cranes. ... Hardly any other order among birds has so little uniformity."

As of 2002, science recognizes 10 families in this ancient group of birds: Eurypygidae (sunbittern), Otididae (bustards), Gruidae (crowned cranes and typical cranes), Aramidae (limpkin), Heliornithidae (sungrebes and finfoots), Psophiidae (trumpeters), Cariamidae (seriemas), Rhynochetidae (kagu), Rallidae (rails, coots, gallinules), and Mesitornithidae (mesites). One of the Gruiformes families recognized by Meise, the Turnicidae (buttonquails), has since been elevated in some taxonomies to order status (parvclass Turnicae; order Turniciformes), though here it will be discussed as part of the Gruiformes.

Gruiformes have a long evolutionary history. With fossil evidence dating back to the middle Eocene, DNA studies indicate the bustards diverged from the remaining Gruiforme lineage around 77 million years ago. DNA and fossil evidence suggests the trumpeters originated in the late Cretaceous or early Tertiary, 60–70 mya. Fossil crowned cranes date back 50 million years, whereas typical cranes first appear in the fos-

sil record during the Miocene, approximately 24 million years ago. The earliest good fossils of true Rallidae were from the Upper Oligocene and Lower Miocene, 20–30 mya. The flightless, extinct, predatory fossil family Phorusrhacidae, beginning 38 mya with South America's Lower Oligocene, are considered by some to be the distant ancestors of the extant seriemas. The earliest fossil limpkins were found in early Eocene sediments from the state of Wyoming, in the United States, dated approximately 54 mya. Fossil kagu have been found on New Caledonia dating back 4,000 years. No fossil sunbitterns, sungrebes, nor finfoots have been discovered.

Physical characteristics

The Gruiformes reflect great diversity in size, ranging from the diminutive 4.7 in (12 cm) American black rail (Laterallus jamaicensis) to the 5.8 ft (176 cm) Sarus crane (Grus antigone), the tallest of all flying birds. Average sizes for families are: sunbittern (17–19 in; 43–48 cm), bustards (16–47 in; 40–120 cm), cranes (35-69 in; 90-176 cm), limpkin (22-28 in; 56-71 cm), sungrebes and finfoots (10-23 in; 26-59 cm), trumpeters (18–21 in; 45–52 cm), seriemas (28–35 in; 70–90 cm), kagu (22 in; 55 cm), rails (5–25 in; 12–63 cm), mesites (12–13 in; 30–32 cm). The species with the smallest average weight is the 8 oz (20 g) American black rail. At 16 oz (40 g), the inaccessible rail (Atlantisia rogersi) is the smallest flightless bird known to exist. On the other end of the scale, male kori bustards (Ardeotis kori) can weigh up to 7.5 lb (19 kg), and some male great bustards (Otis tarda) have been reported to reach 40 lb (18 kg), putting them on par with the mute swan (Cygnus olor) as the heaviest flying birds.

Plumage coloration is typically earth toned, in shades of black, gray, and brown, and often heavily or cryptically streaked or vermiculated. Several typical cranes are the Order: Gruiformes Vol. 9: Birds II



Courtship display of the male kori bustard (*Ardeotis kori*) in Kenya. (Photo by K & K Ammann. Bruce Coleman Inc. Reproduced by permission.)

exceptions, with mostly white and black plumage accented by red patches on the head or neck. The sunbittern is notable for its exceptional chestnut, black, and buff-yellow "eyespots" on the dorsal side of its wings, which it uses in defensive displays. Many cryptically marked male bustards can erect their feathers in magnificent fashion during courtship displays. Several Gruiforme species have bright red or orange legs, bills, or frontal shields. A few rails, most notably among the gallinules, are greenish or purple. Mesites have feather patches that produce powder down, a feature not found in other Gruiformes.

Bill shapes are somewhat variable and are adapted to the type of food taken. Notable is the limpkin's relatively long, slightly decurved bill that bends to the right at its tip, with crosscutting action from the lower mandible, to aid in feeding upon its primary food, the right-handed apple snail (*Pomacea*). In contrast, trumpeters have short, chicken-like bills used to forage among the leaves on the floor of the rainforest for vegetable matter and insects. The cranes have narrow, medium-length bills, which in some species are used to probe in moist soil for tubers and invertebrates.

Distribution

Representatives of the Gruiformes may be found on every continent except Antarctica, and on many oceanic islands. Some families are more limited in distribution than others. The monotypic kagu is severely limited, found only on the island New Caledonia. The mesites are restricted to the island of Madagascar. The trumpeters are found in the tropical forests of northern South America, while the seriemas inhabit the grasslands of central and eastern South America. The monotypic sunbittern is found in tropical Central and South America near water. The monotypic limpkin is found in tropical and subtropical Neotropics (the region that extends south, east, and west of the central plain of Mexico). The bustards are distributed in the Old World, with greatest diversity in Africa. The sungrebes are found in the Neotropics; and the finfoots in Africa, and from India to Malaysia. The cranes, many of which are highly migratory, are found worldwide except Antarctica. They have their greatest diversity of species in Asia, and their greatest diversity of genera in Africa. Rails, gallinules, and coots are also distributed worldwide, except for polar regions and waterless deserts, and they are widely distributed on oceanic islands where many species have become flightless.

Habitat and feeding ecology

As in all other aspects of their biology, the habitats (and associated diets) of Gruiformes are quite variable. The families can be roughly ordered from wet-loving to dry-loving groups. The sungrebes and finfoots are primarily aquatic, inhabiting marshes, lakes, and streams, and feeding upon small insects, aquatic animals, and some seeds and leaves. The sunbittern lives near water in dense tropical forests and swamps. There the birds can be seen walking slowly while they stalk insects and small fish or crustaceans. The limpkin is found near wetland areas, such as in marshes or wooded swamps, where the birds feed on apple snails, as well as insects and some seeds. The cranes frequent freshwater and saline wetlands and open upland country, taking a wide variety of seeds, tubers, and other vegetable and animal matter. The rails also live mainly in or near swamps, marshes, and lakes, and eat a wide variety of vegetable and animal foods. The trumpeter species are found in tropical rainforest, where they forage for fruits, berries, seeds, and other plant material on the forest floor. The kagu eats insects, worms, small frogs, and mollusks in its native forests. The mesites are distributed from lush rainforest to dry scrub, taking fruit, seeds, and insects. The seriemas are found in grassland and pampas, where they hunt insects, small reptiles, and mammals, and occasionally take some vegetable matter. Bustards live in open country, including grassland and dry brush and scrub habitats, eating a variety of seeds, small and large insects, and occasionally small animals.

Behavior

Gruiformes are not particularly gregarious, with some exceptions among the bustards, trumpeters, and the cranes. The sunbittern, limpkin, sungrebes, kagu, and rails tend to be soli-

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tary, secretive, and even highly territorial residents. The seriemas and mesites are more likely to be found in pairs or small family groups.

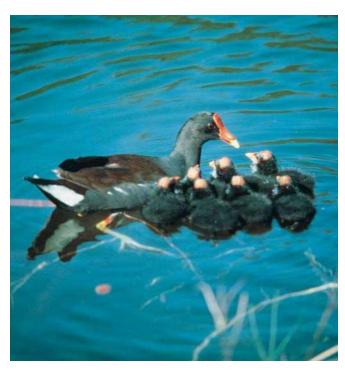
Mating systems range from the monogamy of the cranes to the polygyny/promiscuity of the bustards. Cranes lay from one to four eggs, with the norm being two eggs for most species. Both sexes establish a territory, nest-build, incubate the eggs, and feed the precocial chicks. All species of cranes engage in spectacular dances, by leaping, extending their wings, and sometimes head-bobbing. Dances are presumed to create and maintain pair bonds and to synchronize breeding physiology, so both male and female are ready to breed at exactly the same time. Cranes also vocalize with trumpeting duets known as "unison calls," to strengthen the pair bond. Crane pairs often stay with each other year-round and even for life. In contrast, the males of many bustard species gather in traditional "dispersed leks," or display grounds, to attract females. After choosing the male and mating, the female nests, incubates, and rears the young alone without any help from the male. Males copulate with as many females as are receptive.

Although many Gruiformes are strong fliers, as witness the well-known migrations of many crane species, the members of this order are generally reluctant to fly. Gruiformes have evolved more obligate flightless forms than any other avian order. In fact, the rails seem almost evolutionarily predisposed to have evolve flightlessness. More than one-quarter of all known island rails have lost the ability to fly. Their large and energetically expensive avian flight muscles and associated skeletal apparatus have either disappeared or become greatly reduced in these forms; this appears to have come about through arrested development, known as *neotony*.

Conservation status

The 2000 IUCN Red List of Threatened Species reported on 93 species of Gruiformes. Of these, 22 species were reported Extinct. Another species, the Guam rail (*Gallirallus owstoni*) is listed as Extinct in the Wild. In an effort to save the species from extinction, several Guam rails were brought into captivity and managed as a global population by the Guam Department of Agriculture Aquatic and Wildlife Resources Division, the United States Fish and Wildlife Service (USFWS), and zoological institutions. Zoos participating in the captive gene pool and conservation programs include member institutions of the American Zoo and Aquarium Association's (AZA) Guam Rail Species Survival Plan® (SSP®) under the umbrella of the AZA's Gruiformes Taxon Advisory Group (TAG).

An additional four Rallidae species are listed as Critically Endangered, and 11 more as Endangered. An additional 30 rallids are globally Vulnerable or at risk. The main causes of extinctions and threats to flightless and island rallids are purposely or accidentally introduced exotic mammalian predators: rats, cats, dogs, mongooses, pigs, snakes, and humans. Habitat destruction plays a lesser role, as humans and their introduced livestock modify wetlands, forests, and grasslands.



A common moorhen (*Gallinula chloropus*) family. (Photo by Laura Riley. Bruce Coleman Inc. Reproduced by permission.)

The monotypic family Rhynchochetidae (kagu) is listed as Endangered and legally protected in New Caledonia, with CITES Appendix I status. The main reason for the decline appears to be the introduction of dogs to the island in 1774 by Captain Cook. Logging and deforestation are also affecting kagu habitat. The remaining two monotypic families in the order, the Aramidae (limpkin) and the Eurypygidae (sunbittern), are well distributed in the New World and not in any immediate danger.

Among the Otididae (bustards), nine are globally at risk. The great Indian bustard (*Ardeotis nigriceps*), Bengal florican (*Houbaropsis bengalensis*), and lesser florican (*Sypheotides indica* are listed as Endangered, and appear on Appendix I of CITES. Hunting, habitat loss due to agriculture and grazing, and nest failure due to interference from cattle and crows are the main pressures.

The Gruidae (cranes) are severely at risk. Habitat loss due to agriculture, the degradation of wetlands, and direct hunting have caused eight of the 15 crane species to be globally at risk. At greatest risk is the Critically Endangered Siberian crane (*Grus leucogeranus*). The two Endangered species are the whooping crane (*Grus americana*) and the Japanese crane (*Grus japonensis*). Finally, six crane species are globally Vulnerable: Sarus crane, wattled crane (*Grus carunculatus*), hooded crane (*Grus monacha*), black-necked crane (*Grus nigricollis*), blue crane (*Grus paradisea*), and the white-naped crane (*Grus vipio*).

Order: Gruiformes Vol. 9: Birds II

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Charles Eric Siegel, MS

Mesites and roatelos

(Mesitornithidae)

Class Aves

Order Gruiformes

Suborder Mesitornithes

Family Mesitornithidae

Thumbnail description

Medium-sized birds with long, wide tails, short, round wings, well-developed legs, and decurved bills

Size

11.8-12.6 in (30-32 cm)

Number of genera, species

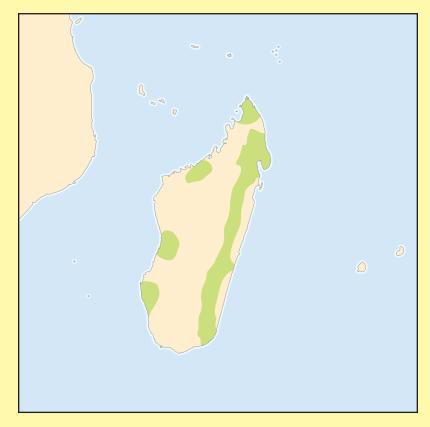
2 genera; 3 species

Habitat

Forest, woodlands, and thicket

Conservation status

Vulnerable: 3 species



Distribution Madagascar

Evolution and systematics

The mesites are thought to be related to the rails (Rallidae), due to anatomical similarities such as breastbone structure. There are also differences, including five pairs of powderdowns and a lack of pervious nostrils. Like other Madagascan families, the mesites are the result of an ancient evolutionary offshoot, and while no fossils have been found, their uniqueness merits them their own suborder (Mesitornithes).

There are two genera: *Mesitornis*, including the white-breasted mesite (*Mesitornis variegata*) and the brown mesite (*Mesitornis unicolor*), and *Monias*, which has only one species, the subdesert mesite (*Monias benschi*). The distinction between the genera is based on bill form and egg form and structure. The species in the genus *Mesitornis* are also known as roatelos.

Physical characteristics

Mesites have an unusual, cylindrical profile, with thick undertail-coverts and a long, wide tail. The wings are short and round, and the legs are well developed. The bill, which is de-

curved, is adapted for foraging on the forest floor. Length is 12–12.5 in (30–32 cm), and only the subdesert mesite exhibits sexual dimorphism.

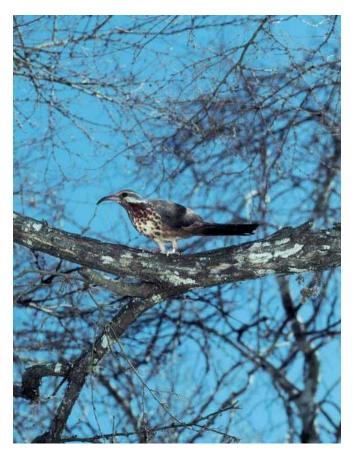
Distribution

The mesites are endemic to Madagascar. The brown mesite has the largest distribution, inhabiting forests in the east of the island. The white-breasted mesite is found primarily in patches of forest in the west and north, and the subdesert mesite occupies a strip of forest 125 mi (200 km) long and 50 mi (80 km) wide between the coast and the hills in the southwest.

Habitat

Three main forest and woodland types are occupied: the lowland humid forests of the east (brown mesite), the dry deciduous forests of the west and north (white-breasted mesite), and the more open, spiny thickets of the southwest (subdesert mesite).

Family: Mesites and roatelos Vol. 9: Birds II



A subdesert mesite (*Monias benschi*) in southwest Madagascar. (Photo by Patti Murray/Animals Animals. Reproduced by permission.)

Behavior

Mesites are thought to be diurnal and, although able to fly, spend much of their time on the ground. Their bobbing gait is reminiscent of a pigeon, breaking into a run or short flight only when threatened. Social units vary in size from three birds in the brown mesite and white-breasted mesite (pair with most recent young) to six or 10 birds in the subdesert mesite (within-group relationships not established).

All three species have a wide vocal repertoire—paired duets are common in the white-breasted and brown mesites—and utter a similar alarm call. Subdesert mesites will vocalize at the sound of another group approaching their ter-

ritory. Both white-breasted and subdesert mesites engage in territorial disputes.

Feeding ecology and diet

The two *Mesitornis* species feed amongst the leaf litter, searching for invertebrates, seeds, and small fruits. The bill is positioned to allow them to lift fallen leaves without flicking them over, thereby minimizing disturbance to potential prey. The longer and more decurved bill of the subdesert mesite is better suited to probing the ground for invertebrates, although it too will take items from the litter.

Reproductive biology

The subdesert mesite is thought to be polygamous, while the two *Mesitornis* species are monogamous. The nests of all three are simple platforms of sticks, in low bushes or forked branches 2–10 ft (0.6–3 m) above the ground. Clutches of one to three eggs are laid during the rainy season, October through April. The incubation period is unknown, and parental responsibilities vary between species. The chicks are precocial and covered with reddish or blackish brown down. They tend to remain with the parents post-fledging, for up to a year in the case of the white-breasted mesite.

Conservation status

All three mesites are classed as Vulnerable due to population declines and decreases in habitat extent and quality. The Madagascan forests are under pressure from slash-and-burn cultivation, charcoal production, and commercial timber extraction. None appears readily able to recolonize areas of regenerating forest, which is a concern. Hunting, and predation by dogs and rats may be significant locally. Conservation areas cover a portion of the populations of the two *Mesitornis* species, but the level of protection afforded is low. The dry, spiny thickets of the southwest, home to the subdesert mesite, are entirely unprotected; a series of community-based conservation areas has been proposed.

Significance to humans

The mesites are all hunted for food, and are well known among local peoples. The brown mesite is not hunted in part of its range, due to a taboo that ranges from engendering human-like respect, to not speaking the bird's name, to simple terror.



1. Subdesert mesite (*Monias benschi*); 2. White-breasted mesite (*Mesitornis variegata*); 3. Brown mesite (*Mesitornis unicolor*). (Illustration by Amanda Humphrey)

Family: Mesites and roatelos Vol. 9: Birds II

Species accounts

White-breasted mesite

Mesitornis variegata

TAXONOMY

Mesites variegata I. Geoffroy Saint-Hilaire, 1838, Madagascar. Monotypic.

OTHER COMMON NAMES

English: White-breasted roatelo; French: Mésite variée; German: Kurzfuss-stelzenralle; Spanish: Mesito Pechiblanco;.

PHYSICAL CHARACTERISTICS

12 in (31 cm); male 3.5–4.0 oz (103–111 g), female lighter. Upperparts rufous brown; throat, eyebrows, and breast pale cream; black crescent-shaped markings on sides of breast and upper belly; nape may be gray.

DISTRIBUTION

Madagascar. Small patches of forest in the west and north of the island, and Ambatovaky in the east.

HABITAT

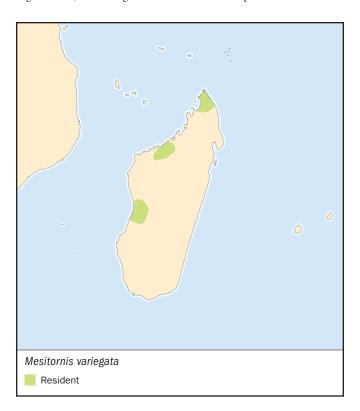
In the west and north: dry, deciduous forest on sandy soils, with sparse understory and thick leaf litter. In the east: lowland humid forest. Sea level to 1,150 ft (350 m).

BEHAVIOR

Terrestrial and secretive. Sedentary; usually found in family groups that defend territories year round.

FEEDING ECOLOGY AND DIET

Feeds among leaf litter and low vegetation, occasionally probing the soil, searching for invertebrates and plant seeds.



REPRODUCTIVE BIOLOGY

Thought to be monogamous. Nests 3–9 ft (1–3 m) above the ground on a platform of sticks, October through April. Female incubates one to three eggs, period unknown. The young remain with parents for up to a year post-fledging.

CONSERVATION STATUS

Vulnerable.

SIGNIFICANCE TO HUMANS

Hunted opportunistically, if irregularly, due to their small size. ◆

Brown mesite

Mesitornis unicolor

TAXONOMY

Mesites unicolor Des Murs, 1845, Madagascar. Monotypic.

OTHER COMMON NAMES

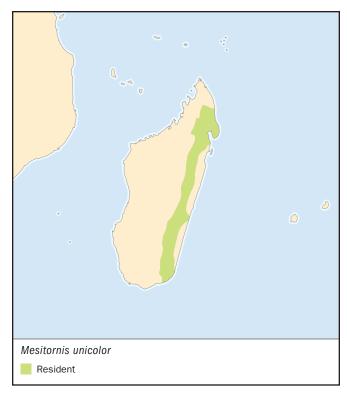
English: Brown roatelo; French: Mésite unicolore; German: Einfarb-stelzenralle; Spanish: Mesito Unicolor.

PHYSICAL CHARACTERISTICS

12 in (30 cm); weights unrecorded. Upperparts rufous brown; underparts lighter. Rufous brown head may have pinkish gray tinge; chin and throat whitish tinged with rufous.

DISTRIBUTION

Eastern forests of Madagascar.



Vol. 9: Birds II Family: Mesites and roatelos

HABITAT

Lowland humid forest with sparse understory and thick leaf litter. Sea level to 3,600 ft (1,100 m).

BEHAVIOR

Terrestrial and secretive. May move to different altitudes with the seasons. Often found in small family groups.

FEEDING ECOLOGY AND DIET

Probably similar to *M. variegata*, taking invertebrates from the forest floor.

REPRODUCTIVE BIOLOGY

Breeds November through December. Only two nests found: both a platform of sticks 3–7 ft (1–2 m) above the ground, containing one egg. Incubation in both cases was by female, but period unknown.

CONSERVATION STATUS

Vulnerable.

SIGNIFICANCE TO HUMANS

Hunted for food in the south of its range. Elsewhere hunting is restricted by taboo. ◆

Subdesert mesite

Monias benschi

TAXONOMY

Monias benschi Oustalet and G. Grandidier, 1903, Vorondreo, Madagascar. Monotypic.

OTHER COMMON NAMES

English: Monias, Bensch's rail; French: Mésite monias; German: Moniasstelzenralle; Spanish: Mesito Monias.

PHYSICAL CHARACTERISTICS

13 in (32 cm); weights unrecorded. Relatively long, decurved bill. Grayish brown upperparts; light underparts; long, white eyebrows. Males have black crescent-shaped markings on underparts; females have rufous throat and breast.

DISTRIBUTION

Coastal forests in southwest Madagascar.

HABITAT

Dry, spiny thickets on sandy soils, with sparse understory and much leaf litter. From sea level to 430 ft (130 m).



BEHAVIOR

Terrestrial and gregarious. Usually found in groups of two to six birds, rarely up to 10. If alarmed, the group will scatter, with birds either remaining motionless in shadow or flying onto low branches where they lie pressed to the bark.

FEEDING ECOLOGY AND DIET

Forages on the ground, probing the soil for invertebrates; occasionally takes prey and small fruits and seeds from leaf litter.

REPRODUCTIVE BIOLOGY

May be polyandrous or polygynous. Breeds November through January. The simple stick nest is built 2–7 ft (0.6–2 m) above the ground, and contains one or two eggs. Parents share incubation and care of the blackish brown chick.

CONSERVATION STATUS

Vulnerable.

SIGNIFICANCE TO HUMANS

Hunted for food. ◆

Resources

Books

BirdLife International. *Threatened Birds of the World*. Cambridge, UK: BirdLife International, 2000.

Dee, T. J. *The Endemic Birds of Madagascar*. Cambridge, UK: International Council for Bird Preservation, 1986.

Evans, M. I., A. F. A. Hawkins, and J. W. Duckworth. "Family Mesitornithidae (Mesites)." In: *Handbook of the Birds of the World*, Vol. 3. *Hoatzin to Auks*, edited by J. del Hoyo, A. Elliott, and J. Sargatal. Barcelona: Lynx Edicions, 1996. Langrand, O. *Guide to the Birds of Madagascar*. New Haven & London: Yale University Press, 1990.

Morris, P. and F. Hawkins. *Birds of Madagascar: A Photographic Guide*. East Sussex, UK: Pica Press, 1998.

Periodicals

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Resources

- Seddon, N., J. Tobias, J. W. Yount, J. R. Ramanampamonjy, S. Butchart, and H. Randrianizahana. "Conservation Issues and Priorities in the Mikea Forest of South-west Madagascar." *Oryx* 34, no. 4 (2000): 287–304.
- Turner, A. D. "A Note on Bensch's Rail *Monias benschi* from Madagascar." *Bull. British Ornithologists' Club* 101, no. 1 (1981): 240–241.
- Woodbury, C. J. "Two Spinal Cords in Birds: Novel Insights into Early Avian Evolution." *Proceedings of the Royal Society of London Series B-Biological Sciences* 265 (1998): 1721–1729.

Organizations

African Bird Club, c/o 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: info@africanbirdclub.org Web site: http://www.africanbirdclub.org/

Other

BirdLife International. "Saving Species Factsheets." (31 January 2002). http://www.birdlife.net/species/ index.cfm?GeoRecID=126>

David G. Hoccom, BSc (Hons)

Buttonquails

(Turnicidae)

Class Aves

Order Gruiformes

Suborder Turnices

Family Turnicidae

Thumbnail description

Small, plump, quail-like terrestrial birds colored in browns and grays, with short legs and a tiny tail

Size

4-9 in (10-23 cm); 0.7-5.3 oz (20-150 g)

Number of genera, species

3 genera; 17 species

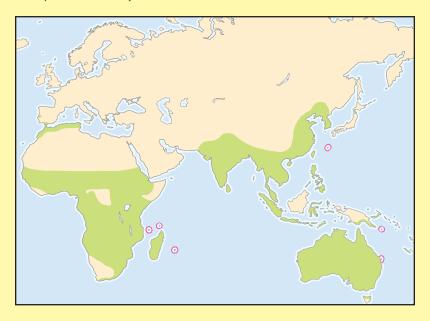
Habitat

Forest, woodlands, heath, scrub, savanna, grassland

Conservation status

Endangered: 3 species; Vulnerable: 3 species;

Near Threatened: 1 species



Distribution

Spain, northwest African coast, sub-Saharan Africa, Madagascar, south and Southeast Asia, New Guinea, Solomon Islands, Australia

Evolution and systematics

Among the many crane-like birds there is no group more problematic to the taxonomist than the buttonquails or hemipodes (family Turnicidae). It challenges the ornithologist to classify it with other orders or to promote it to an order of its own. As noted by Paul Johnsgard in his definitive work Bustards, Hemipodes, and Sandgrouse (1991), "The taxonomic history and evolutionary relationships of the buttonquail assemblage are perhaps as confusing and unsettled as those of any group of birds." Historically, the scanty fossil record was of little help, and by the dawn of the twenty-first century the situation had not changed. DNA comparisons in the 1980s established only that buttonquails are an old group without close relatives, or whose rapid genetic evolution has obscured its origins, although a connection with the Gruiformes cannot be discounted. The distribution of the species and their interrelationships suggest that the family originated on the ancient southern supercontinent Gondwana.

In size, shape, and gait, buttonquails only superficially resemble the true quails, which belong with gallinaceous birds (Galliformes, family Phasianidae). Some quail-like features distinguish buttonquails from the crane-like birds: covered nostrils, brief developmental period before flight (from 10 to 19 days), and early attainment of reproductive capacity (at four or five months of age in captivity). The nature of the downy plumage is also similar to that of gallinaceous birds; furthermore, the innermost primaries of the plumage of the young molt early (although, in contrast to gallinaceous birds, these feathers remain small). Buttonquails also have a very

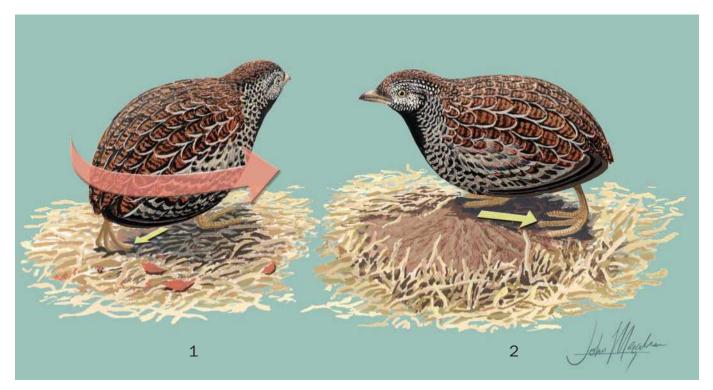
early complete molt of the juvenal plumage and precocious development of the scraping behavior used when feeding. On the other hand, crane-like features of the buttonquails are the absence of a crop, the single but deep notch on each side of the rear margin of the breastbone, doubly speckled eggs, and the manner in which parents hold food in front of the young.

The buttonquails (subfamily Turnicinae) differ from both groups, the gallinaceous and the crane-like birds, in the following ways: the short incubation period of only 12 or 13 days, brooding done by males only, rearing of the young by the males, larger size and brighter coloration of the females, and the females' booming call. Summarizing these characteristics, buttonquails are either a sibling group of all the rest of the crane-like birds and of the wader-gull group and thus a separate order, or they belong among crane-like birds, but at a distance from all other rail, crane, and bustard relatives. By consensus, buttonquails are, as of 2001, retained in their traditional classification with the rails and cranes.

The Australian plains-wanderer (*Pedionomus torquatus*) has traditionally been placed with the buttonquails in its own subfamily (Pedionominae). However, DNA, anatomical, and behavioral evidence suggest that it is instead a shorebird (Charadriiformes) deserving of its own family (Pedionomidae) and related to the seedsnipes (Thinocoridae) of South America.

As of 2001, there were 15 recognized species in the genus *Turnix* and only one species in each of the genera *Ortyxelos* and *Pedionomus*. Among the *Turnix* buttonquails there are

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Barred button quail (Turnix suscitator) at a feeding scrape. (Illustration by John Megahan)

59 subspecies, mostly of those few widespread species whose distributions include many islands in Southeast Asia and Melanesia.

Physical characteristics

Buttonquails are small, dumpy birds (short and thick in build) with small, unadorned heads, short necks, short legs, three toes on each foot (lacking the hind toe), and rudimentary tails. The bill is short, unspecialized, and laterally compressed, being slender in insectivorous species to stout in granivorous species. These birds range in size from 4 in (10 cm) and 0.7 oz (20 g) to 9 in (23 cm) and 5.3 oz (150 g).

Buttonquails are colored in browns, grays, and dull reds. The dorsal surface is colored like the birds' habitat and finely patterned with black mottling, vermiculations (irregular lines), and pale streaks for camouflage. The breast is often more brightly colored, either red or boldly patterned in black and white. Females are larger and more colorful than males. Especially when breeding, females have either dull red on the neck, shoulders, or breast, or black-and-white foreparts. The tiny, gracile lark buttonquail (Ortyxelos meiffrenii) has relatively long wings, black in the center, and almost surrounded with white. Its flight resembles that of a lark; there are only slight sexual differences in plumage. This species is a littleknown bird that looks at first like a relative of the coursers (Glareolidae) when on the ground. Buttonquails of the genus Turnix have wings that are not black and white, although some have boldly spotted wings. The plains-wanderer is longerlegged and more shorebird-like, showing a faint wing bar in lark-like flight. Females have a black-and-white mottled collar and a rusty red breast.

Other characteristics of the buttonquails (Turnicinae) include a single carotid artery and the presence of a fifth secondary feather in each wing (the condition of eutaxis). Their posture is horizontal, and the egg is oval in shape. It is somewhat surprising that buttonquails have no crop, since they feed on seeds. The plains-wanderer differs in having a hind toe, two carotid arteries, no fifth secondary feather (diastaxis), erect posture, and pear-shaped eggs.

Distribution

Buttonquails inhabit the Old World from southern Europe and Africa through south and Southeast Asia to Australia and the Solomon Islands. One *Turnix* species occurs in Europe, two in Africa, one endemic on Madagascar, three in Asia, three endemic in the Philippine and Indonesian archipelagos, and seven in Australasia. *Ortyxelos* occurs only in Africa, and *Pedionomus* occurs only in Australia. The historical distribution of most species has remained largely unchanged, although the common or small buttonquail (*Turnix sylvatica*) has become extinct in Sicily.

Habitat

Buttonquails inhabit the warmer, drier parts of the world, from the tropics and subtropics to the temperate zones, where they occupy low grassy or brushy habitats such as forest or forest clearings, secondary growth, woodland, savanna, and

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grassland. They are entirely terrestrial, living amid the ground layer of tussock grasses, dense crops, or weeds. They feed and roost on the ground, and shelter and nest in cover. They forage in leaf litter and use dry soil for dustbathing. Nests are placed in rank or tussocky grass, often near or beneath a tree, shrub, log, or fallen branch.

Behavior

The various species of buttonquail are found singly, in pairs, or in family groups consisting of a male and dependent young, but sometimes include an adult female as well. In smaller species, family groups may coalesce to form small coveys or loose aggregations.

Members of a pair of buttonquails are sociable toward each other but aggressive toward members of their own sex. Male and female forage in each other's company, and clump together to loaf or roost. In the smaller species, male and female also preen each other's head feathers, and more than one pair may roost together. Females advertise to rivals or prospective mates with a series of eight to 11 booming notes that sound like "oom-oom...," to which the receptive males respond with a trilling, chattering, or clucking call. For her booming call, the female has no more than a dilation of the trachea above the syrinx, so that the accumulated air is expelled as from a bellows. During this, her bill rests on her breast and appears closed; in addition, a ball in the upper esophagus (the "courtship crop") consequently vibrates after having been inflated by swallowed air. The Sicilian name for the common buttonquail, and indeed the Spanish name Torillo for the buttonquail group, is literally "little bull," from the birds' roaring calls. The lark buttonquail is known only to utter soft whistling notes. Female plains-wanderers utter a series of dove-like or bovine "oo-oo..." notes.

These small birds are justly called "battling quails." Not only do they behave like quails, but they are also pugnacious. The females fight among themselves, as they are the ones that occupy and defend the territories. When fighting, they peck mostly at the antagonist's forehead. They have no special weapons such as spurs. Many fights probably are averted owing to the far-carrying calls, which are hard to locate. When a male meets his female again after a long separation, he prostrates himself in an apparent appeasement display, taking a position that invites the female to nestle up to him in the plumage of his head and back.

Aptly described as "ecologically invisible birds," buttonquails are rarely seen and are difficult to find even with hunting dogs. If danger threatens, they squat and freeze, creep through cover, or run away, flushing into flight if pressed. On these occasions they fly low for a short distance, in a straight line, and with a whir. The birds walk about their habitat by day, sometimes on defined trails or runways marked by their footprints in the dust, and loaf in their sheltered roosting sites during the heat of midday as well as sleeping there at night. Buttonquails sometimes forage and call at night. Several times during the day they take a dustbath. When they drink, they keep their heads down and swallow continuously in a sucking action. Plains-wanderers resemble shorebirds in the way they



A small buttonquail (*Turnix sylvatica*) on its nest. (Photo by V. Sinha/VIREO. Reproduced by permission.)

stand on tiptoe and bob their head when scanning for danger; they drink only dew or raindrops.

In warmer temperate regions of their distribution, buttonquails appear to be resident throughout the year, with some birds being sedentary for many months, although there is also a high turnover of individuals. In cool temperate regions at high latitudes and altitudes, buttonquails appear to behave as summer breeding migrants that winter at lower latitudes and altitudes. In tropical and subtropical areas with wet and dry seasons, they follow the rains. Migratory flights take place at night. Plain-wanderers are sedentary unless forced to move by drought or changes to their habitat.

Feeding ecology and diet

Aside from seeds, buttonquails eat plant materials, insects, and snails. They also swallow sand to help grind up their food in the gizzard. Buttonquails forage by walking about, gleaning the ground, litter, and low vegetation. They scratch in the litter by pivoting on one foot and raking with the other, turning a half or complete circle, and sometimes changing feet and reversing direction. This technique leaves a characteristic circular feeding scrape in the soil and litter. Plainswanderers eat seeds and insects pecked from the ground, but do not share the pivoting and raking behavior.

Reproductive biology

In courtship, a female buttonquail puffs up her plumage, cocks her tail, and lets out booming notes explosively while also stamping her feet and scratching the ground. In some

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species the female also spreads her wings while booming at the male. Pairing proceeds to a mutual "rocking" chameleon-like gait backwards and forwards on the feet, increased synchronization of activities, huddling together to roost or dust-bathe, a mutual bowing display, and mutual preening. The female also performs "tidbitting" courtship feeding—giving a soft drumming call while she holds or pecks at a food item for the male to take. One or both birds then perform a "scrape ceremony," in which they go through the motions of preparing a nest site. Female plains-wanderers court males by booming with their wings drooped.

The mating system of *Turnix* buttonquails is sequential polyandry with male parental care, meaning that a female forms a temporary monogamous pair-bond with a male until she has presented him with a clutch of eggs, then finds a new mate while the first male tends the eggs and young alone. In this way a female can produce several clutches of eggs in quick succession in a breeding season. In some cases, monogamy, with some parental care by the female, also occurs. The little-known lark buttonquail appears to be monogamous, although incubation solely by the male suggests that it may, too, be polyandrous. The solitary plains-wanderer is sequentially polyandrous, with male parental care.

Both sexes search for a nesting site by testing several with the "scrape ceremony." The final site, selected by the female, is in grass, often next to a shrub. One of the partners throws dry blades or leaves over its shoulder, and the other builds it into a bowl shape, often with a roof. Usually the two take turns, with the female doing most of the work. Rarely does a covered path lead to the nest. The lark buttonquail's nest is a simple structure in sparse cover and often surrounded by pebbles. That of the plains-wanderer is a simple, grass-lined scrape built by the female, sometimes beneath a few standing grass stems.

The lark buttonquail's clutch consists of two eggs. Clutches of *Turnix* species consist of three to seven eggs, usually four. Until the next to last egg is laid, the female also incubates occasionally; after that she sometimes sleeps close to and touching the male, who incubates alone. The occasional unevenly incubated clutch suggests that the female sometimes shares the task with the male until the eggs hatch. This might take place only if there is no other male for whom she has to provide a clutch. For a precocial bird, the short incubation period of 12 or 13 days is a record. Plain-wanderers lay a clutch of about four eggs that require 23 days for incubation.

Hatching is synchronized, so that all chicks leave the nest together to follow their father about. The chicks, which have loose down, often weigh less than 0.1 oz (2 g), which makes them the smallest of all precocial birds. Buttonquail chicks pick at the gray bill of their father when he approaches and presents them with a termite or a seed. He also broods them and protects them. At one week, juvenal plumage replaces the down and there remains but a slight down on the tips of the feathers. Chicks start to perform the "rocking" gait when 12

days old. When three or four weeks old, the young are independent; they detach themselves from the father, who in turn answers the female's calls and obtains a second clutch to tend. At the age of three and one half weeks, the young peep animatedly; at age six or seven weeks, they are in the middle of their first molt, which is completed by the tenth week. Caged young females have laid fertilized eggs at as early as four or five months of age.

Buttonquails usually lay in spring and summer, although in the tropics they can breed at any time of year when conditions are suitable. In dry habitats, buttonquails wait for the rainy season before they breed.

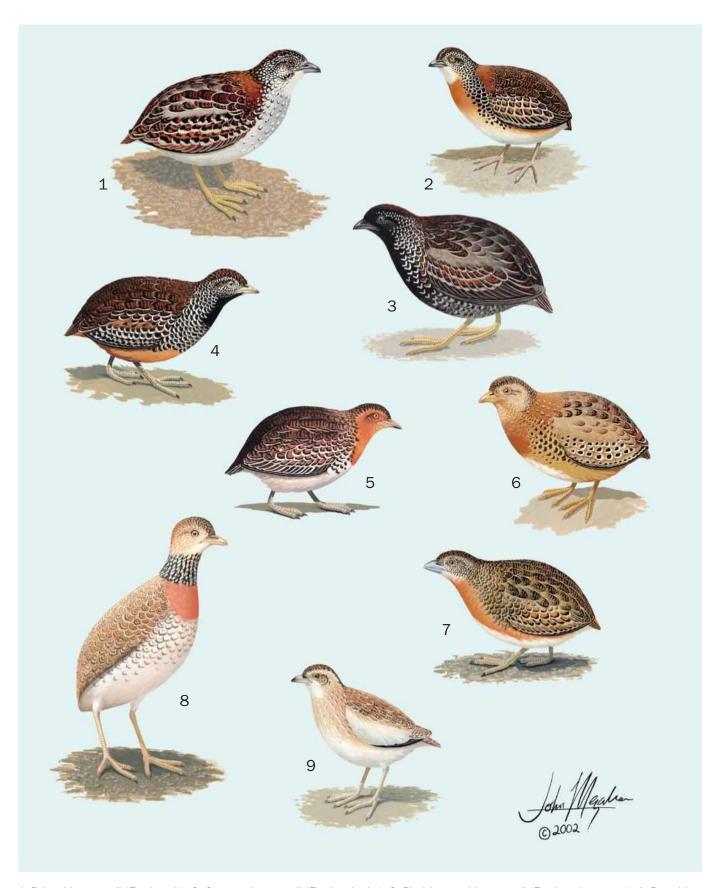
Conservation status

Most buttonguail species remain common, but three Aus-(black-breasted tralian species buttonguail melanogaster, buff-breasted buttonquail Turnix olivii, and plains-wanderer) are rare, and three (spotted buttonquail Turnix ocellata, Worcester's buttonquail Turnix worcesteri, and Sumba buttonquail *Turnix everetti*) are endemic species with restricted ranges on Philippine and Indonesian islands. The black-breasted and buff-breasted buttonquails are on the IUCN Red List as Endangered, the Worcester's buttonquail, Sumba buttonquail, Australian chestnut-backed buttonquail (Turnix castanota), and plains-wanderer are listed as Vulnerable, and the spotted buttonquail is Near Threatened. Three species were listed in the Australian Environment Protection and Biodiversity Conservation Act of 1999: the buff-breasted buttonquail as Endangered, and the black-breasted buttonquail and plains-wanderer as Vulnerable. In 2000 the status of the plains-wanderer was revised to Endangered.

Most buttonquail species are declining in parts of their range, where their habitat has been cleared or converted to a Westernized style of agriculture and pastoralism with its attendant fire. As of 2000, populations of the buff-breasted and black-breasted buttonquails were estimated at 500 and 5,000 breeding individuals, respectively, and that of the plainswanderer at a minimum of 2,500 during droughts.

Significance to humans

Many species of buttonquail are hunted for food by indigenous peoples in developing countries, and they were formerly regarded as game birds elsewhere, although as of 2001 they were no longer legal game birds in most Western countries. They were probably important in the ceremonial life of the Australian Aborigines and perhaps native peoples in other countries. Several species, particularly the common buttonquail and most Australian species, are now well established in aviculture. In some Asian countries the barred buttonquail (*Turnix suscitator*) is exploited in exhibitions similar to those of fighting cocks.



1. Painted buttonquail (*Turnix varia*); 2. Common buttonquail (*Turnix sylvatica*); 3. Black-breasted buttonquail (*Turnix melanogaster*); 4. Barred buttonquail (*Turnix suscitator*); 5. Black-rumped buttonquail (*Turnix hottentotta*); 6. Yellow-legged buttonquail (*Turnix tanki*); 7. Red-chested buttonquail (*Turnix pyrrhothorax*); 8. Plains-wanderer (*Pedionomus torquatus*). 9. Lark buttonquail (*Ortyxelos meifrenii*). (Illustration by John Megahan)

Family: Buttonquails Vol. 9: Birds II

Species accounts

Small buttonquail

Turnix sylvatica

SUBFAMILY

Turnicinae

TAXONOMY

Tetrao sylvaticus Desfontaines, 1787, near Algiers. Most closely related to red-backed buttonquail (*Turnix maculosa*) of Australasia. Nine subspecies recognized.

OTHER COMMON NAMES

English: Striped, small, little, or Kurrichane buttonquail, Andalusian hemipode, bustard quail; French: Turnix d'Andalousie; German: Laufhühnchen; Spanish: Torillo Andaluz.

PHYSICAL CHARACTERISTICS

5.9–6.3 in (15–16 cm); male 1.1–1.6 oz (32–44 g), female 1.4–1.9 oz (39–54 g). Small buttonquail, mostly chestnut with reddish breast and shoulders, scalloped back and wings, spotted flanks, pale eyes, and slender blue-gray bill. Female slightly larger, darker, and more brightly colored. Juvenile smaller and more heavily spotted, with dark eyes. Red-backed buttonquail similar but darker and has yellow bill and legs.

DISTRIBUTION

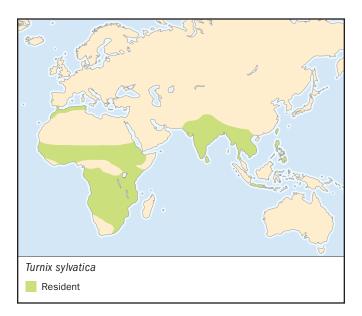
One subspecies in southwestern Spain and northwestern African coast; one subspecies in sub-Saharan Africa; two subspecies in southern and Southeast Asia; four subspecies in Philippine archipelago; one subspecies in Indonesia.

HABITAT

Scrub, thickets, grassland, and farmland.

BEHAVIOR

Terrestrial, diurnal, and partly nocturnal. Migrates at night. Territorial when breeding.



FEEDING ECOLOGY AND DIET

Eats seeds, especially of grasses, and invertebrates obtained by gleaning and scratching on the ground. Mostly insectivorous, or takes seeds and insects in similar proportions.

REPRODUCTIVE BIOLOGY

Breeds in spring and summer in Europe, all months of the year elsewhere, though locally only during the rainy season. Females are sequentially polyandrous, but monogamous locally. Clutch usually four eggs, though up to seven. Incubation 12–15 days. Chicks can fly at 7–11 days, are independent at 18–20 days while still not fully grown, and can breed by four months of age.

CONSERVATION STATUS

Not threatened. Widespread and uncommon to common through most of range, although rare and declining in Europe.

SIGNIFICANCE TO HUMANS

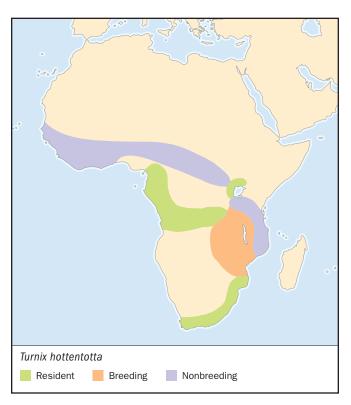
Hunted for food in non-European parts of range; formerly hunted as a game bird in Europe. Established in aviculture. ◆

Black-rumped buttonquail

Turnix hottentotta

TAXONOMY

Turnix hottentottus Temminck, 1815, Cape of Good Hope. Two subspecies recognized. A member of the *T. sylvatica–T. maculosa* group.



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OTHER COMMON NAMES

English: Dwarf, small, African, Natal, Hottentott or South African buttonquail; French: Turnix hottentot; German: Hottentottenlaufhühnchen; Spanish: Torillo Hotentote.

PHYSICAL CHARACTERISTICS

5.5–5.9 in (14–15 cm); male 1.4 oz (40 g), female 2–2.2 oz (58–62 g). Small dark buttonquail with reddish face and breast, barring on sides, spots on flanks, slender bill, and pale eyes. Female slightly larger and redder. Juvenile smaller, less red, and more heavily marked.

DISTRIBUTION

T.b. hottentotta: Southern South Africa; T.b. nana: Sub-Saharan Africa from Nigeria eastward to Uganda and Kenya, south to Angola, and eastern South Africa.

HABITAT

Grassland, savanna, farmland, low herbage, scrub, and edges of thickets.

BEHAVIOR

Terrestrial, diurnal, and partly nocturnal. Migrates at night.

FEEDING ECOLOGY AND DIET

Eats seeds of grasses and low herbage; also eats invertebrates, including insects and larvae, obtained from the ground.

REPRODUCTIVE BIOLOGY

Lays in most months of the year but locally during or at the end of the rainy season. Females are possibly polyandrous. Clutch usually three eggs, though up to six. Incubation 12–14 days.

CONSERVATION STATUS

Not threatened. Uncommon to locally common in most of range but very rare or possibly extinct in South Africa, owing to impacts of pastoral industry.

SIGNIFICANCE TO HUMANS

Hunted for food. Rare in aviculture.

Yellow-legged buttonquail

Turnix tanki

TAXONOMY

Turnix tanki Blyth, 1843, Bengal. Two subspecies recognized. Possibly related to the spotted buttonquail *T. ocellata*, a little-known Philippine endemic.

OTHER COMMON NAMES

French: Turnix indien; German: Rotnacken-Laufhühnchen; Spanish: Torillo Tanki.

PHYSICAL CHARACTERISTICS

6.7 in (17 cm); male 1.2–2.6 oz (35–78 g), female 3.3–4 oz (93–113 g). Rather large buttonquail, grayish with dorsal barring, a pale boldly spotted underside, and yellow bill and legs. Female more brightly colored, with reddish collar. Juvenile smaller, mottled red, and densely spotted.

DISTRIBUTION

T. t. tanki: India, Pakistan, Andaman and Nicobar islands; T. t. blanfordii: Myanmar through Indochina and eastern China, north to Korea, south Amurland, and Ussuriland.



HABITAT

Grassland, farmland, secondary growth on abandoned cropland, grass beneath bamboo thickets, and scrub.

BEHAVIOR

Terrestrial, diurnal, and partly nocturnal. Migrates at night.

FEEDING ECOLOGY AND DIET

Eats seeds, green shoots, and invertebrates obtained from the ground. Mostly granivorous.

REPRODUCTIVE BIOLOGY

Lays from March to November and sometimes in other months, though usually in the rainy season from June to October. Females are sequentially polyandrous. Clutch is usually of four eggs, incubated for 12 days. Chicks can fly at 10 days and acquire adult plumage by seven weeks.

CONSERVATION STATUS

Not threatened. Poorly known, but apparently widespread and common.

SIGNIFICANCE TO HUMANS

Hunted for food. ◆

Barred buttonquail

Turnix suscitator

TAXONOMY

Tetrao suscitator Gmelin, 1789, Java. Eighteen subspecies recognized. Possibly related to Madagascar buttonquail (T. nigricollis).

OTHER COMMON NAMES

English: Common, dusky, Indian, or Philippine buttonquail; French: Turnix combattant; German: Bindenlaufhühnchen; Spanish: Torillo Batallador.



PHYSICAL CHARACTERISTICS

5.9–6.7 in (15–17 cm); male 1.2–1.8 oz (35–52 g), female 1.7–2.4 oz (47–68 g). Medium-sized buttonquail, rusty brown with black-and-white head pattern, barred underside, and pale legs. Female more brightly colored, with variable reddish collar, and, in some subspecies, throat barred black and white rather than solid black. Juvenile smaller and paler, with spotted underside.

DISTRIBUTION

Eight subspecies in mainland south and Southeast Asia from India through Indochina to south China and Malay Peninsula; one subspecies in Sri Lanka; one subspecies in Japanese archipelago; one subspecies in Taiwan; two subspecies in Greater Sunda Islands; three subspecies in Philippine archipelago; one subspecies in Sulawesi; one subspecies in Lesser Sunda Islands.

HARITAT

Grassland, farmland, abandoned cropland, secondary growth, scrub, bamboo thickets, and forest edges.

BEHAVIOR

Terrestrial. Territorial when breeding.

FEEDING ECOLOGY AND DIET

Eats seeds, green shoots, and invertebrates obtained by gleaning and scratching on the ground.

REPRODUCTIVE BIOLOGY

Lays in all months of the year according to locally favorable conditions; apparently avoids the wettest and driest months. Females are sequentially polyandrous. Clutch usually four eggs, though up to six. Incubation 12–14 days. Chicks reach adult size at 40–60 days.

CONSERVATION STATUS

Not threatened. Widespread and common to very common.

SIGNIFICANCE TO HUMANS

Hunted for food. Also, females caged and used in "hen-fights." Established in aviculture. ◆

Black-breasted buttonquail

Turnix melanogaster

TAXONOMY

Hemipodius melanogaster Gould, 1837, Moreton Bay, Queensland. Possibly related to *T. suscitator–T. nigricollis* group, though more likely to *T. varia* group.

OTHER COMMON NAMES

French: Turnix à poitrine noire; German: Schwarzbrust-Laufhühnchen; Spanish: Torillo Pechinegro.

PHYSICAL CHARACTERISTICS

6.7–7.5 in (17–19 cm); male 1.8–4.5 oz (50–127 g), female 2.8–5.6 oz (80–159 g). Large buttonquail with slender bill and pale eyes. Female mottled gray and brown, with black head and breast spotted white. Male smaller, duller, and grayer, lacking black. Juvenile smaller, duller, and more mottled on foreparts.

DISTRIBUTION

Small area of central eastern coast of Australia, in southeastern Queensland, and extreme northeastern New South Wales.

HABITAT

Rainforest, other moist forest, and vine thickets with deep leaf litter. Able to use mature (50 years old) indigenous hoop pine (*Araucaria*) plantations with a closed canopy and well-developed understory, but adversely affected by clearcut logging. In fragmented rainforest within agricultural landscapes, uses only



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those habitat remnants greater than 42 acres (17 hectares) and favors the largest patches greater than 158 acres (64 hectares).

BEHAVIOR

Terrestrial, territorial, and resident unless forced to move by habitat clearance or logging. One observational study inferred that two females maintained non-overlapping home ranges vocally rather than by overt aggression. Each female formed a covey with between one and three males. In the breeding season each male of a covey became solitary and maintained a temporary, exclusive small territory around his nest within the larger territory of the female. The female appeared to rotate among the males, presenting each in turn with a clutch of eggs. In another study, this one of radio-tracked birds, the home range of a male overlapped that of three females, and those of the females overlapped each other to some extent. The birds occupied areas of 5.4-15.1 acres (2.2-6.1 hectares) at a density of 0.4-0.5 individuals per acre (1-1.3 birds per hectare). Roosting sites were between the buttress roots of rainforest trees and changed nightly. In another radio-tracking study, females occupied home ranges of 7.4-10.9 acres (3-4.4 hectares) before logging, and 12.8-44.2 acres (5.2-17.9 hectares) after logging. The home ranges of nonbreeding males averaged 15.3 acres (6.2 hectares), but that of a male tending chicks was 4.7 acres (1.9 hectares).

FEEDING ECOLOGY AND DIET

Eats seeds and invertebrates obtained by gleaning and scratching in ground litter. Mostly insectivorous.

REPRODUCTIVE BIOLOGY

Lays from October to February or March in the wild. Females sequentially polyandrous. In captivity can lay in all months, though usually September to April if conditions are sufficiently warm. Beneath the rainforest canopy, the nest is often a simple scrape lined with leaves, grass, or moss, placed between buttress roots or under a fern amid a ferny or weedy understory. The clutch is usually three or four eggs, rarely five. The incubation period for captive birds is 15–16 days but has been reported for wild birds as 18–21 days, apparently from laying of the first egg to hatching of the clutch. Chicks start to feed themselves at eight days, although the male continues to feed them until they are two weeks old. The young acquire sexually diagnostic plumage at eight to twelve weeks and can breed at four to five months old.

CONSERVATION STATUS

Classified as Endangered by the IUCN and listed on Appendix II of the Convention on International Trade on Endangered Species (CITES). Rare, restricted in range and declining, owing to clearance and fragmentation of specialized habitat.

SIGNIFICANCE TO HUMANS

Well established in aviculture. •

Painted buttonquail

Turnix varia

TAXONOMY

Perdix varia Latham, 1801, Sydney, New South Wales. Closely related to chestnut-backed and buff-breasted buttonquails (*T. castanota* and *T. olivii*, respectively). Three subspecies recognized; that on New Caledonia very distinct and may be full species.

OTHER COMMON NAMES

English: Varied buttonquail; French: Turnix bariolé; German: Buntlaufhühnchen; Spanish: Torillo Pintojo.



PHYSICAL CHARACTERISTICS

6.7–9.1 in (17–23 cm); male 1.9–3.3 oz (53–94 g), female 2.5–4.7 oz (72–134 g). Large buttonquail, reddish with mottled gray breast, slender bill, and red eyes. Female larger and redder. Juvenile smaller, grayer, and more mottled, without red, and with pale eyes.

DISTRIBUTION

T. v. varia: eastern, southeastern, and southwestern Australia, including Tasmania; T. v. scintillans: islands off southwestern Australia; T. v. novaecaledoniae: New Caledonia.

HABITAT

Scrub, grassy woodland, open forest, grassy clearings in dense forest, and heath.

BEHAVIOR

Terrestrial, diurnal, and partly nocturnal. Migrates at night. Strongly territorial.

FEEDING ECOLOGY AND DIET

Eats seeds, green shoots, and invertebrates obtained by gleaning and scratching on the ground.

REPRODUCTIVE BIOLOGY

Lays from late winter to autumn in south and east of range, all months of the year in the tropics. Females are sequentially polyandrous but may form short-term monogamous bonds. Clutch is usually three or four eggs, though up to five. Incubation 13–14 days. Chicks are fed by the male for 7–10 days, can fly at 10 days, are fully feathered at 16 days, and reach adult size at 23 days. Breeding success in one sample was 3.7 chicks per successful nest, and 2.6 chicks per clutch started. Broods averaged 3.5 young in the first week, down to 2.3 in the second.

CONSERVATION STATUS

Not threatened. Widespread and uncommon to locally common; declining in south Australian urbanized and agricultural regions.

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Subspecies on New Caledonia, possibly a full species, rare or extinct. Very similar species *T. castanota* and *T. olivii* of N. Australia classified as Vulnerable and Endangered, respectively.

SIGNIFICANCE TO HUMANS

Established in aviculture.

Red-chested buttonquail

Turnix pyrrhothorax

TAXONOMY

Hemipodius pyrrhothorax Gould, 1841, Aberdeen, New South Wales. Closely related to Worcester's and Sumba buttonquails (*T. worcesteri* and *T. everetti*, respectively), which may be subspecies. Australian little buttonquail *T. velox* also related to this species group.

OTHER COMMON NAMES

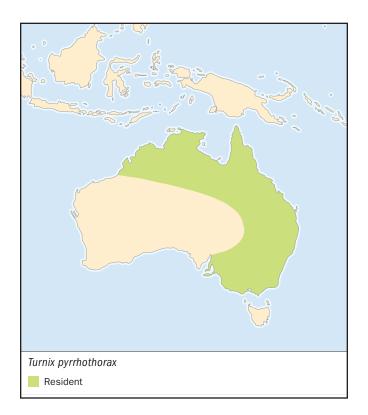
English: Chestnut-breasted, red-breasted, rufous-breasted, or yellow buttonquail; French: Turnix à poitrine rousse; German: Rotbrust-Laufhühnchen; Spanish: Torillo Pechirrufo.

PHYSICAL CHARACTERISTICS

4.7–6.3 in (12–16 cm); male 1–1.6 oz (27–46 g), female 1.5–2.7 oz (43–76 g). Small buttonquail, gray with rusty red breast, scalloped sides, stout bill, and pale eyes. Female larger, with brighter red breast. Juvenile smaller, browner, and more mottled, with scalloped breast.

DISTRIBUTION

Northern and eastern Australia.



HABITAT

Grassland, grassy woodland, and cropland with dense ground cover.

BEHAVIOR

Terrestrial, diurnal, and partly nocturnal. Migrates at night. Territorial when breeding.

FEEDING ECOLOGY AND DIET

Eats seeds and insects obtained by gleaning and scratching on the ground. Mostly granivorous.

REPRODUCTIVE BIOLOGY

Lays in spring and summer in the south of its range and autumn to spring in the tropics. Females sequentially polyandrous. Clutch usually four eggs, though up to five. Incubation 13–18 days. Chicks reach adult size in six to eight weeks and acquire adult-like plumage at two to three months.

CONSERVATION STATUS

Not threatened. Widespread and uncommon to locally common; possibly declining in south Australian agricultural regions. Very similar forms *T. worcesteri* and *T. everetti* classified as Vulnerable; these are very poorly known restricted-range endemics in Philippine and Lesser Sunda islands.

SIGNIFICANCE TO HUMANS

Hunted by Australian Aborigines for food. Established in a viculture. \blacklozenge

Lark buttonquail

Ortyxelos meiffrenii

TAXONOMY

Turnix meiffrenii Vieillot, 1819, Senegal.

OTHER COMMON NAMES

English: Lark-quail, quail-plover; French: Turnix à ailes blanches; German: Lerchenlaufhühnchen; Spanish: Torillo Alaudino.

PHYSICAL CHARACTERISTICS

3.9–5.1 in (10–13 cm); male 0.6–0.7 oz (16–20 g), female larger. Tiny, gracile, courser-like buttonquail, mottled red with pale belly. Wings and tail longer than in *Turnix*, dark with conspicuous white flashes in flight. Female has redder breast and broader white tip to tail. Juvenile duller and paler, more mottled.

DISTRIBUTION

Tropical Africa from Senegal east to Sudan and Kenya, including south Ghana and possibly elsewhere in west Africa.

HABITAT

Dry, sparse grassland, savanna, scrub, and dense shrubland.

BEHAVIOR

Terrestrial. Otherwise little known.

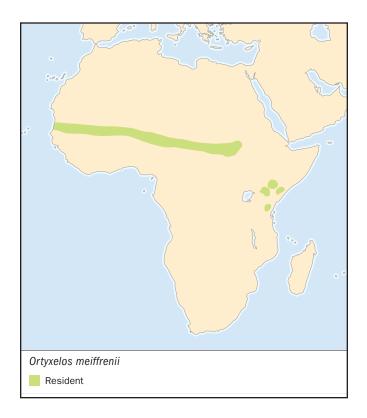
FEEDING ECOLOGY AND DIET

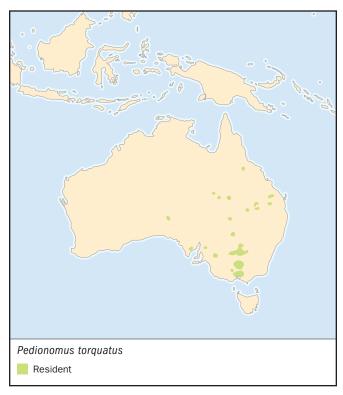
Eats grass seeds and insects obtained from the ground.

REPRODUCTIVE BIOLOGY

Little known. Lays from September to March in the cool dry season. Possibly monogamouns. Clutch is two eggs, incubated by the male.







CONSERVATION STATUS

Not threatened. Widespread and uncommon to locally common; range increasing with expanding deserts.

SIGNIFICANCE TO HUMANS

None known. ◆

Plains-wanderer

Pedionomus torquatus

SUBFAMILY

Pedionominae

TAXONOMY

Pedionomus torquatus Gould near Adelaide, South Australia. Traditionally placed with the Turnicidae, but as of 1990s increasingly recognized as belonging in the Charadriiformes, family Pedionomidae, and allied with the seedsnipes (Thinocoridae).

OTHER COMMON NAMES

English: Collared plains-wanderer/hemipode, turkey quail; French: Pédionome errant; German: Steppenläufer; Spanish: Llanero.

PHYSICAL CHARACTERISTICS

5.9–7.5 in (15–19 cm); male 1.4–2.8 oz (40–80 g), female 1.9–3.4 oz (55–95 g). Buttonquail-like bird with longer legs, small raised hind toe, shorebird-like mannerisms. Mottled and scalloped brown, with pale, scalloped underside. Female larger, with black-and-white mottled collar, reddish upper breast. Juvenile smaller, with spotted underside.

DISTRIBUTION

Inland eastern Australia.

HABITAT

Sparse native grasslands with low herbaceous layer; rarely in stubble or sparse low crops.

BEHAVIOR

Terrestrial, diurnal, and solitary except when pairing or when a male is tending chicks. Sedentary except when forced to move by drought or changes to habitat. Individuals occupy home ranges of 17.3–51.9 acres (7–21 hectares). Stands on tiptoe, with head bobbing, to scan for danger. Roosts solitarily in grass using the same roost nightly.

FEEDING ECOLOGY AND DIET

Eats seeds and insects obtained by gleaning from the ground or sometimes the standing heads of grasses. Lives without surface water but gleans dew and raindrops from vegetation.

REPRODUCTIVE BIOLOGY

Lays in spring and summer in temperate southern parts of its range, and autumn to early winter in subtropical northern parts. Possibly sequentially polyandrous. Clutch is usually four eggs, though up to five. Incubation 23 days. Young are independent after two months and can breed by one year old.

CONSERVATION STATUS

Classified as Vulnerable, revised to Endangered in 2000 by the IUCN and listed on Appendix II of CITES. Fairly widespread, but rare and declining owing to loss of native grasslands to agriculture.

SIGNIFICANCE TO HUMANS

Rare in aviculture. •

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Resources

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Stephen Debus, MSc

Cranes (Gruidae)

Class Aves

Order Gruiformes

Suborder Grues

Family Gruidae

Thumbnail description

Large birds with long neck and legs, usually gray or white plumage

Size

35-70 in (90-176 cm); 4.4-26.5 lb (2-12 kg)

Number of genera, species

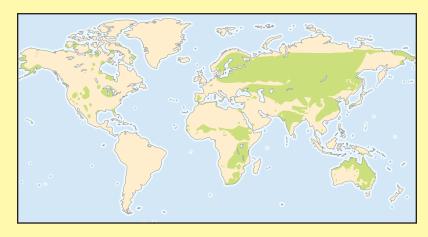
4 genera; 15 species

Habitat

Typically inhabit shallow wetlands from tropical areas to the Arctic

Conservation status

Vulnerable: 5; Endangered: 6



Distribution

Present in all regions except Antarctica and South America

Evolution and systematics

Cranes are an ancient family that dates back some 40–60 million years to the end of the Age of the Dinosaurs in the remote Eocene. More than a dozen extinct species are represented in fossil records.

The Gruidae's closest relative is the New World limpkin of the family Aramidae. Somewhat smaller than cranes, limpkins have an upright stance and loud calls reminiscent of cranes. The next closest relative to the cranes and limpkins are the New World trumpeters of the family Psophidae. Native to the tropical forests of South and Central America, the jumpy behavior and the plumage of trumpeters somewhat resembles that of the most primitive of cranes, the crowned cranes. These close links of cranes to New World families suggests that the pro-crane originated in the New World and subsequently expanded into Asia where their closest relatives are bustards of the family Otidae—a family that is restricted to the Old World. From Asia, ancient cranes probably extended their ranges into Africa and Australia.

Crowned cranes are placed in the subfamily Balearicinae, and differ from cranes of the subfamily Gruinae in many ways. Crowned cranes have loose plumage and the inability to tolerate extreme cold. Gruinae cranes have compact plumage and are cold-hardy. Balearicinae cranes have elongated hind toes (hallux) and perch in trees. Gruinae cranes have vestigial short hind toes and seldom perch in trees. As the name suggests, crowned cranes have elaborate bristle-like feathers on the hind part of their heads that look like golden crowns. While Gruinae cranes lack this plumage, portions of the heads of most species are covered by predominantly bare red skin that is used in display. The trachea of crowned cranes proceeds directly from the neck to the lungs in contrast to the trachea of the Gruinae that coils to varying degrees into the

sternum. The prevalence of extinct species of crowned cranes in fossil records in North America, suggests that the Balearicinae or its ancestor gave rise to the Gruinae. Today there are two living species of Baleariciae, both of the genus *Balearica* and both restricted to wetlands amidst the grasslands and savannas of sub-Saharan Africa.

The Gruinae includes thirteen species of the typical cranes. Although comparative studies of their DNA by American scientist Dr. Carey Krajewski suggest they all can be considered members of a single genus *Grus*, the species are divided into three genera—*Grus*, *Anthropoides*, and *Bugeranus*—based on anatomical and behavioral evidence.

The *Grus* includes 10 species divided into four subgroups, the Siberian; the sandhill; the Group of Five (Eurasian, whooping, hooded, black-necked and red-crowned); and the Group of Three (brolga, sarus, and white-naped). *Anthropoides* includes demoiselle and blue cranes, while *Bugeranus* has the wattled crane.

The Siberian is the enigma of the Gruinae. Although resembling the whooping crane with glistening white plumage and black primary flight feathers, the red facial comb is restricted to the area in front of the eyes, giving it a nun-like look and a pattern somewhat similar to that of the comb of the wattled crane. The reduced coiling of its trachea and its feeding behavior is also similar to the wattleds. But these similarities with *Bugeranus* are perhaps the consequence of convergent evolution. DNA of the Siberian suggest the species is definitely a *Grus* but with a more distant relationship to the remaining nine species within that genus.

The sandhill has some behavioral links to Siberian cranes but more DNA, anatomical, and behavioral links to the Group of Three. Within the Group of Three, DNA suggests the white-naped of Asia and the brolga of Australia are more Family: Cranes Vol. 9: Birds II



Display behavior of the red-crowned crane (*Grus japonensis*) on Hokkaidō, Japan. (Photo by Akira Uchiyama. Photo Researchers, Inc. Reproduced by permission.)

closely related to each other than to the sarus of south Asia. Anatomical evidence suggests the brolga and the sarus are more closely aliened. DNA suggests the red-crowned crane is most distant within the Group of Five, and that the Eurasian, whooping, hooded, and black-necked cranes are closely related to each other. Perhaps the whooping crane arose from a stock of Eurasian cranes that immigrated into North America from Asia.

DNA suggests that the wattled crane is closely related to the demoiselle and blue cranes. Wattled cranes are adapted to African wetlands while the *Anthropoides* species live predominantly in grasslands in southern Africa (blue) and in Asia and north Africa (demoiselle). Perhaps the demoiselle cranelike ancestor from Asia radiated into African wetlands and grasslands to become the wattled and the blue cranes.

Physical characteristics

Cranes are large, long-legged, long-necked birds that typically inhabit shallow wetlands. They have loud calls that can carry for several miles.

Distribution

Cranes occur on all continents except Antarctica and South America.

Habitat

Most cranes nest in wetlands, where they also feed. Many species use freshwater wetlands in their summer breeding areas, but may use saltwater coastal marshes in their wintering ranges. Two species of cranes predominantly inhabit grasslands.

Behavior

Cranes of northern latitudes migrate thousands of miles (kilometers) south to wintering areas. When prevailing winds are correct, cranes climb mid-morning thermals to glide. While gliding they are not in "V" formation. However, when flap-flying without the aid of thermals, they do fly in "V" formation. For each crane population there are usually one or two traditional staging areas where the cranes remain for several weeks during migration. Otherwise, when migrating, cranes fly until late in the afternoon or evening and then roost opportunistically at available wetlands. Juvenile cranes remain close to their parents during migration and throughout most of the winter. Sometimes they accompany their parents back to natal areas in spring, and sometimes they leave their parents before or during the spring migration.

Cranes that live in warm climates typically breed during the wet season or seasons and gather in flocks during the dry season. Flocking is usually greatest just before the onset of the next breeding season and is presumed to facilitate integration of juveniles in sub-adult flocks and genetic mixing as new pairs form in the flocks.

Crane calls

Cranes are well known for their trumpet-like calls. Aldo Leopold said it best, "When we hear his voice we hear no mere bird. He is the trumpet in the orchestra of evolution. The sadness discernable in some wetlands stems from their once having harbored cranes. Now they stand humbled adrift in history."

Within the Gruidae, there is an evolutionary progression from the simpler displays in the ancient crowned cranes through a progression of "middle species" to the most elaborate displays in Siberian and red-crowned cranes. The most fundamental call in all cranes is the low, purr-like contact call. It is given by cranes that are familiar with one another in a flock, between members of a pair, and from a parent crane to its egg and chicks. Apparently it signals compatibility and well being. In sharp contrast to the soft contact call is a nasal hiss or deep growl, both of which signal acute aggression.

The black crowned cranes have one single-syllable loud honk-like call that appears to suffice in many circumstances. Likewise, the gray crowned crane has a two-syllable call that is commonly performed. Crowned cranes are unique in possessing an inflatable sac beneath the head that is inflated when performing a series of boom-like calls at the onset of the breeding season. This gular sac is larger in the gray crowned crane and at least in captive cranes "booming" is more frequently performed in gray crowned than in black crowned cranes.

Within the Gruinae, there is a whole series of distinct and somewhat complicated calls that are difficult to describe. The alarm call immediately causes other cranes to become alert and perhaps to fly. The flight intention call signals just that. The loud flight call perhaps helps maintain flock cohesion. The low groan call signals acute pain. The piercing guard call warns of both danger and of the individual's aggression. The trumpeting and prolonged unison call—a duet of mated pairs—is a threat to other cranes. The duration and the in-

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tensity of the calls can vary depending on the condition of the crane emitting the call.

Crowned cranes have honk-like calls. Anthropoides have low broken calls that are remarkably similar to the calls of sand-hills. Wattled cranes are generally silent, and when they do call, the voice is high-pitched and somewhat squeaky. Siberian cranes have soft flute-like calls that are simpler in structure than the call of other Grus species. Sarus have the loudest and shrillest calls of cranes, and brolgas have the lowest calls. As its name suggests, the whooping crane has a penetrating call that carries for great distances over the wetlands.

The voice of the Gruinae cranes is modified by coiling of the trachea in the sternum. The trachea of Siberian cranes and wattled cranes makes a slight dip into the sternum: their calls are high frequency and of less intensity than in other cranes. In the remaining Gruinae species there are varying degrees of coiling, the most advanced being in the Group of Five (Eurasian, whooping, hooded, black-necked, and redcrowned) where the length of the trachea is doubled by two coils that penetrate the entire length of the sternum. The tracheal rings fuse with the sternal bone to create a plate between the tracheal passage and air sacs on the outer side of the sternum. The vibrations of these bones are believed responsible for the amplification of the calls of the crane. If an operation is performed to bypass the sternum and lead the trachea directly from the lower neck to the bronchi, the crane's voice becomes a whisper.

Individual cranes can be identified by "voice prints." Remarkable research by German scientist Dr. Bernard Wessling reveals that recordings of guard calls and unison calls of Eurasian, red-crowned, and whooping cranes can be used to identify individuals. Catching cranes for individual marking with color bands is difficult for humans and dangerous for cranes. Voice printing provides many new opportunities for research to better understand the biology and thus the needs of the endangered cranes.

Threats and dances

The head is the most important unit for communication in cranes. Not only is it the outlet of calls, but also it has many visual features used in communication.

Crowned cranes have bare skin on the sides of the head, tiny black fur-like feathers on the forehead, and elaborate crests. They are the only cranes that commonly all preen each other's heads in what appears to be both a maintenance activity and a sexual display.

The *Anthropoides* have completely feathered heads with elongated plumes on the side of the head that can be raised during display to increase the apparent size of the head. During display a blue crane elevates these feathers creating a cobra-like look. A triangle of white plumes form just behind the bright red eye of the demoiselle, and can be elevated and fanned open. Wattled cranes elongate their drooping flaccid wattles. Blue, demoiselle, and wattled cranes all use their bills while displaying.

The *Grus* species have areas of conspicuous red skin on their heads. In Siberian cranes the red skin extends from the

eye down along a central groove in the upper mandible. The portion on the top of the head is pulled back slightly when the crane displays. In sandhills, as in Siberians, the red extends from the facial area over the top of the head. When not displaying, the red area can be pulled forward so the backside of the head is then covered by gray feathers.

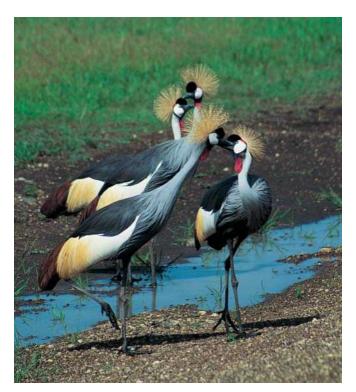
In the Group of Three (brolga, sarus, and white-naped), the sides of the head are covered by bare red skin, and in the brolga and sarus the red continues down the upper portion of the neck. The feathers covering the ear holes are conspicuous as gray circles surrounded by red skin. The Group of Five somewhat like the sandhill, have red on the top of the head that can be pulled down over the back of the head in display. The ability to voluntarily expand and contract the size of the area of bare red skin gives the crane an ability to communicate in degrees.

Cranes that fear other cranes often adopt a submissive posture and reduce the display component of their heads. With neck retracted and feathers slightly ruffled, a crane communicates submission. In sharp contrast, a crane that communicates aggression and/or sex holds its neck and head high, elevates the inner half of the toes above the substrate, sleeks is plumage, protrudes its thighs, and displays its tertials. From this classic threatening posture a crane can perform a series of complex threat postures and rapid sequence of postures.

The following outlines common threat displays of several species:

- Crowned—upright, then ruffles wings with head lowered and then head up.
- Blue—neck up, head puffed, head lowered to near ground and at same time ruffles elongated tertials, raises head and puffs sides of head while simultaneously moving tail back and forth rapidly.
- Wattled—open wings, held open for a second, closed rapidly, false preens shoulder feathers, head up, ruffles wings, tail back and forth rapidly.
- Siberian—flaps with strength with head lowered to ground level, ruffles, snaps head and neck up and false preens shoulder with wing dropped vertically.
- White-naped—exaggerated flap of wings and head and neck lowered between legs as wings open, as wings close head and neck brought up and then back over the back in spring-like manner, head up, wings ruffled and at same time head and neck lowered to false preen the thigh.
- Red-crowned—exaggerated flap of wings, with wrists closed, humeri raised high over back, red of head turned sideways against black elevated tertials.

One of the highest intensity threat displays is the crouch threat, whereby a crane sits on the ground in front of an adversary in a posture that resembles incubation posture. The beak is often pressed into the substrate and the wings are Family: Cranes Vol. 9: Birds II



Gray crowned crane (*Balearica regulorum*) courtship at Maasai Mara National Reserve in Kenya. (Photo by Mitch Reardon. Photo Researchers, Inc. Reproduced by permission.)

sometimes partially opened. From this prostrate-like posture, a crane can leap up and attack.

If threat displays do not resolve a conflict, cranes engage in a ritualized fight that usually does not injure the participants. The combatants approach each other in threat posture, face each other, and then leap up with legs folded. The feet strike at the opponent's breast and both birds are vigorously pushed in opposite directions. During this split second of contact, the dominance relationship is established. When the cranes land, they are separated by several meters. The subordinate bird usually slowly walks away in reduced threat posture. Through this ritualized combat serious injuries are avoided and social relationships are determined. This type of conflict frequently occurs when cranes gather in flocks.

Territorial cranes are acutely aggressive to other cranes. If an intruder approaches a piece of defended real estate, in the majority of the species, the resident pair releases a unison call for an extended period. This display usually results in the departure of the intruders. However, if the intruder continues to penetrate the territory, the resident birds often attack with vigor and the intruder departs. Seldom will an intruder attempt to stand up to the attacks of a resident pair. There is a significant psychological advantage to holding a territory.

Feeding ecology and diet

Cranes can be divided into three groups based on beak proportions and associated foraging behavior: the short-

beaked, the medium-beaked, and the long-beaked. The shorter the beak, the more dependent a species is on uplands; conversely, a longer beak allows for a wetland-dependent species.

The short-beaked cranes include the *Balearica*, *Anthropoides*, and the lesser sandhill. *Balearica* and *Anthropides* forage predominantly in grasslands and agricultural fields, while the lesser sandhills feed in more upland and drier portions of the tundra. During migration and on their wintering grounds these sandhills also forage in grasslands and agricultural fields. The short beaks of these cranes are adapted for grasping insects, seeds and for grazing in a manner somewhat similar to the grazing of geese.

The medium-beaked cranes include five other subspecies of sandhills, Eurasian, hooded, and black-necked cranes. These cranes often forage in uplands like the short-beaked cranes. Harvested grain fields rife with gleanings are particularly important to these cranes during the nonbreeding season. During the breeding season, as well as feeding in nearby and drier uplands, these cranes also forage on a wide variety of plant and animal life in the wetlands.

The long-beaked cranes can be divided into two groups: the diggers (Siberian, wattled, and the Group of Three) and the catchers (red-crowned and whooping). In a quest for the flesh tubers of sedges, the diggers excavate holes up to approximately 1.6 ft (0.5 m) deep in wet mud. Although the diggers can be catchers and the catchers can be diggers, the diggers typically dig in wet soils for the nutrient rich portions of aquatic plants, while the catchers gently probe the bottoms for live animals.

Cranes that have adapted to a human-altered habitat by foraging in pastures and harvested fields are more successful than species restricted to wetlands. Gleaning in agricultural fields in southern areas of both North America and Eurasia, have undoubtedly contributed to the increase in numbers of demoiselle, sandhills, and Eurasians into the hundreds of thousands. Conversely, the more dependent on aquatic habitat, the more endangered the species. The Siberian crane is the most wetland dependent of the diggers and it is considered to be the most endangered species of cranes, although not the rarest—a distinction held by the more wetland-dependent of the catchers, the whooping crane.

Young cranes require a high-protein diet of live animal food independent of the beak type and foraging habitat of adults. Foraging patterns with the young cranes closely resemble those of adult cranes with the exception that the families usually spend more time in wetlands. The Balearicinae forage for live animal food in both wetlands and neighboring uplands. The *Anthropoides* pairs walk quickly with their juveniles through the uplands on a seemingly urgent quest of insects and other small animals. The medium-beaked cranes forage in both aquatic and upland habitats, while the long-beaked cranes are more restricted to the wetlands.

Vegetation stomping is performed to flush insects that are then grabbed. This behavior is most prevalent in crowned cranes and is included in a ritualized manner in their courtship Vol. 9: Birds II Family: Cranes

dance. Cranes of all species will trample down dense emergent aquatic vegetation to create a flat open habitat for their chicks. Presumably the vegetation forms a mat on which the chicks can walk and from which they can more readily catch insects.

Reproductive biology

Cranes are monogamous birds and usually pair in their second or third year and start to breed in their fourth or fifth year. Pairs defend breeding territories that usually include many acres (hectares) of open wetlands or grasslands. A low platform nest is constructed of materials available in the wetland. A clutch of two eggs is typical. The incubation period of about one month is followed by a prefledging period of about 2–3 months.

Young cranes are precocial and remain with their parents for about 9 months. If there is more than one juvenile in a family, there is usually a dominance hierarchy among the chicks. Parents partially feed the juveniles and dominant birds receive proportionately more food from the parents. In times of food scarcity, subordinate juveniles are the first to perish. Most successful pairs usually rear only a single offspring per breeding attempt. After juveniles fledge, cranes usually abandon their territories and gather in flocks and feed in areas of food abundance. At night they roost in flocks in shallow water to better escape terrestrial predators.

Cranes that are completely white (Siberian, whooping, redcrowned) or that have white necks (white-naped, wattled), tend to breed on wide expanses of wetlands far from terrestrial predators. They use white to make themselves conspicuous on their territories. Intruding conspecifics can readily see the white residents and easily avoid contact with them and their land. The gray cranes tend to nest on smaller wetland often near uplands. Rather than making themselves conspicuous, these cranes have evolved strategies to hide at the nest. Sandhills and Eurasian, and to a lesser extent black-necked and hooded, apply iron-rich mud to their backs that stains the feathers a reddish-brown color. With the neck lowered while incubating, a painted crane blends with the pile of mud and dead wetland vegetation that constitutes the nest. Undoubtedly, they are much less obvious to predators than are white cranes.

In contrast to the wattled and *Grus*, the blue and demoiselle cranes often lay their eggs on the ground in grasslands and do not build a nest. These gray cranes are the same color as many weathered rocks and are usually difficult to spot. They nest in a spot that provides a commanding view of the surrounding area. If danger approaches the crane simply stands up and calmly walks away from the nest, making it extremely difficult to pinpoint the location of the eggs.

In South Africa, where gray-crowned, blue, and wattled cranes inhabit the same wetlands and grasslands, the breeding strategies of the three species are easily compared. Crowned cranes nest in dense aquatic vegetation and are usually impossible to see from land. Their strategy is to hide. Blue cranes nest in the short grass and look like a gray stone or if the grass is taller are hidden but for the white-topped

head peering above the grass. In contrast, the wattled crane builds a large platform nest in an open area of a small pond in the wetland. The pond, the nest, and the huge crane with a white neck are all conspicuous. The wattled crane makes itself conspicuous to conspecific intruders. Apparently, it is large enough to defend itself from most predators.

Crane eggs vary in color from white to dark brown. Crowned crane eggs appear white from a distance but have a slight blue tint. Sarus and brolgas lay bright white eggs. These species breed in tropical and subtropical areas where temperatures are sometimes so hot that exposure to sunlight is a threat to the survival of the embryo. These cranes must shade their eggs from the sun. The light color of the eggs might help deflect heat from sunlight. In contrast, cranes that breed in the coldest areas (lesser sandhill, Siberian, and black-necked) have the darkest eggs, perhaps an adaptation to absorb more heat from sunlight. The remaining species are intermediate except for the red-crowned crane in which some females lay almost completely white eggs. This leads to speculation that perhaps in prehistoric times, red-crowned cranes might have nested further south in east Asia where heat is more extreme during the breeding season.

Conservation status

Fifteen species survive today and of these, five are considered Vulnerable and six are Endangered.

Whooping crane conservation

In resettlement time, tall grass prairies covered much of the landscapes of what is the "food basket of the world." The deep roots of the prairie grasses built rich soils. Wetlands of the tall grass prairie provided habitat for the whooping cranes. These cranes probably only numbered in the low thousands. For the pioneers, a big bird was a meal, and whooping crane eggs were treasured by egg collectors. The whooping cranes disappeared as a breeding resident from the prairies in 1922.

A remnant flock of whooping cranes survived by breeding in a wilderness wetland area of northern Canada, an area protected within the borders of Wood Buffalo National Park. These cranes migrate about 2,175 mi (3,500 km) to spend the winter along the coast of Texas in Aransas National Wildlife Refuge. The population reached its lowest point in 1941 with just 15 survivors. DNA studies of the pre- and post-bottleneck populations indicate that perhaps as few as three females were breeding when the population was at its lowest. Through widespread public education, the whooping crane became a household word in Canada and the United States. The cranes responded to protection and remarkably their numbers climbed to about 180 birds at the turn of the twenty-first century.

Although a pair of whopping cranes usually lay a clutch of two eggs, they seldom are successful in rearing two chicks. The second egg and later the second chick seem to be for insurance should something happen to the other egg or chick. As a safeguard against extinction, in 1966 the Canadian and U.S. governments established a captive population of whooping cranes by collecting one egg from each of several whooping crane nests. The eggs were taken by air in a

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A sandhill crane (*Grus canadensis*) takes flight from its morning roost. (Photo by C.K. Lorenz. Photo Researchers, Inc. Reproduced by permission.)

portable incubator to the Patuxent Wildlife Research Center in Maryland. During many springs over the next three decades, eggs were harvested from the wild cranes and taken to captive breeding centers. Today there are about 120 whooping cranes in captivity at three major breeding centers and three zoos.

Banding studies indicate that the whooping crane can breed in its third year, although most breeding first happens when the cranes are 4–5 years old. Population modeling suggests whooping cranes live for 25–30 years if they survive the first few years when mortality is heaviest. One whooping crane might be capable of breeding for more than two decades.

In captivity, whooping cranes usually take 6–8 years before they start breeding. However, whereas wild cranes lay but two eggs per breeding season, captive birds can be induced to lay 6–8 eggs per year if the eggs are removed as they are laid. One pair of captive whooping cranes is capable of contributing 4–6 offspring in a single breeding season. It might take a wild pair of cranes a decade to fledge that number of offspring.

As well as serving as a "species bank," the captive population is also a source of whooping cranes for release programs. The traditional group of cranes that migrates between Canada and the United States faces a variety of threats. The intercoastal canal traverses the core wetland area used by cranes at the Arkansas National Wildlife Refuge. Barges filled with toxins travel through the refuge every day, and one spill of chemicals could be the demise of most of the whooping cranes. Whooping cranes forage on blue crabs in tidal pools where the salinity is reduced by rainwater and fresh water inflow from inland rivers. Inland stream flow is being blocked for agriculture and urban use. If the salinity of the tidal pools reaches a certain level, the blue crabs become scarce and the cranes are forced to fly to inland oak savanna areas to feed on

acorns and other foods. During winters when an adequate supply is not available for the cranes, 6–7 cranes have died. The "old" flock of whooping cranes, although slowly increasing, is by no means secure.

Since 1976, efforts have been made to start new wild populations of whooping cranes using birds reared from eggs collected from the "old" population of wild cranes, and from eggs and birds produced by the captive breeding centers. Between 1976 and 1988, about 300 whooping crane eggs were substituted into the nests of wild sandhill cranes in Idaho. The sandhills raised and migrated with 77 whooping cranes. But unfortunately, the whooping cranes appear to have been sexually imprinted on sandhill cranes. Not a single conspecific pairing occurred. Before the program was discontinued, a mixed pair of sandhill and whooping crane produced a single hybrid—a Whoophill.

In the mid1980s, ethologist Dr. Robert Horwich developed a remarkable new technique for rearing cranes in captivity known as "costume-rearing." Using this technique, problems associated with sexual imprinting are avoided and birds are reared that are afraid of humans and can be released into the wild. Crane-costumed keepers cloaked in white and wearing a hand puppet that resembles the head of a whooping crane, rear chicks that are exposed to real live whooping cranes in adjacent enclosures.

There was a nonmigratory breeding population in southwest Louisiana that was extirpated in the 1940s. Since 1993, more than 200 costume-reared whooping cranes have been released on the Kissimmee prairie of south-central Florida in an effort to start a nonmigratory population in that area. Bobcat predation has been a major mortality factor.

In 1993, an experiment began in Wisconsin to establish a new migratory population of whooping cranes in eastern North America. Costume-reared cranes were trained to follow ultralight aircraft. Based on preliminary work with sand-hill cranes, in which the birds were led south behind an ultralight and returned on their own to natal areas in spring, it is hoped a new and successful migratory population will be established between breeding grounds in central Wisconsin and wintering grounds on the northwest coastal wetlands of peninsular Florida. In the autumn of 2001, 6 whooping cranes migrated south behind the ultralight. Five survived the winter, and all 5 migrated back to Wisconsin without assistance. Finally, whooping cranes might be returned to the rich prairie wetlands of the great plains.

Siberian crane conservation

The Siberian crane shares many threats with the whooping crane. Both species breed in the far north of respective continents; both species migrate across a continent; and both species must use wetlands that occur near heavily populated areas. But while the whooping crane has only one population, the Siberian crane has three—all of which breed in Russia. One group migrates from western Siberia to Iran. A second group breeds 620 mi (1,000 km) due north of the first group and migrates to India. A third group breeds on the tundra of eastern Siberia and winters in China. The western group

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numbers fewer than 12 birds. The central group has declined during recent decades from 75 birds to a single pair. The eastern group numbers approximately 3,000.

Prior to massive public education along the flyway through the heart of North America, many whooping cranes were probably shot. Hunting remains a problem along flyways used by Siberian cranes in west Asia. And just as the conservation along the coast of Texas is vital to the survival of whooping cranes in winter, the conservation of wetlands in Iran, India, and China is vital to the conservation of the Siberian crane. Whooping crane management is based on the comparatively well-funded activities of specialists in Canada and the United States. Funds for Siberian crane management are extremely limited, and 12 nations (Afghanistan, Azerbaijan, China, India, Iran, Kazakhstan, Pakistan, Russia, Turkmenistan, Uzbekistan) must participate if the three populations of Siberian cranes are to be maintained and/or restored.

In 1976, Russian ornithologist Dr. Vladimir Flint, in collaboration with the U.S.-based International Crane Foundation (ICF), began a major program for the conservation of the Siberian crane. Hatching eggs were transported from the tundra breeding grounds of eastern Siberia to ICF and the Oka Nature Reserve south of Moscow. A flourishing captive population has been established and many eggs and birds are available for release programs.

In 1978, Iranian ornithologists discovered the remnant population of Siberian cranes in the Caspian lowlands. The cranes spend the winter inside a waterfowl trapping complex where shooting is banned. It was not until 1996 that Russian scientists discovered their breeding grounds west of the town of Uvat in southwest Siberia.

The year 1981 was a banner year for the Siberian crane. That year the breeding grounds of the central population were discovered on the basin of the Kunovat River in western Siberia, the wintering grounds of the eastern population were discovered at Poyang Lake, China, and the species bred for the first time in captivity.

Although the well-known Keoladeo National Park in India provided sanctuary for the central population of Siberian cranes, winter counts in India show a steady decline of cranes, presumably as a result of hunting along the 3,100 mi (5,000 km) migration route. The breeding area of the central population has been protected both for the cranes and for the in-

digenous local people, the Khanty, some of whom continue to live a traditional lifestyle.

The eastern population holds the largest share of the Siberian cranes. The major breeding area in Russia has been protected as Kytalic Nature Reserve, while the major wintering area in China has been protected as Poyang Lake Nature Reserve. Likewise, several important wetlands in northeast China have been conserved to protect breeding habitat of redcrowned and white-naped cranes and migration staging areas for Siberian cranes. However, there are concerns that water diversion projects in China, designed to meet the needs of humans, might negatively impact wetlands vital to the welfare of the eastern population.

In 1993, the Convention for Migratory Species headquartered in Bonn, Germany, developed, in collaboration with ICF, a Memorandum of Understanding on the Conservation of the Siberian Crane. This agreement has been signed by most of the range states. Every two years delegates from the range states meet to report on conservation actions and to refine recovery programs for the three populations of Siberian cranes.

A number of experiments have been undertaken to augment the western and central populations, but as yet none have met with confirmed success. Several captive-reared cranes released with the wild cranes in India and Iran failed either to join the wild cranes or to migrate. Although scientists have not confirmed the survival of captive-reared Siberian cranes released with wild cranes on the breeding grounds of the wild Siberian cranes, and on the migration staging areas of Eurasian and Siberian cranes in Western Russia, local people near the release areas have reported in subsequent years the presence of color-banded Siberian cranes. Now Russian scientists are exploring the possibility to leading captive-reared Siberian cranes south behind hang gliders, rather than behind ultralight aircraft as is being done in North America for whooping cranes.

Significance to humans

Humans have been intrigued by the grace and beauty of cranes since ancient times. Today they are a symbol of good luck in many parts of the world, and appear on coins and as national symbols. The whooping crane is a special conservation symbol in North America, because of its recovery from the brink of extinction.



1. Sandhill crane (*Grus canadensis*); 2. Demoiselle crane (*Anthropoides virgo*); 3. Siberian crane (*Grus leucogeranus*); 4. Wattled crane (*Bugeranus carunculatus*); 5. Gray crowned crane (*Balearica regulorum*); 6. Sarus crane (*Grus antigone*); 7. Whooping crane (*Grus americana*); 8. Redcrowned crane (*Grus japonensis*); 9. Eurasian crane (*Grus grus*). (Illustration by Barbara Duperron)

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Species accounts

Gray crowned crane

Balearica regulorum

SUBFAMILY

Balearicinae

TAXONOMY

Arthropoides regulorum Bennett, 1834, South Africa. Two subspecies.

OTHER COMMON NAMES

English: Blue-necked crane, royal crane; French: Grue royale; German: Südafrikanischer kronenkranich; Spanish: Grulla Coronada Cuelligrís.

PHYSICAL CHARACTERISTICS

Height 39–43.3 in (100–110) cm; wingspan 71–79 in (180–200 cm); weight 6.6–8.8 lb (3–4) kg. Distinctive crown of gold feathers. Pale gray neck and red throat wattles.

DISTRIBUTION

Eastern Africa from Kenya to South Africa, west to Zambia, also Angola and Namibia.

HABITAT

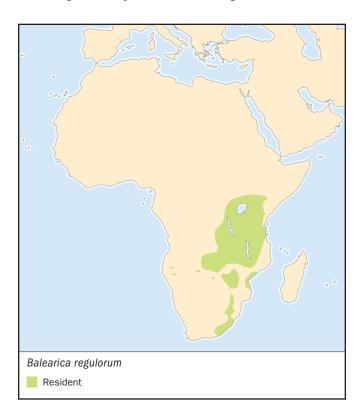
Uses wetlands and grasslands or savanna.

BEHAVIOR

These birds perch in trees and use ground nests, or rarely tree nests, abandoned by other large birds.

FEEDING ECOLOGY AND DIET

Wide range of food preferences, including seeds and insects.



REPRODUCTIVE BIOLOGY

Breed in wetland-grassland areas.

CONSERVATION STATUS

Not threatened. The most abundant crane in Africa, though populations have declined. Continued wetland drainage may threaten its future, as many live and forage outside of protected areas.

SIGNIFICANCE TO HUMANS

Gray-crowned cranes are the national bird of Uganda and regarded as a sacred bird or symbol in Kenya, Namibia, South Africa, and Zambia. ◆

Demoiselle crane

Anthropoides virgo

SUBFAMILY

Gruinae

TAXONOMY

Ardea virgo Linnaeus, 1758, India. Monotypic.

OTHER COMMON NAMES

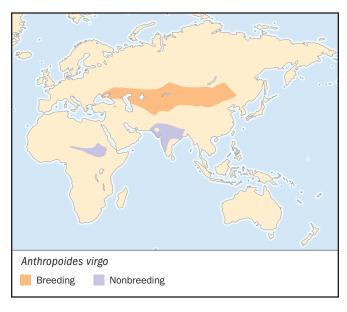
French: Grue demoiselle; German: Jungfernkranich; Spanish: Grulla Damisela.

PHYSICAL CHARACTERISTICS

Height 35.4 in (90 cm); wingspan 59–67 in (150–170 cm); weight 4.4–6.6 lb (2–3 kg). All gray, but with black neck and head, and white ear tufts behind eye to upper neck.

DISTRIBUTION

Eastern Europe across central Asia to eastern China. Small populations in Morocco and Turkey. Winter in Africa, Pakistan, and India.



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HABITAT

Grassland near streams or other wetlands.

BEHAVIOR

Aggressively defend their nesting sites.

FEEDING ECOLOGY AND DIET

Generally grass seeds and other plant materials; also some insects, worms, lizards, and other small vertebrates.

REPRODUCTIVE BIOLOGY

Eggs are laid in nests made of pebbles, or laid on the ground, in upland or desert areas with some vegetation to hide the incubating parent.

CONSERVATION STATUS

Not threatened, though listed on CITES Appendix II. Legally protected in many countries.

SIGNIFICANCE TO HUMANS

Good luck symbols in Mongolia and parts of India, and generally revered in Islamic countries. ◆

Wattled crane

Bugeranus carunculatus

SUBFAMILY

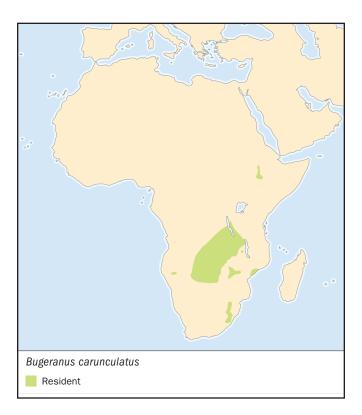
Gruinae

TAXONOMY

Ardea carunculata Gmelin, 1789, Cape of Good Hope. Monotypic.

OTHER COMMON NAMES

English: Great African wattled crane; French: Grue caronculée; German: Klunkerkranich; Spanish: Grulla Carunculada.



PHYSICAL CHARACTERISTICS

Height 69 in (175 cm); wingspan 90.5–102.3 in (230–260) cm; weight male 18.3–18.7 lb (8.3–8.5 kg), female 15.6–17.4 (7.1–7.9 kg). Body and wings gray and black, white neck, wattles white with some red skin.

DISTRIBUTION

South-central Africa, with some populations in Ethiopia, South Africa, Namibia, and in the Zambezi Delta on Africa's east coast.

HABITAT

Dependent on wetlands.

BEHAVIOR

Nonmigratory. Rarely leave their territories.

FEEDING ECOLOGY AND DIET

Their primary food is sedge tubers, which they find in shallow wetlands.

REPRODUCTIVE BIOLOGY

Many nests contain only a single egg. Incubation lasts up to 40 days, and the fledgling period is 103 days or more.

CONSERVATION STATUS

Endangered, and listed on CITES Appendix II. Protected throughout much of their range.

SIGNIFICANCE TO HUMANS

These birds receive great attention in South Africa as one of the nation's most endangered birds. ◆

Siberian crane

Grus leucogeranus

SUBFAMILY

Gruinae

TAXONOMY

Grus leucogeranus Pallas, 1773, central Siberia. Monotypic.

OTHER COMMON NAMES

English: Great white crane, Siberian white crane, Asiatic white crane; French: Grue de Sibérie; German: Schneekranich; Spanish: Grulla Siberiana.

PHYSICAL CHARACTERISTICS

Height 55 in (140 cm); wingspan 82.6–90.5 in (210–230 cm); weight 11–19 lb (5–8.6 kg). White crane with dark red mask around bill and eyes. Serrated bill tip.

DISTRIBUTION

Russia; winters in China, Iran, and India.

HABITAT

Uses wetlands for nesting, breeding, and roosting.

BEHAVIOR

Migrate long distances over international borders.

FEEDING ECOLOGY AND DIET

During winter and while migrating, the cranes feed on tubers. While nesting, they feed on invertebrates, cranberries, frogs, mollusks, aquatic insects, and fish.

REPRODUCTIVE BIOLOGY

Usually lay 2 eggs, incubated for 29 days. Chicks fledge at 70-75 days.

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CONSERVATION STATUS

Endangered, and listed on CITES Appendix I. Strict dependence on wetlands makes it susceptible to habitat loss due to development, dam building, and oil exploration.

SIGNIFICANCE TO HUMANS

Revered by Khanty people in western Siberia and Yakatian people in eastern Siberia. Treasured as "Lily of Birds" by Indians. •

Sandhill crane

Grus canadensis

SUBFAMILY

Gruinae

TAXONOMY

Ardea canadensis Linnaeus, 1758, Hudson Bay, Canada. Six subspecies.

OTHER COMMON NAMES

English: Little brown crane, Canadian crane; French: Grue du Canada; German: Kanadakranich; Spanish: Grulla Canadiense.

PHYSICAL CHARACTERISTICS

Height up to 47.2 in (120 cm); wingspan 63–82.6 in (160–210 cm); weight 7.3–12 lb (3.3–5.4 kg). Gray body, neck, and head with bare red forecrown.

DISTRIBUTION

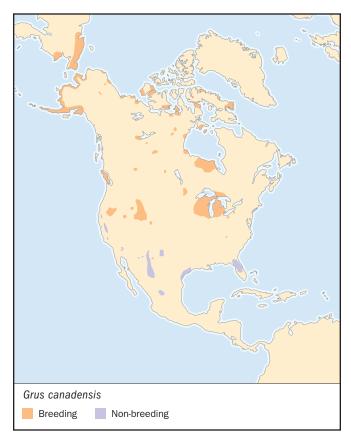
Across North America from Quebec west to British Columbia and north to Alaska and eastern Siberia. Additional populations in Pennsylvania, Ohio, Maine, and the Northwest (U.S.). Winter in Florida, Texas, New Mexico, Arizona, California, and Mexico. Nonmigratory subspecies found in Florida, Mississippi, and Cuba.

HABITAT

Wetland areas. May use savannas and agricultural fields in wintering areas.

BEHAVIOR

Three subspecies are migratory; three are nonmigratory.



FEEDING ECOLOGY AND DIET

Omnivorous. Diet includes grains, berries, insects, and rodents.

REPRODUCTIVE BIOLOGY

Usually lays 2 eggs, incubated for 29–32 days. Chicks fledge at 50–90 days.

CONSERVATION STATUS

Four subspecies Not threatened, though listed on CITES Appendix II. Two subspecies, the Mississippi and the Cuban sandhill, are Threatened.

SIGNIFICANCE TO HUMANS

The most abundant of all cranes, it has been a part of Native American culture for over 1,000 years. ◆

Sarus crane

Grus antigone

SUBFAMILY

Gruinae

TAXONOMY

Ardea antigone Linnaeus, 1758, India. Three subspecies.

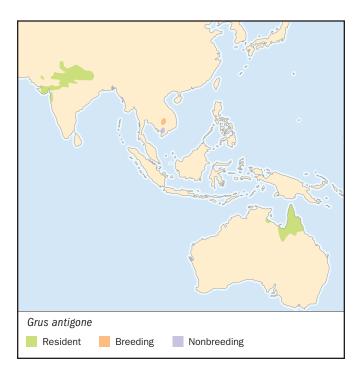
OTHER COMMON NAMES

English: Sharpe's crane; French: Grue antigone; German: Saruskranich; Spanish: Grulla Sarus.

PHYSICAL CHARACTERISTICS

Height up to 69 in (176 cm); wingspan 86.6–110.2 in (220–280 cm); weight 11–26.5 lb (5–12 kg). Gray body, red skin on head, throat, and upper neck.

Family: Cranes Vol. 9: Birds II



DISTRIBUTION

Northern and central India, southeastern Pakistan, southern Myanmar, Cambodia, southern Laos, Vietnam, and northern Australia.

HABITAT

Wetlands, including seasonally flooded savannas and humanmade areas such as canals, irrigation ditches, and fields.

BEHAVIOR

Subspecies in India and Australia is generally nonmigratory, but population in southeast Asia is locally migratory.

FEEDING ECOLOGY AND DIET

A generalist, its diet includes plants, grains, insects, fish, and other small vertebrates.

REPRODUCTIVE BIOLOGY

Lays 2 or 3 eggs, incubated for 31–34 days. Chicks fledge at 85–100 days.

CONSERVATION STATUS

Endangered, and listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Regarded as omens for good crops in India. •

Eurasian crane

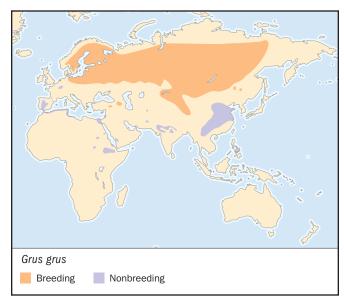
Grus grus

SUBFAMILY

Gruinae

TAXONOMY

Ardea grus Linnaeus, 1758 Sweden. Monotypic.



OTHER COMMON NAMES

English: Common crane; French: Grue cendrée; German: Kranich; Spanish: Grulla Común.

PHYSICAL CHARACTERISTICS

Height 45 in (114 cm); wingspan 71–78.7 in (180–200 cm); weight male 11–13.4 lb (5–6.1 kg), female 10–13 lb (4.5–5.9 kg). Gray body with black primaries. Head and neck are dark with white stripe from behind eyes down neck. Crown has red skin patch.

DISTRIBUTION

The most widely distributed of all cranes, they occupy an area extending across the Scandinavian countries south to Germany and then east to eastern Russia and China. Winter in Spain, northern Africa, the Middle East, India, Indochina, and China.

HABITAT

Shallow wetlands. In winter range, it may forage in agricultural fields and pastures.

BEHAVIOR

Migrates throughout Asia, Europe, and northern Africa.

FEEDING ECOLOGY AND DIET

Omnivorous, including tubers, stems, leaves, berries, and other plant material; also invertebrates (worms and insects) and some small vertebrates (snakes, fish, rodents).

REPRODUCTIVE BIOLOGY

Typically lays 2 eggs, incubated for 28–31 days. Chicks fledge at 65–70 days.

CONSERVATION STATUS

Not threatened, though listed on CITES Appendix II. Its habitat would benefit from increased protection in heavily populated areas of Europe.

SIGNIFICANCE TO HUMANS

Their yearly return to the Scandinavian countries is heralded as a sign of spring. ◆

Vol. 9: Birds II Family: Cranes

Whooping crane

Grus americana

SUBFAMILY

Gruinae

TAXONOMY

Ardea americana Linnaeus, 1758, Hudson Bay, Canada. Monotypic.

OTHER COMMON NAMES

English: Whooper, big white crane; French: Grue blanche; German: Schreikranich; Spanish: Grulla Trompetera.

PHYSICAL CHARACTERISTICS

Height 5 ft (150 cm), wingspan 7–8 ft (200–230 cm). Weight: male 16 lb (7.3 kg), female 14 lb (6.4 kg). White with black wingtips, legs, and feet; black facial markings; and a bare patch of red skin on its head.

DISTRIBUTION

Wood Buffalo National Park in west-central Canada; winters at Aransas National Wildlife Refuge on the Gulf Coast of Texas.

HABITAT

Currently use ponds and marshes; historically used potholes and other wetlands of North American plains and prairies. Winter habitat includes coastal marshes.

REHAVIOR

Wild flock is migratory, as well as an experimental flock in the Rocky Mountains. An experimental flock in Florida is nonmigratory, and has dispersed from its original release area.

FEEDING ECOLOGY AND DIET

Omnivorous, its diet includes blue crabs, small fish, rodents, berries, tubers, grain, insects, and other invertebrates.



REPRODUCTIVE BIOLOGY

Whooping cranes are monogamous. Both parents take turns incubating two eggs for a period of 29–30 days. Both eggs may hatch, but usually only one chick survives the first few months to reach fledging age.

CONSERVATION STATUS

Endangered, and listed on CITES Appendix I.

SIGNIFICANCE TO HUMANS

After near extinction and subsequent precarious recovery, it has become a symbol of conservation in North America. ◆

Red-crowned crane

Grus japonensis

SUBFAMILY

Gruinae

TAXONOMY

Ardea (Grus) japonensis P.L.S. Müller, 1776 Japan. Monotypic.

OTHER COMMON NAMES

English: Japanese crane, Manchurian crane; French: Grue du Japon; German: Mandschurenkranich; Spanish: Grulla Manchü.

PHYSICAL CHARACTERISTICS

Height 59 in (150 cm); wingspan 86.6–98.4 in (220–250 cm); weight 15.4–22 lb (7–10 kg). White body with black neck and white nape. Red skin on crown.

DISTRIBUTION

Most breed in the Amur River basin near the China-Russia border and winter in coastal areas of China and on the Korean peninsula, many within the Korean Demilitarized Zone (DMZ). A nonmigratory population remains year-round on Hokkaidō, Japan.



Family: Cranes Vol. 9: Birds II

HABITAT

More aquatic, using marshes and other deep wetland areas. Winter habitat includes rivers, freshwater wetlands, and coastal salt-marshes.

BEHAVIOR

Well-known for their elaborate courtship dances.

FEEDING ECOLOGY AND DIET

A generalist, it feeds on insects, fish, rodents, and plants.

REPRODUCTIVE BIOLOGY

Lays 2 eggs, incubated for 29–34 days. Chicks fledge at about 95 days.

CONSERVATION STATUS

Endangered, and listed on CITES Appendix I.

SIGNIFICANCE TO HUMANS

The "sacred crane" is widely revered in the Orient as a symbol of fidelity in marriage, good luck, long life, and love. These cranes are often the subjects of poems, mythology, and art. ◆

Resources

Books

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Wessling, Bernhard. "Individual Recognition of Cranes, Monitoring and Vocal Communication Analysis by Sonography." IV European Crane Workshop. European Crane Working Group, 2000.

Organizations

International Crane Foundation. P.O. Box 447, Baraboo, WI 53913-0447 USA. Phone: (608) 356-9462. Fax: (608) 356-9465. E-mail: explorer@savingcranes.org Web site: http://www.savingcranes.org

George William Archibald, PhD

Limpkins (Aramidae)

Class Aves

Order Gruiformes

Suborder Grues

Family Aramidae

Thumbnail description

Medium-sized wading birds with a long downcurved bill, long legs, long neck, rounded wings and tail, an erect stance, and a distinctive limplike gait; brownish plumage is streaked and spotted with white

Size

26 in (66 cm); wingspan 40 in (102 cm); up to 2.4 lb (1.1 kg)

Number of genera, species

1 genus; 1 species

Habitat

Tropical and subtropical wetlands and lake and river margins

Conservation status

Many local populations are declining, but the species is not threatened.



Distribution

Florida, Mexico, Central America, tropical and subtropical South America

Evolution and systematics

The limpkin (*Aramus guarauna*) is the only member of the family Aramidae (which was described by Bonaparte in 1842). Limpkins are related to and intermediate in morphology and behavior to the cranes (family Gruidae) and rails (family Rallidae).

Physical characteristics

Limpkins are medium-sized wading birds with an erect stance, long legs, spreading toes, an elongate down-curved bill, and rounded wings and tail. The body length is about 26 in (66 cm), the wingspread 40 in (102 cm), and the weight is up to 2.4 lb (1.1 kg). The plumage is dark brown with white spots on the lower neck, breast, and outer wings. There is little physical difference between male and female limpkins.

Distribution

Limpkins range widely in tropical, subtropical, and warm-temperate regions of the Americas, from the southeastern

United States (mostly on the Florida peninsula), through some islands of the West Indies, much of Mexico, Central America, and most of South America east of the Andes as far south as central Argentina.

Habitat

Limpkins inhabit a wide range of brushy and forested shallow-water wetlands, including the marshy edges of ponds, lakes, and slow-flowing rivers. They usually roost in shrubs or in the top of dead trees.

Behavior

Limpkins may live a solitary life or occur in breeding pairs or in small loose groups. They are difficult to see when roosting quietly in dense shrubbery but do not hide when active, especially while searching for food. In this respect their behavior is closer to that of cranes rather than to that of the much shyer rails. Limpkins can swim well. They fly slowly with an outstretched neck and with wings rising and

Family: Limpkins Vol. 9: Birds II



Limpkin (Aramus guarauna). (Illustration by Michelle Meneghini)

falling in a deliberate rhythm. The name limpkin comes from the bird's walking gait, which is somewhat awkward and resembles a limp. Limpkins are nonmigratory over much of their range, but in parts of South America they may move between habitats used during the wet and dry seasons. Limpkins have an unmistakable, loud, discordant, wild-sounding scream or wail, as well as a quieter clicking sound. Their shrill cries are most often heard in early morning, at night, or on heavily clouded days. Their calls have earned limpkins several colloquial nicknames, such as wailing bird, crying bird, and crazy widow.

Feeding ecology and diet

Limpkins feed almost exclusively on large freshwater mollusks known as apple snails (genus *Pomacea*). Limpkins find these snails in shallow water by searching visually and by probing carefully on the muddy bottom using their long bill. They extract the snail meat and leave an empty shell. Young limpkins take small snails from the bill of the parent and swallow them with the shell intact. Limpkins also eat

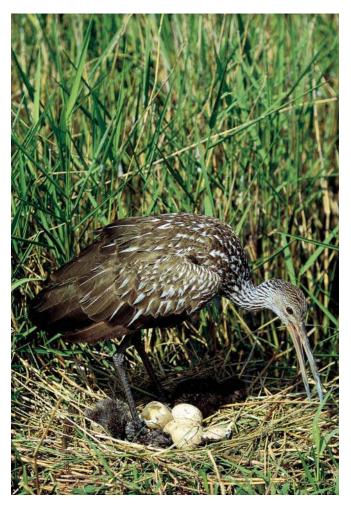
mussels, insects, crayfish and other aquatic crustaceans, worms, small reptiles, frogs, and plant seeds.

Reproductive biology

A pair of limpkins builds a nest near water, either on the ground within dense vegetation or in a bush or tree 20 ft (6 m) or sometimes higher above the ground. The nest is a platform constructed of reeds and grasses and lined with finer plant fibers. The female lays from four to eight eggs, each measuring about 2.2 in long by 1.7 in wide (56 mm x 44 mm) and ranging in color from whitish to pale brown with brown and gray spots. The incubation period is not exactly known. Both parents tend the eggs, and both parents cooperate in the care of their young, which are dark brown, downy, and precocial (capable of leaving the nest within about a day after birth).

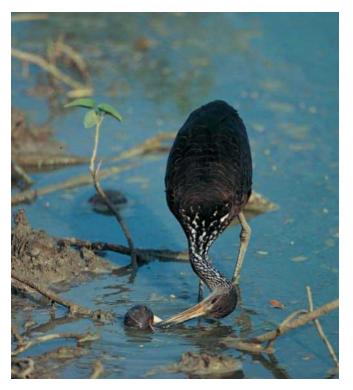
Conservation status

Limpkins are not listed as being at risk globally by the IUCN or in the United States by the U.S. Fish and Wildlife



Limpkin (*Aramus guarauna*) hatching eggs. (Photo by Bill Dyer. Photo Researchers, Inc. Reproduced by permission.)

Vol. 9: Birds II Family: Limpkins



A limpkin (*Aramus guarauna*) eats a snail. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)

Service. Limpkins are, however, designated a species of special concern by the state of Florida. At the turn of the twentieth century, limpkins were hunted almost to extirpation in the United States, mostly as a source of meat. Since then limpkins have been protected and their populations have substantially recovered. However, many of the wetland areas inhabited by limpkins have been destroyed or degraded by filling, dredging, pollution, and other human influences. Habitat degradation has caused the species to decline in overall abundance in the last few decades of the twentieth century and to disappear from local parts of its range.

Significance to humans

Limpkins are not often hunted anymore. They are appreciated by birders and other naturalists, which can contribute to local economic benefits through ecotourism. The wailing cries of limpkins make them of cultural significance to aboriginal peoples who inhabit remote parts of the species' range.

Resources

Books

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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>

Bill Freedman, PhD



Class Aves

Order Gruiformes

Suborder Rhynocheti

Family Rhynochetidae

Thumbnail description

Medium-sized, agile, flightless birds with ashgray and white plumage, orange-red legs and bill, dark-red eyes, long crest feathers, and black-and-white cross-banded wings

Size

Averages 22 in (55 cm); 2 lb (900 g)

Number of genera, species

1 genus; 1 species

Habitat

Forests and certain shrublands

Conservation status

Endangered



DistributionNew Caledonia

Evolution and systematics

Kagus (*Rhynochetos jubatus*) are rather oddballs among birds because they are a mixed bag of physical characteristics, some of which are unique to Rhynochetidae, but most of which are shared with other bird families. The name "Rhynochetos" refers to the unique rolled corns or nasal flaps that cover its nostrils. Kagus look like rails (Rallidae) and occupy a niche similar to Rallidae; however, kagus also exhibit light coloration and abundant, widely distributed powder-downs, much like herons (Ardeidae). Kagus have a unique blood composition compared to other bird species, consisting of one-third the number of red blood cells and three times the hemoglobin content. Early morphological comparisons correctly placed kagus in Gruiformes. Subsequent DNA and morphological comparisons by J. Cracraft and P. Houde et al. suggest that the kagu's closest living relative is the South American sunbittern (Eurypygidae). These findings imply that the Rhynochetidae have an ancient, Gondwana origin.

Physical characteristics

Although flightless, kagus have large wings. They are medium-sized (1.5–2.4 lb [700–1,100 g]), quite compact, and

agile birds that move surprisingly fast. Their dark-red eyes and orange-red, long legs and large bill contrast with their ash-gray and white plumage. A striking feature of the kagu's appearance, and usually concealed, is the patterning on the wings, which somewhat resembles that on the sunbittern's wings. The patterning consists of a dominant design of black-and-white cross-bands with a smaller area of brown "overlay" also running across the primaries. Their long crest feathers extend to the lower back and are difficult to spot unless raised. No secondary sexual dimorphism is known. The brown-and-fawn color of chicks gradually changes into a dull, adult-like plumage and is completely adult after about two to three years.

Distribution

Identified by Verreaux and Des Murs in 1860, kagus are endemic to New Caledonia where they live in only a small area of the mainland's forests.

Habitat

The main habitat for kagus is humid forest where the birds can find sufficient small invertebrates and reptiles in the soil Family: Kagus Vol. 9: Birds II



Male kagu (Rhynochetos jubatus). (Illustration by Dan Erickson)

and litter and on low vegetation. Kagus also forage in more shrub-like vegetation if there is enough food available. Kagus have been reported foraging on beaches. In a 1991 survey, they were found at low altitude to over 4,600 ft (1,400 m) on New Caledonia's high peaks.

Behavior

Kagus are diurnal and roost at night, usually on low branches. In colder, winter conditions at higher altitudes, they mainly roost in natural shelters formed by rocks or tree roots. Kagus generally roost alone but sometimes do so next to partners and offspring, particularly in the breeding season. Preening is mostly carried out at the roost.

Mated pairs are territorial and defend areas of around 50 acres (20 ha) throughout the year. Although partners spend much of their day foraging and mostly alone, their first chore of the day is often to sing a distinctive duet. The male and female alternate in singing a sexually distinctive chorus that can be heard up to 1.2 mi (2 km) away. Some people liken this chorus to the yapping of a young dog.

In addition to their song, kagus are best known for their distinctive displays. For defense, the wings are opened to reveal their patterning and positioned forward-facing in an attention-grabbing display that might have acted to confuse past predators. This display is remarkably similar in form and function to the "frontal display" of the sunbittern. Kagus use a "strutting" display in courtship and in disputes with other birds. They take an upright pose with the crest raised and fanned and the wings held down and forward in the form of a cape. They then slowly circle around each other in a ballet-like dance. A captured bird held by the feet will also instinctively open its wings to reveal the patterning and bring them together as "shields" to cover its head.

Feeding ecology and diet

Kagus eat most types of small animal prey available to them. This behavior is consistent with the large amount of time they spend foraging and suggests that food is usually difficult to obtain. Prey includes a wide range of animals, like invertebrate larvae, amphipods, spiders, centipedes, orthoptera (e.g., crickets), cockroaches, millipedes, beetles, snails, worms, and lizards. Although they are generalists in the types of prey they eat, kagus seem to select larger, more rewarding food items when food supplies are abundant. Individuals have reportedly been seen catching small animals in shallow water. Kagus' unique nasal flaps may protect the nares when they forage in soil and water.

Kagus spend much of their foraging time motionless while trying to detect prey. They certainly use their relatively large, rather forward-facing eyes to notice prey movement, but they must also use other means, like vibration and/or sound, to pinpoint out-of-sight prey (e.g., in soil) that they capture. Once prey is detected, kagus spring into action and launch their bills into the likely spot where the prey is hidden. This foraging strategy results in characteristic "divets" in the soil made by birds digging with their bills. Food is most abundant for kagus during the summer wet-season storms from January to March.

Reproductive biology

Kagu pairs are monogamous and form long-term partnerships. Like many island birds that evolved with low predation, kagus have low rates of reproduction. They generally lay a single one-egg clutch each year. The breeding season is wellknown only at low altitudes, where the main nesting period is in the cool season from June to August, with most eggs laid



Kagu (*Rhynochetos jubatus*) chick plumage appears to resemble the forest floor. (Photo by Gavin R. Hunt. Reproduced by permission.)

Vol. 9: Birds II Family: Kagus

in July. This period is outside the time of peak food supplies, but wet season conditions may be unsuitable for nesting and birds molt in those months.

One-egg clutches are laid in simple, open-ground nests that sometimes involve nest-building using layered leaves. Incubation in the wild lasts 34–35 days and is shared by both sexes, who each take 24-hour shifts. Most chicks hatch with closed eyes and stay in the nest for the first few days. The chicks then gradually move away from the nest as they follow their parents.

Kagu parents are very attentive toward chicks and share feeding duties, bringing small prey to them. Both parents defend chicks aggressively and can also feign injury to draw an intruder away from the young. Chicks are brooded at night by one of the parents until they are about 6 weeks old, when they begin to perch. Parents feed the chicks for around 14 weeks until they become independent. Independent offspring can reside on their natal territories for many years before they establish their own territories, during which time they may assist their parents in protecting chicks. Males can start breeding around two years of age. Kagus can live for over 30 years in captivity.

Conservation status

Kagus are Endangered and listed in Appendix I of CITES. The species is fully protected in New Caledonia. The minimum number of kagus known in 1991 was 654 birds, including 163 in Parc Rivière Bleue reserve. The kagu population has declined because of habitat loss, introduced mammalian predators, and hunting and capture by humans. The main threat comes from roaming dogs who find the kagus to be easy prey. Wild pigs, cats, and rats also take a toll on the kagu population. Consequently, the unforgettable sound of many kagu pairs duetting in the early-morning dawn is absent from in most of New Caledonia's forests.

Local recovery efforts begun in 1977 have greatly increased the kagu's chances of survival. Kagus are bred in captivity and then released into Parc Rivière Bleue where some have successfully paired and raised young with wild partners. The number of birds in the Parc has increased substantially since the early 1980s due to predator control and the release of the captive-bred individuals under the guidance of Y. Létocart. Other kagus are mostly unprotected and at substantial risk



An adult kagu (*Rhynochetos jubatus*) display for territorial defense against an intruding kagu. (Photo by Gavin R. Hunt. Reproduced by permission.)

from predation. Another large kagu reserve is needed to ensure the species' survival over the long term.

Significance to humans

The kagu played a part in some indigenous Kanak cultures; for example, kagu feathers were worn by the chiefs and their song was used in war dances. However, kagus seem to have always been a source of meat for the Kanak people on an island where native terrestrial game was limited. Europeans continued the hunting and had a tradition of keeping kagus as pets, but this practice has ceased. Kagus hold a prominent place in New Caledonian national culture as a bird emblem and a unique tourist attraction.

Resources

Books

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Family: Kagus Vol. 9: Birds II

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Organizations

Ligue pour la Protection des Oiseaux. La Corderie Royale, B.P. 263, 17305 Rochefort cedex, France. Phone: +33 546 821 234. Fax: 33 546 839 586. E-mail: lpo@lpo-birdlife.asso.fr Web site: http://www.lpo-birdlife.asso.fr

Other

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Gavin Raymond Hunt, PhD

Rails, coots, and moorhens

(Rallidae)

Class Aves
Order Gruiformes
Suborder Grues
Family Rallidae

Thumbnail description

Small to medium-sized birds with short and deep to long and slender bill, moderately long neck, broad wings, short, soft tail, and strong legs

Size

4.7-24.8 in (12-63 cm); 0.7 oz-9.13 lb (20.41 g-4.14 kg)

Number of genera, species

33 genera; 134 species

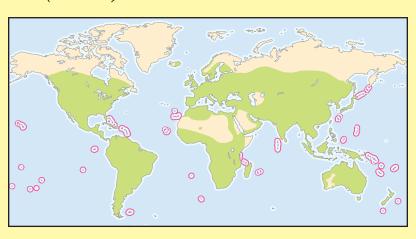
Habitat

Wetlands, grasslands, forest, and dense scrub

Conservation status

Extinct in the Wild: 1 species; Critically Endangered: 4 species; Endangered: 12 species; Vulnerable: 16 species; Near Threatened: 9 species; Data Deficient: 4

species



Distribution

Worldwide, except for polar regions and waterless deserts; widely distributed on oceanic islands

Evolution and systematics

The Rallidae is by far the largest family in the Gruiformes. In some classifications the family has been assigned to its own order Ralliformes, while others have allied with to the Charadriiformes; DNA evidence suggests that it shares a common ancestor with both gruiform and charadriiform birds. Skeletal morphology suggests a close alliance with the Psophiidae (trumpeters) and the Heliornithidae (sungrebes and finfoots), and a phylogenetic study of the Gruiformes using morphological characters, published by Bradley Livezey in 1998, places the families Psophiidae, Aramidae (limpkin), Gruidae (cranes), Heliornithidae and Rallidae together in the suborder Grues. On the basis of DNA evidence that the Rallidae may have had a distinct lineage for a long time, it has also been proposed that the rails should be elevated to their own suborder, the Ralli, alongside the Grues.

Fossil evidence tells us little about the origins of the Rallidae. The earliest rail fossils are from the Lower Eocene, about 50 million years ago, but the family may have existed earlier than this. DNA-DNA hybridization studies suggest that rails may have diverged from the other gruiform groups as long as 86 million years ago, in the Upper Middle Cretaceous. The first adequate diagnostic material on fossil rail genera comes from the Upper Oligocene and Lower Miocene, 20–30 million years ago, and by then the birds had attained a morphology similar to that of modern rails. Most continental fossil rails from Pliocene and Pleistocene deposits have been assigned to modern genera.

The geographic origins of modern rails have been obscured by the antiquity, cosmopolitan distribution, and inadequate taxonomy of the family. However, Storrs Olson has shown that the greatest number of rail species and peculiar genera, and the most primitive species, are found in the Old World tropics. The New World has fewer groups, most of which are apparently derived from Old World stem groups. A few genera appear to have specialized and radiated in the New World, some of which (e.g. *Rallus* and *Fulica*) have reinvaded the Old World.

Several classifications have been proposed for the family. The generally accepted classification, published in 1973 by Olson, listed 35 genera in two subfamilies, the Himantornithinae and Rallinae, the former containing one species, *Himantornis baematopus*, the nkulengu rail of Africa. Livezey's classification also recognizes these subfamilies. Sibley and Ahlquist have suggested that the flufftails (*Sarothrura*) of Africa and Madagascar diverged from the rest of the group about 60 million years ago and should be separated into a family Sarothruridae within its own superfamily, the Sarothruroidea.

In this work we follow Olson and Livezey's subfamily treatment and Olson's taxonomic treatment regarding genera—modified to some extent by subsequent studies. Within the family, 33 genera containing 134 extant species and 312 subspecies are recognized, following the list published in 1998 in the book *Rails: a guide to the rails, crakes, gallinules and coots of the world* by Barry Taylor.



American coot (*Fulica americana*) hatchling in its nest, Saskatchewan, Canada. (Photo by S.E. Cornelius. Photo Researchers, Inc. Reproduced by permission.)

Two "natural groups" within the Rallidae are usually recognized: the crakes, rails, and wood-rails, most of which are terrestrial; and the gallinules (including moorhens) and coots, which are more aquatic. The term "rail" is applied to the whole family and also to longer-billed species in many genera, while "crake" is applied mostly to the smaller, short-billed, species, particularly in the genera *Laterallus* and *Porzana*. "Gallinule" can cover all the birds in the second group except the coots, though it is often restricted to *Gallinula* and *Porphyrio*.

Physical characteristics

The rails are a relatively homogeneous group of birds, ranging in size from the tiny black rail (*Laterallus jamaicensis*), 4.7 in (12 cm) long and weighing 0.7 oz (20 g), to the flightless takahe (*Porphyrio mantelli*) 24.8 in (63 cm) long and weighing up to 9.2 lb (4.2 kg). The sexes are usually similar in size but in a few species the male is markedly larger than the female.

Rail plumage is often cryptic, common colors being somber browns, chestnut, black, blue-gray, or gray, but the *Porphyrio* gallinules are predominantly iridescent purple, blue, or green. The upperparts are often spotted, barred, or streaked and the flanks strongly barred, while the undertail-coverts may contrast strongly with the rest of the plumage. In most species the sexes are very similar in appearance, exceptions including the flufftails and the New Guinea *Rallina* forest-rails. Only the watercock (*Gallicrex cinerea*) shows any significant seasonal change in plumage color or pattern. The juvenal plumage is often a duller, less patterned version of the adult plumage.

The downy plumage of most species is black or dark brown, but the nkulengu rail chick is cryptically patterned with brown, black, and white, closely resembling precocial chicks of other orders. Some chicks, especially those of coots (*Fulica*), have distinctively colored filoplumes or bristles. Coots, gallinules (*Porphyrio*), and moorhens (*Gallinula*) have brightly colored bare skin on the head, and such prominent features act as signals for feeding.

The bodies of rails are often laterally compressed, allowing easy movement through dense vegetation, and the neck can be quite long. The wings are short, broad, and rounded. In some species the alula has a sharp claw, used by the young, and possibly also by adults, when climbing. Short flights are usually low and weak, but some species migrate or disperse over long distances. The tail is short and soft.

The bill shape is variable: from long and thin to short and fine, straight or slightly down-curved; or short and laterally compressed; or short and heavy. It is often brightly colored. Gallinules and coots have a frontal shield that may be of a contrasting color to the bill. Shield and bill colors often become duller in the nonbreeding season, when the shield may also shrink.

Rails have strong, often long, legs. The toes are often long, for walking on marsh vegetation. In some species the legs and feet are brightly colored. Coots have the pelvis and legs modified for diving, and lateral lobes on the toes aid swimming.

Flightlessness is a well-known feature of the family and all flightless rails occur on islands. Of the 134 extant rail species, 41 are known only from islands, including New Guinea, New Zealand, and Madagascar, and 24 (59%) of these are flightless. Flightlessness has evolved many times within the family, often and repeatedly on predator-free islands. The energetic cost of flight is high and flight muscles and associated structures average 20–25% of body weight in typical birds. Where such costs do not convey the benefits of dispersal and escape from predators it is obviously advantageous to become flightless. The muscles and bones of the wing and pectoral girdle are greatly reduced, the feathers become loosely constructed and the leg muscles usually become better developed.

The strong tendency of rails to become flightless suggests a predisposition to the condition, and rails are pre-adapted to coping with some of its restrictions. Thus many volant species are behaviorally flightless, avoiding predators by running. Many are temporarily flightless during wing molt, and the postnatal development of flight in most species is slow.

Distribution

Rails occur throughout the world, being absent only from polar regions, waterless deserts, and mountains above the snow line. Of the 33 rail genera, four (*Porzana*, *Porphyrio*, *Gallinula*, and *Fulica*) occur worldwide. The genus *Porzana* includes 13 species of small rails, one of which, Baillon's crake (*Porzana pusilla*), ranges from western Europe through Africa and Asia east to Japan and Australasia.

The genus *Porphyrio* has five species of medium to very large gallinules, including the purple swamphen (*Porphyrio porphyrio*), which has a similar range to Baillon's crake. In the genus *Gallinula*, the common moorhen (*Gallinula chloropus*) occurs from the Americas east through Africa and Eurasia to the Malay Archipelago; farther east it is replaced by the very similar dusky moorhen (*Gallinula tenebrosa*). Although moorhens are commonly regarded as wetland birds, two species occur in forest: the Samoan moorhen (*Gallinula pacifica*) and the San Cristobal moorhen (*Gallinula silvestris*). The center of the coots' species diversity is in South America, where eight of the 11 species occur.

The relatively unspecialized genus *Gallirallus*, with 10 extant and five recently extinct species, is distributed largely from Indonesia through Australasia to western Pacific islands. Seven extant species are flightless, as were all the recently extinct species. The islands in this region also support 17 other endemic rails, eight flightless, and seven of these in five endemic genera. The genus *Gymnocrex* contains three species of very distinctive, long-legged forest rails of Indonesia and New Guinea, one of which, the Talaud rail (*Gymnocrex talaudensis*) was discovered only in 1996.

Africa and Madagascar have 23 endemic rail species, with 15 species in six endemic genera, including *Sarothrura* (the flufftails). In comparison, 51 rail species occur only in the Americas, including 27 in eight endemic genera, the most diverse of which is *Laterallus*, with nine species. South and Central America are home to all seven species of the wood-rails (*Aramides*). Six of the nine *Rallus* species occur only in the Americas, including the well-known clapper and king rails (*Rallus longirostris* and *R. elegans*).

Most Holarctic rails are migratory, and five of the nine species that breed in the western Palaearctic winter in sub-Saharan Africa. All rails that breed in North America are migratory to some extent. Relatively little is known about the migrations of species that breed from India east to Japan and south through the Oriental region, but evidence suggests that many birds that breed in the northern regions of Asia move south after breeding. Even less is known about the movements of South American rails, but most of the species known or suspected to be migratory or dispersive inhabit wetlands or wet grassland. All rails occurring widely in Australia are migratory, dispersive, nomadic, or irruptive. In Africa, some species move away from the equator to breed during the rains.

The widespread occurrence of rails on oceanic islands reflects these birds' powers of dispersal and their tendency to vagrancy. The high degree of long-distance vagrancy in the family is also indicative of the readiness with which rails are blown off course by unfavorable winds as a result of their rel-



Common coots (*Fulica atra*) engage in territorial fighting near Arundel, United Kingdom. (Photo by Roger Wilmshurst. Photo Researchers, Inc. Reproduced by permission.)

atively poor flight performance. The purple gallinule (*Porphyrio martinica*) is a vagrant to South Africa, but there are no instances of African rails occurring in the Americas.

Habitat

The cosmopolitan distribution of the family reflects the ability of rails to adapt to a great diversity of habitat types, both natural and artificial, including wetland, grassland, savanna, scrub, and forest.

Although the greatest number of species occurs in wetland habitats, many species occupy forest habitats in tropical regions. The most primitive living rail, the nkulengu rail, is a forest bird, as are the members of other primitive or unspecialized genera such as *Aramides, Canirallus*, and *Gymnocrex*. Species in the most specialized or derived genera such as *Rallus, Porzana, Gallinula*, and *Fulica* are aquatic or marshdwelling. This suggests that forest was the primitive habitat of the family.

Rails occupy all types of vegetated wetlands, plus some open water habitats. Freshwater wetland habitats include swamps, bogs, marshes, floodplains, pans, ponds, ditches, rice fields, and vegetation fringing streams, rivers, canals, and lakes. Some species, such as the white-browed crake (*Porzana cinerea*) of Asia and Australasia, and *Porphyrio* species, prefer floating vegetation, on which they search for food. Some rails occur at coastal wetlands such as lagoons, saltmarshes, tidal creeks, and mudflats, while mangroves are an important habitat for species such as some South American *Aramides* woodrails. Coots, the most aquatic rails, occupy fresh to saline waterbodies.

Forest habitats range from low to high altitudes and include primary and secondary growth, riverine and swamp forest, overgrown and abandoned cultivation at forest margins, banana groves, cassava plantations, and dense evergreen or deciduous thickets. Substrates may be clear, with leaf-litter, soft earth or mud, or may have dense herbaceous vegetation. Some species, such as the gray-throated rail (*Canirallus oculeus*) of Africa and Woodford's rail (*Nesoclopeus woodfordi*) of the



A gray-necked wood-rail (*Aramides cajanea*) preens in Venezuela. (Photo by Erwin and Peggy Bauer. Bruce Coleman Inc. Reproduced by permission.)

southwest Pacific, occur at forest streams, swamps, or muddy patches, but others are not associated with wet areas.

A few species occur in dense grassland habitats, which may be wet to predominantly dry, the latter including savanna, pampas, meadows, and crop fields. Grassland habitats may be permanently or seasonally occupied; for example, the African crake (*Crex egregia*) occurs in seasonally moist to wet grassland, which is frequently burned during the dry season, forcing the birds to emigrate after breeding.

Most rails do not have specialized diets and this enables many to exploit ephemeral or atypical habitats. They are able to colonize islands where, in the absence of competitors and predators, they can radiate to occupy almost any available terrestrial niche. They are capable of adapting to harsh conditions on remote oceanic islands. The recently extinct Ascension rail (*Atlantisia elpenor*) lived on Ascension Island, where the terrestrial environment consists of bare, waterless tracts of lava and ash. It apparently obtained its food and water from the eggs and regurgitated prey of the seabirds, which formerly nested on Ascension in great numbers. The spotless crake (*Porzana tabuensis*) of the Pacific region, has successfully colonized islands. It normally occurs in a great variety of wetland and scrub habitats, but on some islands it occupies dry rocky habitats with no water.

For rails that feed chiefly on invertebrates, the structure of the vegetation and the nature of the substrate are the most important factors influencing habitat choice. The Virginia rail (*Rallus limicola*) avoids marshes with high stem densities or large amounts of residual vegetation—features that impede movement—whereas vegetation height is not important if adequate overhead cover is present. It needs shallow water and a substrate with a high invertebrate abundance, and is most common in wetlands with 40–70% upright emergent vegetation interspersed with open water, mudflats, or matted vegetation. The buff-spotted flufftail (*Sarothrura elegans*) occupies natural forests and thickets, but also areas dominated by alien vegetation. Its invertebrate food is equally abundant on substrates below exotic vegetation and those below indigenous plants.

Behavior

Most rails are solitary or occur in pairs, family parties, or small groups. The most gregarious species are the coots, most of which associate in large monospecific flocks outside the breeding season. Some gallinules and moorhens also associate in loose flocks when not breeding. The black-tailed native-hen (*Gallinula ventralis*) of Australia may occur in flocks of up to 20,000 birds during its periodic irruptions.

Wetlands and lush grasslands are structurally simple and may be highly productive, with food concentrated in a narrow spatial range. In such conditions it may be possible for males to control territories in which two or more females can breed, relegating less successful males to suboptimal territories, or to none at all. This strategy may apply to the yellow rail and the corncrake, while polyandry in the striped crake may have evolved in response to great variability in breeding conditions and the availability of abundant food in the breeding habitat.

In the promiscuous *Porphyrio* and *Gallinula* species, social structure and mating systems are complex. The common moorhen is normally monogamous, but immatures from earlier broods, and sometimes other mature birds, often help care for chicks. Polyandrous trios and cooperative nesting also occur, while intraspecific brood parasitism is regular. Monogamy prevails in most races of the purple swamphen, but in two races birds often live in communal groups. In New Zealand, stable groups, usually of kin, hold permanent territories and are polygamous, usually with two to seven breeding males, one to two breeding females, and one to seven nonbreeding helpers (offspring from previous matings). Unstable groups are usually non-kin and are promiscuous, with much aggression and many male members, and are largely unsuccessful. Within a stable group mate-sharing is total and multiple paternity prevails. Dominant females lay in a common nest and all group members care for the young. Habitat saturation and a shortage of prime breeding territories appear to be responsible for this breeding strategy.

Agonistic behavior in rails is common and often conspicuous. In the purple swamphen, the position of the tail and wings is important in agonistic display, while differing body postures indicate aggression or anxiety. Moorhens and coots share similar agonistic displays, in which the degree of prominence of the frontal shield is often an important component.

Rails are territorial, many species defending territories only while breeding. Winter feeding territories are maintained by the water rail (*Rallus aquaticus*), the spotted crake (*Porzana porzana*), and the African crake, and this phenomenon is probably more widespread than is known.

Most rails are very vocal, with an extensive repertoire, as is to be expected in birds that inhabit dense cover where visual contact is often very limited and communication by sound is important. Calls include screams, squeals, trills, whistles, whines, hoots, moans, booms, rattles, clicking and ticking notes, snoring noises, humming and buzzing sounds, trumpets, roars, grunts, barks, frog-like croaks, and snake-like hisses; calls of some small species may be very insect-like. The advertising and territorial calls of many species are given in a repetitive series, are often loud, and are given most commonly in the early morning, the evening, and at night.

Most rails normally keep within dense cover and are adept at moving around without causing any noise or disturbance of the vegetation. When alarmed, most run rather than fly, and they can melt quietly and rapidly into cover, compressing the body laterally for easy passage through vegetation. Rails often walk with bobbing head and flicking tail. Tail jerking is used in visual orientation and signaling between conspecific individuals, but in the common moorhen and the purple swamphen it is also directed toward potential predators as an alertness signal and pursuit deterrent.

Many rails are predominantly crepuscular. Some terrestrial and marsh species forage at night as well as by day and it is possible that nocturnal activity is largely confined to species of open habitats where visibility at night is relatively good. Rails that forage in tidal areas are often active during low tides at night. Most rails normally roost singly, in pairs, or in family groups, generally on the ground in dense cover, but sometimes above ground in dense vegetation such as bushes and trees.

Feeding ecology and diet

Rails are characteristically omnivorous, generalized feeders, often opportunistic and able to take advantage of new food sources. In general the most aquatic species, such as the gallinules and coots, are largely herbivorous, while those that inhabit terrestrial and marshy habitats are either omnivorous or take predominantly animal food, at least in the breeding season.

Many rails appear to feed largely on the most abundant foods available at any time. A few species take only a restricted range of prey or plant material, and such specialization is usually a reflection of the limited variety of suitable food available. Thus rails that forage in mangroves feed largely on crabs, examples being the chestnut rail (*Eulabeornis castaneoventris*) and the rufous-necked wood-rail (*Aramides axillaris*).

Invertebrates are the principal diet of many species, and commonly include worms, mollusks, crustaceans, spiders, and insects. Some rails take vertebrate prey, including small fish, amphibians and their tadpoles, small reptiles (lizards, snakes, and turtle eggs and hatchlings), and the eggs and young of other birds, while a few will eat carrion. Forest-



A common moorhen (*Gallinula chloropus*) at its nest in England. (Photo by Roger Wilmshurst. Bruce Coleman Inc. Reproduced by permission.)

dwelling rails probably eat fewer plant foods than those in other habitats.

Many types of plant foods are eaten by rails, including seeds, fruits, shoots, stems and leaves, tubers, bulbs, rhizomes and roots, as well as marine and filamentous algae, fungi, lichens, and ferns. Cultivated plants such as vegetables, cereal and fodder crops, fruit, and taro are taken by some species. Coots are almost entirely herbivorous, but some aquatic insects, mollusks, and crustaceans are taken, and coots will sometimes eat eggs, fish, carrion, duck-food pellets, and even food scraps from campsites.

Although most rails drink fresh water, some species are able to survive on oceanic islands with no fresh water. These rails may drink salt water or may obtain most of their water from their food. Thus the white-throated rail (*Dryolimnas cuvieri*) drinks salt water on Aldabra, and the buff-banded rail (*Gallirallus philippensis*) can exist on islands with no fresh water. Some rails, such as the saltmarsh-dwelling clapper rail, possess well-developed supra-orbital (nasal) glands, which function in the excretion of salt.

Bill size and shape provide a good indication of a rail's foraging habits. Species with long thin bills probe for invertebrate food in shallow water, soft ground, and litter, while those with small, fine bills take small invertebrates and seeds from the substrate, shallow water, and low vegetation. Those



An American coot (*Fulica americana*) feeds its young in southwest Idaho. (Photo by William H. Mullins. Photo Researchers, Inc. Reproduced by permission.)

with straight bills of moderate length and depth take a wide variety of small to large food items, chiefly by probing, gleaning, digging, sifting leaf-litter, stabbing at large prey, and raking in earth and mud. Thick-billed species tear and slice vegetation, and dig or pull up the underground parts of plants.

Some gallinules use the foot to grasp and manipulate food. The purple swamphen uses its bill to pull out emergent plants and then grasps them in the foot while eating the bases.

Only coots regularly dive for food, but coots and *Gallinula* species regularly up-end when feeding. The white-browed crake often feeds while swimming, floating with the neck extended parallel with the surface and reaching out to capture insects.

Some species show seasonal variations in the proportions of animal and plant food taken, and this may reflect seasonal changes in the availability of food, the use of different habitats when birds are on migration or in wintering areas, or the need for a greater consumption of protein in the breeding season to satisfy the requirements for egg-laying. Many species increase their intake of animal food in the spring and summer, and of plant food in the autumn and winter. Most rail chicks, even those of herbivorous species, are fed primarily on animal food.

Reproductive biology

With the exception of some coots, moorhens, and gallinules, little is known about the breeding of most rails. The nest, eggs, and young of 23 species remained undescribed in 2001.

Monogamy is the predominant mating system in the family. This is to be expected because, although rail chicks are precocial or semi-precocial, they need intensive care at an early age, when they are fed, guarded and brooded by their

parents. A non-monogamous mating system occurs in the wild in only five rails: the corncrake (*Crex crex*), the purple swamphen, the common moorhen, the dusky moorhen and the Tasmanian native hen (*Gallinula mortierii*), and in captivity in the yellow rail (*Coturnicops noveboracensis*) and the striped crake (*Aenigmatolimnas marginalis*).

Most species appear to breed seasonally, during the spring and summer in temperate regions and during the wet seasons in the tropics. Most exceptions to this pattern involve tropical or subtropical species that may have extended or ill-defined breeding periods.

Some species may breed throughout the year if conditions remain suitable, examples from Africa being the common moorhen and the red-knobbed coot (*Fulica cristata*). Studies of some rails in southwest Australia have shown that in most species the laying period is correlated with peak rainfall, day length, and temperature. The timing of vegetation development is often important to the initiation of nesting in rails of marshy habitats. Thus in the state of Ohio, peak nest initiation of the common moorhen occurs when vegetation height is 18–40 in (45–100 cm) and its growth rate is greatest. The breeding season of the Tasmanian native-hen is determined by rainfall, as it depends on fresh young plant growth.

Courtship feeding and allopreening are common, and aggressive-looking courtship chases often lead to copulation. In some species the male's courtship display involves bowing, and may involve the display of bold flank patterns or contrastingly colored undertail-coverts. Gallinules, moorhens, and coots show the most complex courtship and mating behavior. In the purple swamphen, courtship usually starts with allopreening but the male may also present aquatic plant material in his bill to the female, and the female solicits copulation by adopting the arch-bow posture. Coots and moorhens share similar components in their sexual displays, including a bowing-and-nibbling ceremony (in which one bird is submissive while the other preens it), a greeting and passing ceremony, and a courtship chase.

Nests are usually concealed in thick ground vegetation, often near or over water, but some species nest in dry areas and some in trees. Nest materials are often gleaned from the vegetation closest to the nest site, and nests are often built by both sexes. The nest is usually cup-shaped, but is domed in some species, including most Laterallus crakes. Nests in grass and emergent vegetation often have surrounding vegetation woven into a concealing canopy over the bowl, while nests in wetlands often have ramps up to the bowl. Some species build nests that float or are attached to aquatic vegetation. The giant coot (Fulica gigantea) and horned coot (Fulica cornuta) build enormous permanent nests of aquatic vegetation which, in the horned coot, is usually placed on a conical mound of stones, up to 13 ft (4 m) in diameter at its base, about 2 ft (60 cm) high and about 3 ft (1 m) in diameter at the top. The structure may weigh about 1.5 tons; each stone weighs up to 1 lb (450 g) and both adults collect stones and carry them to the nest in the bill.

Rail eggs are usually approximately oval, smooth, and fairly glossy. The ground color is white to dark tan, usually blotched or spotted with red-brown, gray, mauve, or black. Clutch size



The giant coot (Fulica gigantea) builds its nest of aquatic vegetation in the puna zone of the Peruvian Andes. (Photo by F. Gohier. Photo Researchers, Inc. Reproduced by permission.)

varies from one to 19 (most frequently five to 10), and dumping or laying by more than one female in the same nest may occur. Incubation is by both sexes in most species, and incubation periods are 13–31 (usually 15–19) days per egg. Hatching may be synchronous or asynchronous.

Rail chicks hatch covered in down and are precocial or semi-precocial, usually leaving the nest after one to three days. Chicks are usually fed bill-to-bill at first and are normally tended by both parents, in some species also by helpers. The fledging period is four to eight weeks but in the giant coot it is about four months. Chicks' legs and feet grow rapidly, reaching full size before the rest of the body, but the growth of the wings is generally much retarded. The young usually become independent as soon as they are fully fledged. First breeding usually occurs when the birds reach their first year.

One or two broods are usually reared, and many species will re-lay several times after failure. Nesting success varies widely in the few species for which figures are available, often depending on factors such as food supply, predation, and flooding. In general, early nests are often more successful than later ones. In North American species, nesting success is given as: 10–100% for the clapper rail, 81% for the king rail, 53% for the Virginia rail, 49–91% for the purple gallinule and over 80% for the American coot (*Fulica americana*). In many species hatching success is often high, whereas chick survival may be much lower.

Conservation status

The IUCN Red List of birds, published in 2000, shows that, of the 134 living rail species, 33 (almost 25%) are Threat-

ened, including four that are Critically Endangered, 12 Endangered, 16 Vulnerable and one, the Guam rail (*Gallirallus owstoni*) Extinct in the Wild. A further nine species are listed as Near Threatened and four as Data Deficient. Thus the survival of 62 species (46%) of rails gives cause for concern.

Of 20 rail taxa (16 species and four subspecies) that have become extinct since 1600, 17 (85%) were flightless. The extinction of these rails provides a classic example of the particular vulnerability of island endemics. The principal causes of extinctions among island rails have been introduced mammalian predators such as cats, dogs, rats, mongooses, and pigs, indiscriminate hunting by the first people to visit the islands, and habitat destruction by introduced goats, rabbits, and fire. Introduced predators have probably been responsible for more extinctions than any other cause. Several extant island species are still at risk from the possible accidental introduction of mammalian predators to their islands.

Habitat destruction does not seem to be a critical problem for any threatened island rail at present, but is certainly a major threat to many continental species. For example, the plainflanked rail (*Rallus wetmorei*) has a very restricted distribution in coastal Venezuela, where its mangrove and lagoon habitats are being destroyed by housing development, oil exploration, and diking.

Many rails are probably undergoing a continual population decline, largely through habitat loss. The wholesale and enormous destruction of indigenous forests is a severe threat to some species, especially in southeast Asia and South America. Palustrine wetlands are under threat worldwide and are disappearing at an alarming rate. Small crake species, such as the black rail, which inhabit the edges of marshes,

are generally more threatened by habitat destruction than are other rails, which live in the interiors of marshes or alongside open water.

Great efforts have been made to save some threatened species, involving captive breeding and reintroduction of birds into the wild, habitat management, and predator control. The takahe and the Guam rail are two good examples.

Significance to humans

Rails have had little association with humans and have no significant place in art, literature, or legend. This is presumably because most rails are unobtrusive, cryptic, and hard to see; many people are not even aware that they exist.

However, one rail did excite the interest of ancient civilizations. The purple swamphen is depicted climbing on papyrus stems in the Egyptian wall paintings at Medum. The Greeks and Romans refrained from eating the "Porphyriõn" but imported the birds and placed them in palaces and temples, where they walked around freely as worthy guests by virtue of the nobleness of their bearing, the graciousness of their nature, and the beauty of their plumage.

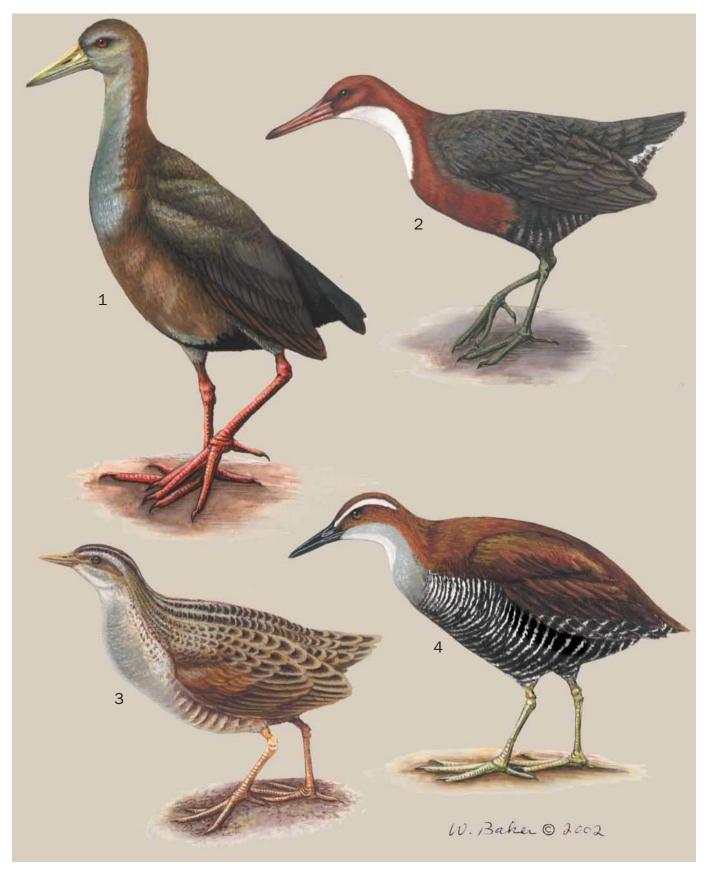
Local superstitions about rails include those held by some African peoples to explain the strange calls heard from forest or marsh. The song of the buff-spotted flufftail, one of the most evocative sounds of the African rainforest, is sometimes believed to be the wail of a banshee, or the sound of a chameleon mourning for its mother, whom it killed in an argument over some mushrooms. The extinct Kosrae crake

(*Porzana monasa*) of the Caroline Islands remains a legend among the islanders, since it was regarded as a sacred bird before the arrival of Christian missionaries.

In the Cocos-Keeling Islands, the buff-banded rail (Galli-rallus philippensis) is apparently used to hatch chicken eggs in place of domestic hens. In Bangladesh the watercock (Gallicrex cinerea) is used as a fighting bird, as in cockfighting. In South America the giant wood-rail (Aramides ypecaha) is often kept in captivity and individuals are sold in village shops.

Rails have long been hunted for food and sport in many parts of the world and the Eurasian coot (Fulica atra) is still shot in Mediterranean countries for these purposes. In Europe the corncrake (Crex crex) was commonly hunted for food in the past, and is still caught in Egypt during the ancient practice of quail netting. In the United States the larger rails may still be hunted legally and in Audubon's time soras (Porzana carolina) and clapper rails (Rallus longirostris) were heavily hunted. People in Africa, Asia, and South America often trap forest rails, while marsh rails are widely hunted in Asia. Rail eggs are regarded as highly palatable, and common moorhens were formerly extensively exploited for their eggs in Asia. The giant coot is also exploited for its eggs.

The larger rails may occasionally damage crops or pasture. The Tasmanian native-hen has been falsely accused of this, and was at one stage declared vermin. The purple swamphen is said to do considerable damage to growing rice crops in India and Bangladesh, but such damage must be highly localized. The purple gallinule is regarded as a pest in rice fields in some Neotropical areas.



1. Giant wood-rail (*Aramides ypecaha*); 2. White-throated rail (*Dryolimnas cuvieri*); 3. Corncrake (*Crex crex*); 4. Guam rail (*Gallirallus owstoni*). (Illustration by Wendy Baker)



1. Talaud rail (*Gymnocrex talaudensis*); 2. Spotted rail (*Pardirallus maculatus*); 3. Laysan rail (*Porzana palmeri*); 4. Striped crake (*Aenigmatolimnas marginalis*). (Illustration by Wendy Baker and Amanda Humphrey)



1. Forbes's forest-rail (*Rallina forbesi*); 2. Black rail (*Laterallus jamaicensis*); 3. Inaccessible rail (*Atlantisia rogersi*); 4. Buff-spotted flufftail (*Sarothrura elegans*). (Illustration by Wendy Baker)



1. Giant coot (Fulica gigantea); 2. White-breasted waterhen (Amaurornis phoenicurus); 3. Chestnut rail (Eulabeornis castaneoventris); 4. Takahe (Porphyrio mantelli). (Illustration by Amanda Humphrey and Wendy Baker)

Species accounts

Buff-spotted flufftail

Sarothrura elegans

SUBFAMILY

Rallinae

TAXONOMY

Gallinula elegans A. Smith, 1839, Durban, South Africa. Two subspecies.

OTHER COMMON NAMES

French: Râle ponctué; German: Tropfenralle; Spanish: Polluela Elegante.

PHYSICAL CHARACTERISTICS

6–6.7 in (15–17 cm); 1.4–2 oz (39–61 g). Male has orange-chestnut foreparts and buff-spotted upperparts; female golden brown with buff-spotted upperparts and barred underparts. Juvenile gray-brown.

DISTRIBUTION

S. e. reichenovi: Guinea east to Democratic Republic of Congo (Zaire) and Uganda, south to north Angola; S. e. elegans: southern Sudan and Ethiopia south to South Africa.

HABITAT

Forest, thickets, and abandoned cultivated areas.

BEHAVIOR

Territorial when breeding. Diurnal, but breeding males sing mostly at night, giving a loud, repeated, hollow hoot "oooooo," sometimes for 12 hours or more. Some populations sedentary, others have seasonal movements.



FEEDING ECOLOGY AND DIET

Takes terrestrial invertebrates.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds during rains. Lays three to five white eggs in domed nest of dead leaves or grass on ground. Incubation 15–16 days; young independent at 19–21 days.

CONSERVATION STATUS

Not threatened. Widespread, locally common. Probably holds its own because it colonizes degraded forest habitats and exotic vegetation.

SIGNIFICANCE TO HUMANS

Its hooting vocalization has given rise to many local legends. ◆

Forbes's forest-rail

Rallina forbesi

SUBFAMILY

Rallinae

TAXONOMY

Rallicula forbesi Sharpe, 1887, Owen Stanley Range, New Guinea. Four subspecies recognized.

OTHER COMMON NAMES

English: Forbes's chestnut rail; French: Râle de Forbes; German: Nymphenralle; Spanish: Polluela de Forbes.



PHYSICAL CHARACTERISTICS

8–10 in (20–25 cm); 3–3.2 oz (87–91 g). Foreparts chestnut; rear upperparts and wings blackish-brown, spotted buff in female; rear underparts barred. Juvenile duller and browner.

DISTRIBUTION

R. f. steini: central New Guinea; R. f. parva: northeastern New Guinea (Adelbert range); R. f. dryas: northeastern New Guinea (Huon Peninsula); R. f. forbesi: southeastern New Guinea.

HABITAT

Montane forest.

BEHAVIOR

Poorly known and secretive

FEEDING ECOLOGY AND DIET

Invertebrates, small vertebrates, and seeds.

REPRODUCTIVE BIOLOGY

Roosting nest a football-sized domed structure of leaf skeletons and moss on the ground. One breeding nest was a platform in a tree. Eggs probably four to five, white.

CONSERVATION STATUS

Not threatened. Not uncommon locally in the east, probably scarce or rare in west.

SIGNIFICANCE TO HUMANS

Regularly hunted for food. ◆

Black rail

Laterallus jamaicensis

SUBFAMILY

Rallinae

TAXONOMY

Rallus jamaicensis Gmelin, 1789, Jamaica. Four subspecies recognized.

OTHER COMMON NAMES

French: Râle noir; German: Schieferralle; Spanish: Polluela Negruzca.

PHYSICAL CHARACTERISTICS

4.7–6 in (12–15 cm); 0.7–1.6 oz (20.5–46 g). Small and dark, nape to mantle orangy- to reddish brown, upperparts and rear underparts barred or spotted white. Undertail-coverts cinnamon in two races. Female paler on foreparts; juvenile browner, plainer. Hatchlings covered with black down.

DISTRIBUTION

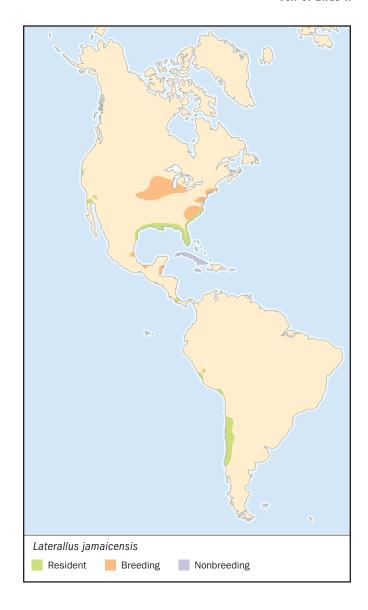
L. j. coturniculus: California; L. j. jamaicensis: eastern United States and eastern Central America, winters from coastal southern and eastern United States to Guatemala and Greater Antilles; L. j. murivagans: coastal central Peru; L. j. tuerosi: lower Junin, Peruvian Andes; L. j. salinasi: southern Peru, central Chile and western Argentina

HABITAT

Marshes and wet grassland.

BEHAVIOR

Territorial when breeding. Some populations migratory, others sedentary. Male's breeding "kic-kic-kerr" call distinctive.



FEEDING ECOLOGY AND DIET

Eats mainly small invertebrates; also fish, tadpoles, and seeds.

REPRODUCTIVE BIOLOGY

Monogamous; occasional polygyny possible. Breeds in summer in United States, during rains in South America. Nest a bowl of grasses or rushes with a woven canopy, low in marsh vegetation. Eggs two to 13; color is buffy to pinkish-white, with brown speckling concentrated at larger end. Incubation 17–20 days.

CONSERVATION STATUS

L. j. tuerosi is Endangered and is known from only two sites at lower Junin, where it is at risk from pollution and water level fluctuations. Other races are Lower Risk/Near Threatened. Most United States populations declined drastically in twentieth century.

SIGNIFICANCE TO HUMANS

None known. ◆

Guam rail

Gallirallus owstoni

SUBFAMILY

Rallinae

TAXONOMY

Hypotaenidia owstoni Rothschild, 1895, Guam. Monotypic.

OTHER COMMON NAMES

French: Râle de Guam; German: Guamralle; Spanish: Rascón de Guam.

PHYSICAL CHARACTERISTICS

11 in (28 cm); 6–10.7 oz (170–303 g). Nearly flightless. Upperparts olive-brown; foreneck to breast gray; underparts and remiges barred black and white. Juvenile has less gray; chick covered with black down.

DISTRIBUTION

Formerly on Guam, Mariana Island. Reintroduced to Rota, northern Mariana Island, and Guam.

HABITAT

Forest, woodland, scrub, grassland, and agriculture.

BEHAVIOR

Territorial; secretive and wary.

FEEDING ECOLOGY AND DIET

Opportunistic and omnivorous, taking mollusks, insects, geckos, seeds, fish, and carrion. Often forages at edges of fields and roads.



REPRODUCTIVE BIOLOGY

Monogamous. Breeds all year. Nest a cup of grass, on dry ground in dense grass; eggs one to four (usually three to four); white to pinkish in color with small spots of pink or blue concentrated at the large end. Incubation 19 days; young sexually mature at 16 weeks.

CONSERVATION STATUS

Formerly abundant throughout Guam, despite being hunted; 1960s population estimated at 80,000. After 1968 it declined rapidly due to predation by the accidentally introduced brown tree snake (*Boiga irregularis*), and by 1987 it was Extinct in the Wild. It survives in captive-breeding facilities on Guam and at 14 zoos in the United States (about 180 birds in 1999). From 1987 birds were introduced to the snake-free island of Rota, where they bred from 1999. It was reintroduced to Guam in 1998, into a protected area.

SIGNIFICANCE TO HUMANS

None known. ◆

White-throated rail

Dryolimnas cuvieri

SUBFAMILY

Rallinae

TAXONOMY

Rallus cuvieri Pucheran, 1845, Mauritius. Two subspecies recognized.

OTHER COMMON NAMES

French: Râle de Cuvier; German: Cuvierralle; Spanish: Rascón de Cuvier.



PHYSICAL CHARACTERISTICS

12–13 in (30–33 cm); 5–8 oz (138–223 g) (aldabranus), 9–9.7 oz (258–276 g) (cuvieri). Orangy- to reddish brown foreparts, prominent white chin and throat, greenish olive upperparts, barred flanks and white lateral undertail-coverts. Juvenile duller and browner.

DISTRIBUTION

D. c. cuvieri: Madagascar; D. c. aldabranus Aldabra Atoll.

HABITAT

Forest, marsh, and mangroves (cuvieri); coral scrub (aldabranus).

BEHAVIOR

Permanently territorial. Often confiding. Vocal, with grunts, clicks, squeals, and a song of loud whistles; often calls at night. The Aldabra race is flightless.

FEEDING ECOLOGY AND DIET

Eats mainly invertebrates; also turtle eggs and hatchlings, and scraps at campsites (Aldabra).

REPRODUCTIVE BIOLOGY

Monogamous; pair bond permanent. Breeds during rains in Madagascar (October through March); on Aldabra lays in Dec. Nest a bowl of leaves and grass on the ground, or a few twigs and leaves among rocks. Eggs three to six (usually three to four); young independent at 12–15 weeks.

CONSERVATION STATUS

Not threatened. Nominate race common. In 2001 3,500–8,000 *aldabranus* individuals occurred naturally on three islands. Reintroduced to Picard Island in 1999, where it breeds and has a predicted population of 2,500 birds. Its survival depends on preventing the spread of feral cats and the introduction of populations to other islands to safeguard against extinction by catastrophic events.

SIGNIFICANCE TO HUMANS

None known. ◆

Corncrake

Crex crex

SUBFAMILY

Rallinae

TAXONOMY

Rallus crex Linnaeus, 1758, Sweden. Monotypic.

OTHER COMMON NAMES

French: Râle des genêts; German: Wachtelkönig; Spanish: Guión de Codornices.

PHYSICAL CHARACTERISTICS

10.6–12 in (27–30 cm); 4.6–7.4 oz (129–210 g). Streaked upperparts, tawny upperwing-coverts, barred flanks and blue-gray face, foreneck, and breast. Juvenile duller, with no gray.

DISTRIBUTION

Breeds in Europe and central Asia, east to western China and central Siberia; winters in Africa, mainly from Democratic Republic of Congo (Zaire) and southern Tanzania south to eastern South Africa.



HABITAT

Breeds mainly in grass meadows; winters in grassland and savanna.

BEHAVIOR

Most active at dawn and dusk. Breeding male's rasping "krekkrek" call given all night.

FEEDING ECOLOGY AND DIET

Many invertebrates; also seeds and grass blades. Normally forages within cover.

REPRODUCTIVE BIOLOGY

Serial polygyny regular, males mating with two or more females. Breeds April and August. Nest a cup of vegetation on the ground in dense vegetation. Eggs six to 14 (usually eight to 12); incubation 16–20 days, by female only; chicks independent at 10–20 days, fledged at 34–38 days. One to two broods per season; breeding success low on agricultural land.

CONSERVATION STATUS

In 1999 a total of 1.7–3 million singing males estimated. Western European populations declined rapidly during the twentieth century due to changing grassland management. Considered Vulnerable because of the potential for similar widespread land-use changes in its eastern European strongholds.

SIGNIFICANCE TO HUMANS

Some migrating birds are trapped for food. ◆

Inaccessible rail

Atlantisia rogersi

SUBFAMILY

Rallinae

TAXONOMY

Atlantisia rogersi Lowe, 1923, Inaccessible Island, Tristan da Cunha. Monotypic.

OTHER COMMON NAMES

French: Râle atlantis; German: Atlantisralle; Spanish: Rasconcillo de Tristan da Cunha.

PHYSICAL CHARACTERISTICS

5–6 in (13–15.5.cm); 1.2–1.7 oz (34–49 g). Smallest flightless bird. Male gray-black, with dark brown back and wings; narrow white barring on upperwings and underparts. Female paler, browner; juvenile black.

DISTRIBUTION

Inaccessible Island.

HABITAT

All island vegetation types from tussock grass to boulder beaches.

BEHAVIOR

Territorial, with small territories 0.025–0.1 acres (0.01–0.04 ha). Partly subterranean, using tunnels through vegetation and cavities under boulder beaches.

FEEDING ECOLOGY AND DIET

Eats invertebrates; also seeds and berries.

REPRODUCTIVE BIOLOGY

Monogamous; pair bond permanent. Lays October through January. Nest domed, on ground in dense vegetation; of dead



grass or sedges. Eggs: two. May retain immature plumage for two years, suggesting delayed maturity. Fertility possibly low; chick mortality high.

CONSERVATION STATUS

Abundant, with a population of 8,400–10,000 birds in 1992; possibly at carrying capacity. Vulnerable: permanently at risk from the accidental introduction of predators and other chance events.

SIGNIFICANCE TO HUMANS

None known.

Giant wood-rail

Aramides ypecaha

SUBFAMILY

Rallinae

TAXONOMY

Rallus ypecaha Vieillot, 1819, Paraguay. Monotypic.

OTHER COMMON NAMES

French: Râle ypécaha; German: Ypecaharalle; Spanish: Cotara Ipacaá.

PHYSICAL CHARACTERISTICS

16–19.3 in (41–49 cm); 1.2–1.9 lb (565–860 g). Olive-brown and vinous-chestnut, with gray face and foreneck, and black rear body. Juvenile paler and duller.



DISTRIBUTION

Eastern and southeastern Brazil, Bolivia, Paraguay, Uruguay, and northeastern Argentina.

HABITAT

Marshes, swamps, fields, and gallery forest.

BEHAVIOR

Often bold and inquisitive. Stance upright, gait elegant. Solitary, but congregates in the evening for a communal display, rushing around with a powerful chorus of screams, shrieks, and wheezes.

FEEDING ECOLOGY AND DIET

Arthropods, mollusks, seeds, and fruit; forages in early morning and evening.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds September through February (Uruguay). Nest of grass and stems, on ground or in trees, usually near water. Eggs: four to seven. In captivity, incubation 24 days; young independent at eight to nine weeks.

CONSERVATION STATUS

Not threatened. Formerly locally common to abundant, it may have suffered less from habitat destruction than its forest-dwelling congeners.

SIGNIFICANCE TO HUMANS

Often kept in captivity. Hunted in Argentina. •

Talaud rail

Gymnocrex talaudensis

SUBFAMILY

Rallinae

TAXONOMY

Gymnocrex talaudensis Lambert, 1998, Karakelong I., Talaud Archipelago.

OTHER COMMON NAMES

French: Râle de Talaud; German: Talaudralle; Spanish: Cotara.

PHYSICAL CHARACTERISTICS

Approximately 13–14 in (33–35 cm). Chestnut foreparts, olivegreen upperparts, tawny remiges, blackish underparts and tail, yellow bill and legs, and white facial skin. Only the holotype is described.

DISTRIBUTION

Karakelong Island, Talaud Archipelago, Indonesia.

HABITAT

Long wet grass and scrub, including at forest edges.

BEHAVIOR

Extremely shy; seen only once in the four years after its discovery.

FEEDING ECOLOGY AND DIET

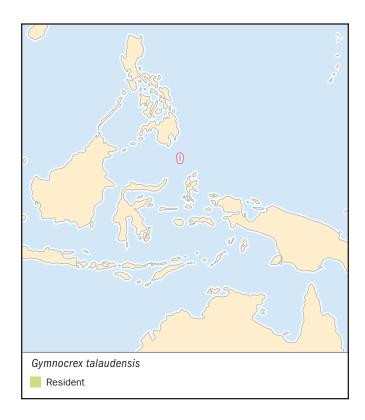
Snails and beetles.

REPRODUCTIVE BIOLOGY

Not known.

CONSERVATION STATUS

Endangered, with a very small range; faces habitat loss and degradation.



SIGNIFICANCE TO HUMANS

Trapped for food. ♦

White-breasted waterhen

Amaurornis phoenicurus

SUBFAMILY

Rallinae

TAXONOMY

Gallinula phoenicurus Pennant, 1769, Sri Lanka. Four subspecies recognized.

OTHER COMMON NAMES

French: Râle à poitrine blanche; German: Weißbrust-Kielralle; Spanish: Gallineta Pechiblanca.

PHYSICAL CHARACTERISTICS

11–13 in (28–33 cm); 5.8–11.6 oz (165–328 g). Dark upperparts, white face and underparts, tawny-rufous rear underparts, and yellow bill and legs. Juvenile duller. Chick black and fluffy.

DISTRIBUTION

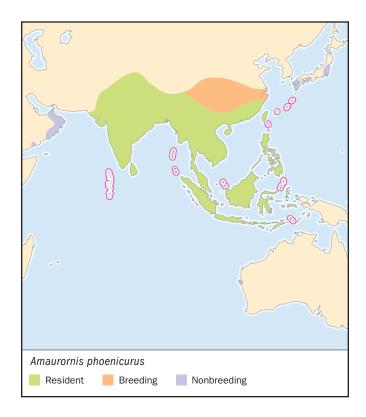
A. p. phoenicurus: Pakistan and India east to Japan, and south through southeastern Asia to Sundas; northern populations winter to the south, reaching Arabia; A. p. insularis: Andaman and Nicobar Island; A. p. midnicobaricus: central Nicobar Island; A. p. leucomelanus: Sulawesi, western Moluccas, Lesser Sundas.

HABITAT

Marshes, grass, forest, scrub, and mangroves.

BEHAVIOR

Not particularly shy. Perches, climbs, and swims well. Territorial when breeding. Characteristic calls include roars, grunts, cackles and croaks; often vocal at night.



FEEDING ECOLOGY AND DIET

Takes invertebrates, small fish and some plant material. Forages on land and in water.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds all months, mainly during rains. Nest a cup of twigs, stems, and leaves, close to the ground and near water. Eggs three to nine; color is dull brownish to white/gray with reddish spots and marks. Incubation 20 days by both parents.

CONSERVATION STATUS

Not threatened. Common to local over much of its range, which is expanding northeast. Uses humanmade habitats, even in built-up areas.

SIGNIFICANCE TO HUMANS

None known. ◆

Laysan rail

Porzana palmeri

SUBFAMILY

Rallinae

TAXONOMY

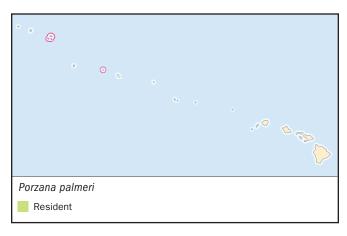
Porzanula palmeri Frohawk, 1892, Laysan I.

OTHER COMMON NAMES

French: Marouette de Laysan; German: Laysansumpfhuhn; Spanish: Polluela de Laysan.

PHYSICAL CHARACTERISTICS

5.9 in (15 cm). Flightless. Light brown, streaked darker on upperparts, ashy-gray from face to breast; some white flank markings. Juvenile buff on underparts.



DISTRIBUTION

Recently extinct; occurred on northwestern Hawaiian Islands; naturally on Laysan Island, introduced to Midway Atoll.

HABITAT

Tussock grass and scrub thickets.

BEHAVIOR

Was active, restless, pugnacious and presumably territorial. Showed little fear of humans. Called communally after dusk, with a warbling or rattling song.

FEEDING ECOLOGY AND DIET

Ate principally insects; also spiders, birds' eggs, carrion, and some plant material. Approached people for food.

REPRODUCTIVE BIOLOGY

Apparently monogamous. Bred mainly April through July. Nest a cup or ball of grass in shelter of tussock or other vegetation. Eggs two to three.

CONSERVATION STATUS

Formerly common on Laysan I.; habitat destruction by introduced rabbits led to its extinction between 1923 and 1936. Introduced to two islands on the Midway Atoll in 1891 and 1910, it thrived but was exterminated by rats that came ashore from a U.S. Navy landing craft in 1943.

SIGNIFICANCE TO HUMANS

None known. ◆

Striped crake

Aenigmatolimnas marginalis

SUBFAMILY

Rallinae

TAXONOMY

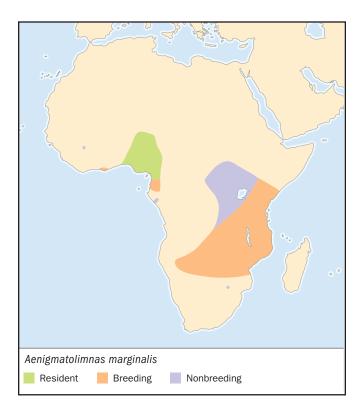
Porzana marginalis Hartlaub, 1857, Gabon. Monotypic.

OTHER COMMON NAMES

French: Marouette rayée; German: Graukehl-Sumpfhuhn; Spanish: Polluela Culirroja.

PHYSICAL CHARACTERISTICS

7–8.3 in (18–21 cm); 1.5–2.2 oz (41.5–61 g). Male dark brown with white streaks on upperparts; anterior underparts pale cinnamon; rear underparts orangy- to reddish brown. Female has gray foreparts; juvenile duller and plainer.



DISTRIBUTION

Ivory Coast east to Cameroon and south to Congo; eastern Democratic Republic of Congo (Zaire) to Kenya and south to northeast South Africa. In south, largely a wet season visitor, retreating towards equatorial regions after breeding.

HABITAT

Seasonally inundated grassland, pans, and marsh edges.

BEHAVIOR

Diurnal and secretive. Territorial when breeding; female gives ticking advertising call, often at night.

FEEDING ECOLOGY AND DIET

Invertebrates, small fish, and frog tadpoles. Forages in grass, mud, and shallow water.

REPRODUCTIVE BIOLOGY

In captivity is sequentially polyandrous, female mating with two or more males. Breeds mainly during rains. Nest a bowl of grass or sedges in vegetation over water. Eggs: four to five. Incubation: 17–18 days, by male only; young cared for by male; fledge at 28 days; one to three broods per season.

CONSERVATION STATUS

Possibly uncommon throughout range; sometimes locally common after good rains.

SIGNIFICANCE TO HUMANS

None known. ◆

Spotted rail

Pardirallus maculatus

SUBFAMILY

Rallinae

TAXONOMY

Rallus maculatus Boddaert, 1783, Cayenne, French Guiana. Two subspecies recognized.

OTHER COMMON NAMES

French: Ràle tacheté; German: Fleckenralle, Spanish: Rascón Overo.

PHYSICAL CHARACTERISTICS

10–12.6 in (25–32 cm); 4.6–7.7 oz (130–219 g). Long-billed; blackish brown, heavily streaked white on foreparts and barred on flanks; undertail-coverts white; bill yellow-green with red base. Juvenile duller; three morphs: dark morph (almost plain), pale morph (pale underparts), and barred morph (barred underparts).



DISTRIBUTION

P. m. insolitus: Mexico to Costa Rica; P. m. maculatus: Cuba, West Indies, and from Colombia and Ecuador to eastern Brazil and northern Argentina.

HABITAT

Marshes, swamps, and wet grassland.

REHAVIOR

Generally secretive. Gives a distinctive rasping screech "g'reech" and gruff pumping notes. Territorial when breeding.

FEEDING ECOLOGY AND DIET

Invertebrates; also small fish and some plant material. Forages in mud or shallow water.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds mainly June through September. Nest a cup of grass or rushes, low in marsh vegetation, often over water. Eggs two to seven.

CONSERVATION STATUS

Not threatened, though poorly known and overlooked; may be locally common.

SIGNIFICANCE TO HUMANS

None known. ◆

Chestnut rail

Eulabeornis castaneoventris

SUBFAMILY

Rallinae

TAXONOMY

Eulabeornis castaneoventris Gould, 1844, Flinders R., Gulf of Carpentaria. Two subspecies recognized.

OTHER COMMON NAMES

French: Râle à ventre roux; German: Mangroveralle; Spanish: Cotara Australiana.

PHYSICAL CHARACTERISTICS

17.3–20.5 in (44–52 cm); 1.2–2.0 lb (550–910 g). Thickset, with gray head and pinkish brown underparts. Three color morphs, with upperparts olive, chestnut, or olive-brown. Juvenile has duller bare parts.

DISTRIBUTION

E. c. castaneoventris: northern coast of Australia; E. c. sharpei: Aru Island.

HABITAT

Dense mangroves.

BEHAVIOR

Diurnal and nocturnal, according to tidal cycle. Shy, secretive, and alert. Has a strutting walk; runs very swiftly. Gives a characteristic harsh screech. Territorial when breeding.

FEEDING ECOLOGY AND DIET

Eats mainly crabs; also other invertebrates. Uses stones as anvils to break shells of hermit crabs.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds September through February. Nest a bulky platform of sticks, grass, leaves, bark and seaweed, in mangroves. Eggs four to five young fledged at nine weeks.



CONSERVATION STATUS

Not threatened. Patchily recorded; possibly overlooked. Probably not uncommon locally.

SIGNIFICANCE TO HUMANS

None known.

Takahe

Porphyrio mantelli

SUBFAMILY

Rallinae

TAXONOMY

Notornis mantelli Owen, 1848, Waingongoro, North Island, New Zealand. Nominate race of North Island recently extinct, may merit species status; one extant race *P. m. hochstetteri*.

OTHER COMMON NAMES

French: Talève takahé; German: Takahe; Spanish: Calamón Takahe.

PHYSICAL CHARACTERISTICS

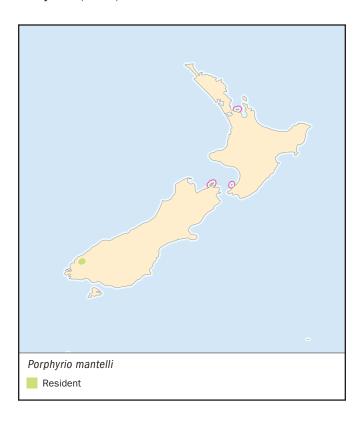
24.8 in (63 cm); 4–9 lb (1.8-4.2 kg). Flightless; thickset, with massive red bill, and purple and green plumage; undertail-coverts white. Juvenile brownish-gray. Chick has black fluffy down and black bill that turns red in the adult stage.

DISTRIBUTION

Fiordland, South Island, New Zealand; also introduced to four nearshore islands.

HABITAT

Alpine tussock grassland, scrub and beech forest (Fiordland); pastures (islands).



BEHAVIOR

Strongly territorial; permanent territories 5–148 acres (2–60 ha), much smaller on islands. Shy; normally has slow, deliberate walk but runs quickly. During winter snow, descends from grassland to forest or scrub up to 6.2 miles (10 km) away.

FEEDING ECOLOGY AND DIET

Eats leaf bases of alpine grasses; in winter also seeds and fern rhizomes. On islands eats introduced grasses.

REPRODUCTIVE BIOLOGY

Breeds mainly October through December. Nest a bowl of grass on ground. Eggs one to three (usually two); pale buff color with blotches of mauve and brown; incubation 29–31 days. Young dependent on adults for food for four months. Age of first breeding two years. Survival to one year 27–71%; survival on islands 89%.

CONSERVATION STATUS

"Rediscovered" in 1948; some translocated to islands in 1984–1991. Captive-bred birds are released into all populations. Endangered, with a very small population (100–160 birds from 1980 to 2000 in Fiordland; 55 adults on islands in 1998). Island populations breed successfully.

SIGNIFICANCE TO HUMANS

Possibly hunted widely in the past. •

Giant coot

Fulica gigantea

SUBFAMILY

Rallinae

TAXONOMY

Fulcia [sic] gigantea Eydoux & Souleyet, 1841, Peru. Monotypic.

OTHER COMMON NAMES

French: Foulque géante; German: Riesenbläßhuhn; Spanish: Focha gigante.

PHYSICAL CHARACTERISTICS

19–23 in (48–59 cm); 4.5–5.3 lb (2.02–2.4 kg). Heavy-bodied, with small head and knobs above eyes. Dark slate-gray with white on undertail-coverts. Bill and shield white, yellow and red; legs red. Juvenile dark dull gray, with paler underparts and dark bare parts. Adults normally too heavy to fly.

DISTRIBUTION

Andes of central Peru, Bolivia, north Chile, and northwestern Argentina.

HABITAT

Ponds and lakes in highlands of puna zone.

BEHAVIOR

Permanently territorial. Quite confident unless persecuted.



FEEDING ECOLOGY AND DIET

Vegetarian, taking mostly aquatic vegetation; also grazes on shore. Feeds from water surface, up-ends, occasionally dives.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds all year, peaking in winter. Nests in water c. 3 ft (1 m) deep; nest permanent; of aquatic vegetation, often resting on bottom of lake and 3 ft (1 m) wide and up to 10 ft (3 m) long at waterline, projecting up to 20 in (50 cm)

above water. Eggs three to seven; young fed until two months old; fledge at four months.

CONSERVATION STATUS

Locally scarce to common. In 1998 considered Vulnerable in Chile

SIGNIFICANCE TO HUMANS

Many eggs are taken by people at some sites. ◆

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Barry Taylor, PhD

Sungrebes (Heliornithidae)

Class Aves
Order Gruiformes
Suborder Heliornithes
Family Heliornithidae

Thumbnail description

Medium-sized aquatic birds with long neck, sharply pointed bill, short legs, and brightly colored, lobed (rounded) toes; sexes differ in head and neck plumage

Size

10.2–23.2 in (26–59 cm); 0.26–1.9 lb (120–880 g)

Number of genera, species

3 genera; 3 species

Habitat

Thickly vegetated margins of rivers, lakes, and swamps

Conservation status Vulnerable: 1 species

Distribution

Central and South America, sub-Saharan Africa, south and southeast Asia

Evolution and systematics

On the basis of skeletal and muscular characteristics, the family Heliornithidae is included in the Gruiformes, but its relationships to other families within the order are unclear. Similarities in superficial features and feather lice suggest a close link with the Rallidae, but there are also strong superficial resemblances to other waterbird families not considered closely related, especially the grebes (Podicipedidae). DNA-DNA hybridization suggests that the closest relative of the sungrebe (Heliornis fulica) may be the limpkin (Aramus guarauna) but material from the other sungrebe species has not been studied.

The family contains three monospecific genera. Similarities between the masked finfoot (*Heliopais personata*) and the African finfoot (*Podica senegalensis*), and differences between these species and the sungrebe, have led to the proposed separation of the sungrebe into the subfamily Heliornithinae and the other species into the subfamily Podicinae.

Physical characteristics

Sungrebes have a long neck; slender body; sharp pointed bill; brightly colored feet with lobed toes and sharp claws; and a long, broad tail. The African finfoot has a claw on the mobile first digit of each wing, which may be used when climbing. It also has stiffened rectrices and often swims with the tail spread flat on the water. This feature may increase maneuverability in water or on land. The masked finfoot has less stiffening and the sungrebe none.

The legs and feet are brightly colored: orange in the African finfoot, pea green in the masked finfoot, and yellow with

black stripes in the sungrebe. Bill colors are also bright. All species have predominantly brown upperparts (spotted white in the African finfoot), a patterned head and neck with a white stripe down the side of the neck, and white underparts (variably barred with brown in the African finfoot). The very dark race *Podica senegalensis camerunensis* of the African finfoot lacks spotting on the upperparts and white on the head and neck.

In all species the sexes differ somewhat in the head and neck plumage pattern. The African finfoot varies in size, both geographically and sexually (males may be 25% larger than females).

Distribution

The family is distributed across three continents. The African finfoot is widespread in sub-Saharan Africa, except in the arid northeast and southwest, while the sungrebe occurs widely in Central America and northern South America. The masked finfoot ranges from Bangladesh and northeast India to Southeast Asia, the Malay Peninsula, and Sumatra. This wide geographic distribution suggests an ancient lineage, while similarities among the widely separated species suggest that the family formerly had a wider and more continuous distribution.

Habitat

All species require water with fringing, dense cover. Habitats range from coastal creeks and mangrove swamps to mountain streams up to about 6,600 ft (2,000 m) above sea level. The birds may inhabit fast-flowing streams, but most often

Family: Sungrebes Vol. 9: Birds II



This sungrebe (*Heliornis fulica*) is well camouflaged in its habitat. (Photo by R. & N. Bowers/VIREO. Reproduced by permission.)

they occur on still or slow-moving water at ponds, lakes, dams, estuaries, rivers, and streams. They are rarely found far from shoreline cover, which may be woody, with overhanging trees or bushes, or emergent. African finfoot are sometimes found on water adjacent to bare rocks. Other habitats include flooded rainforests, papyrus swamps, and reedbeds with woody vegetation.

Behavior

Members of the sungrebe family are usually recorded singly, in pairs, and in family groups; and probably permanently territorial. Sungrebe species are most active in the early morning and the evening and are usually very shy, skulking, and elusive. The birds keep close to cover when swimming, and when disturbed, they seek fringing cover or freeze with the head lowered and the body submerged. Sungrebes swim well, with exaggerated backward and forward movements of the head and neck, but these species also move nimbly on land, with the body carried quite erect, climbing into trees and bushes to roost.

Vocalizations are rarely heard. The African finfoot makes a booming sound when breeding, the masked finfoot utters a bubbling call, and the sungrebe has an "eeyooo" territorial call.

Although no species is known to be regularly migratory, newly available waterbodies are colonized quite rapidly, and vagrancy is recorded in the sungrebe and the masked finfoot. The latter species may be a passage migrant and winter visitor in Thailand and is possibly a winter visitor to the Malay Peninsula and Sumatra.

Feeding ecology and diet

All species eat predominantly insects, especially adult and larval midges, mayflies, and dragonflies but also grasshoppers, flies, and beetles. Mollusks are frequently taken, and crustaceans (shrimps, crabs, and prawns), worms, millipedes, and spiders are recorded in their diet. Frogs, tadpoles, small fish, and small amounts of seeds and leaves are eaten.

Much food is taken from the water surface. Some items are picked from rocks and fringing or overhanging vegetation, with birds sometimes jumping out of the water to take prey. They also forage on land, especially along banks.

Reproductive biology

Sungrebes are monogamous and usually breed when water levels are high. Courtship in the African finfoot involves one bird raising and opening its wings alternately while swimming, while the other bird makes a snapping sound from cover. Courting sungrebes swim in counter circles with lowered necks and half-raised wings.

The nest is a shallow bowl of sticks, twigs, grass, and reeds lined with dead leaves and usually built in thick vegetation over water, especially on clumps of debris caught in branches after floods. Clutch size is two to three eggs in sungrebe species, although some sources note up to seven eggs in a nest. In sungrebe species, both sexes share nest building and incubation responsibilities. Incubation periods appear remarkably short: only 10–11 days in the sungrebe, which is unique in the family in having altricial (naked and helpless) chicks, born blind, that are carried around by the male in a pocket of skin under each wing. The chicks of the other species are semi-precocial (precocial describes young covered in down that are able to move about when first hatched); those of the African finfoot remain in the nest for at least two days after hatching.

Conservation status

The masked finfoot is classed as globally Vulnerable with a small population (2,500–10,000 birds in 2000) that is declining due to the loss and degradation of wetlands, deforestation, mangrove destruction, agriculture, disturbance, and hunting. The African finfoot is Vulnerable in South Africa, where its population was 500–1,000 individuals in 2000 and where it is threatened by rapid habitat loss. Such threats must apply to all species throughout their ranges, as their habits everywhere are under great pressure. Because all species of the sungrebe family are inconspicuous, significant population declines may easily pass unnoticed.

Significance to humans

Sungrebe habitats are usually not densely populated by human beings, and the retiring birds of this family rarely come into contact with people. They do not compete with people for food resources, and their population densities are so low that they often are not a significant human food item or hunting target, although the globally threatened masked finfoot is hunted and its eggs and chicks are also taken. Sungrebe species do not figure significantly in local legends.

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Species accounts

African finfoot

Podica senegalensis

TAXONOMY

Heliornis senegalensis Vieillot 17, Senegal. Four subspecies.

OTHER COMMON NAMES

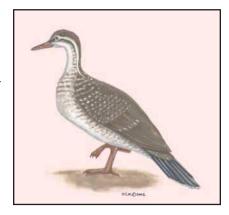
English: Peter's finfoot; French: Grébifoulque d'Afrique; German: Binsenralle; Spanish: Avesol Africano.

PHYSICAL

CHARACTERISTICS 13.8–23.2 in (35–59 cm); 0.74–1.93 lb (338–879 g). Orange feet, brown or blackish back with variable white spotting. Underside light with variable barring.

DISTRIBUTION

P. s. senegalensis: Senegal east to eastern Democratic Republic of Congo (Zaire), Uganda, northwestern Tanza-



Podica senegalensis

nia and Ethiopia; *P. s. somereni*: Kenya and northeastern Tanzania; *P. s. camerunensis*: southern Cameroon, Congo and northern Democratic Republic of Congo; *P. s. petersii*: Angola east to Mozambique and south to eastern South Africa.



HABITAT

Permanent rivers, streams, and still waterbodies densely fringed with reeds and overhanging trees; also mangroves and flooded forests.

BEHAVIOR

Territorial, each pair defending several hundred yards (meters) of waterway.

FEEDING ECOLOGY AND DIET

Forages in water and on land, taking invertebrates and small vertebrates.

REPRODUCTIVE BIOLOGY

Breeds when water levels are high. Monogamous; lays two to three eggs; incubation at least 12 days, by female; young semiprecocial.

CONSERVATION STATUS

Widespread; locally quite common but uncommon in eastern Africa and considered Vulnerable in South Africa.

SIGNIFICANCE TO HUMANS

None known.

Sungrebe

Heliornis fulica

TAXONOMY

Colymbus fulica Boddaert, 1783, Cayenne. Monotypic.



Family: Sungrebes Vol. 9: Birds II

OTHER COMMON NAMES

English: American finfoot; French: Grébifoulque d'Amérique; German: Zwergbinsenralle; Spanish: Avesol Americano.

PHYSICAL CHARACTERISTICS

10.2–13 in (26–33 cm); 0.26–0.33 lb (120–150 g). Yellow and black banded feet, upper bill dark in male, red in female, lower bill pale. White throat, black on top of head to back of neck, brown back and pale underneath.

DISTRIBUTION

Southeastern Mexico through Central and



Heliornis fulica

South America south to Bolivia and northeastern Argentina.

CO

HABITAT

Forest rivers and streams and freshwater lakes and ponds, with dense fringing and overhanging vegetation.

REHAVIOR

Permanently territorial; male defends about 200 yd (180 m) of stream bank.

FEEDING ECOLOGY AND DIET

Feeds from water surface, occasionally on land; eats mainly aquatic insects.

REPRODUCTIVE BIOLOGY

Breeds in spring (northern part of range) or during rains. Two to three eggs; incubation 10–11 days, by both sexes; young altricial.

CONSERVATION STATUS

Not threatened. Widespread but rarely observed; numbers unknown. Regarded as common to uncommon; population density probably low.

SIGNIFICANCE TO HUMANS

None known. ◆

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Barry Taylor, PhD

Sunbitterns

(Eurypygidae)

Class Aves
Order Gruiformes
Suborder Eurypygae
Family Eurypygidae

Thumbnail description

Elegant, bittern-like bird with a long bill, slender neck, and long orange legs; plumage mottled and cryptic except for spectacular sunburst pattern hidden in wings; primarily black head with white striping above and below the ruby-red eyes; sexes similar in appearance

Size

18-21 in (46-53 cm) in length; 6.3-7.8 oz (180-220 g); recorded up to 9 oz (255 g)

Number of genera, species

1 genus; 1 species

Habitat

Tropical forested riparian areas

Conservation status

Not threatened



DistributionCentral and South America

Evolution and systematics

The taxonomic placement of the sunbittern (Euypyga helias) has been a subject of debate through the years. Due to the lack of fossils with which to study, the species has been classed primarily on morphological and behavioral characteristics. It is believed to be most closely related to the kagu (*Rhynocetus jubatus*) of New Caledonia and both species may have originated from the Mesozoic birds of Gondwana. Egg-white protein analysis, hidden patterns in the wings, and soft, lax feathers are a few of the shared similarities. A relationship to the painted-snipes (Rostratulidae) has also been suggested, but lacks the egg-white protein affinity shared with the kagu. Otherwise, the species seems to be most closely related to rails and bustards.

Physical characteristics

The common name is derived from the normally concealed wing markings which reveal a "sunburst" on opening. The bill is fairly straight and long, upper mandible black, and lower bright orange. The legs are also orange. The sunbittern has a long slender neck and long fan-shaped tail with two broad stripes of chestnut and black. The head is black with white stripes above

and below the eyes and across the cheeks. The iris is red. Overall plumage is cryptic, and individuals are perfectly camouflaged when in dappled sunlight due to the mottled plumage. Neck and breast are brown, upperparts chestnut, all barred with black. The throat is white, abdomen buff. In *Eurypyga helias helias*, the bill is more slender and the black dorsal bars of the upperparts are wider. *E. helias major* may be differentiated by a stouter bill and narrow black bars, whereas the Peruvian race *E. helias meridionalis* exhibits more red on the hindneck with narrower black bars on the rump and upper tail. Sexes are similar, although males may be slightly more colorful.

Distribution

E. belias major: Along most of the Caribbean slope of Central America, Columbia west of the Andes, south to western Ecuador.

E. helias helias: East of the Andes, through Amazonian regions of Colombia, Venezuela, and Guineas; also northern Brazil, central Ecuador, and northeastern Peru.

E. belias meridionalis: Tropical zones of South Peru.

Family: Sunbitterns Vol. 9: Birds II

Habitat

Forested areas with an open understory near swift-moving rocky streams. Also inhabits slower-moving creeks, river sandbars, swamps, and pond edges. Typically found at altitudes of 300–4,000 ft (100–1,200 m), but documented at 5,000 ft (1,500 m). Although thought to be nonmigratory, birds that occupy territories with a long dry season may have to travel short distances to find suitable forest habitat bordering permanent water sources.

Behavior

Usually found singly or in pairs. Tends to walk with a deliberate gait, making periodic flights across deep water. If alarmed or disturbed, may fly to perch on low tree branches. Wary, but not shy.

The frontal display, a defensive response to threat or disturbance, was once believed to be a part of courtship. The wings are opened and rotated forward, exposing the usually hidden sunburst pattern. The tail is raised and fanned, while the breast is lowered and the head is pointed toward the intruder, resulting in a bird appearing much larger. The broken-wing display is similar to that employed by many other species of birds, whereby one wing is dragged along the ground in the hopes of distracting potential predators from the nest site to chase the "injured" adult.

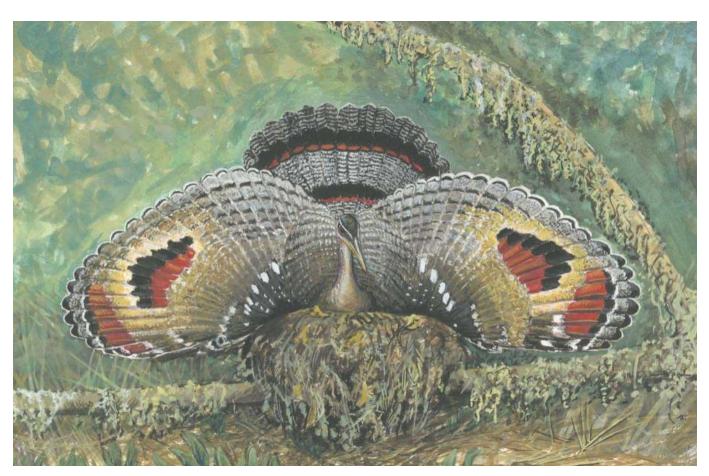
Likely to hiss if disturbed, and this, along with swaying of the neck is commonly used as a method of defense by both adults and chicks. The song, a high, ringing whistle, is most commonly heard in early morning. The alarm call is much harsher and consists of a loud repetition of six to eight notes, similar to "ka, ka, ka..."

Feeding ecology and diet

Stalks prey deliberately, with neck retracted. Spears prey with quick jabs. Also picks and gleans in leaf litter or thick moss lining the forest floor. Typically hunts alone, slowly, and methodically. The diet is diverse including vertebrates such as small fish, tadpoles, and frogs. Invertebrates include spiders, flies, water beetles, cockroaches, katydids, dragonfly and dobsonfly larvae, snails, and crustaceans such as crabs and shrimp. Freshwater eels, toads, earthworms, and moths may also be hunted. Sunbitterns frequently wash their food before eating, and the likelihood is increased if feeding young. This likely aids in rinsing foul-tasting or noxious adherents.

Reproductive biology

The first observations of sunbittern breeding were made in 1865 in the London Zoological Garden where a captive pair raised two nestlings. Both sexes share in nest building,



Sunbittern (Eurypyga helias) alarm display. (Illustration by Wendy Baker)

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incubation, and the subsequent brooding, feeding, and protection of the young.

The breeding cycle begins with the rainy season, when ample mud is available for nest-building. Courtship and pair-bonding rituals include flight displays, head-bobbing, excessive preening, begging displays, duet rattles, and numerous calls and trills. Courtship flight displays have been observed just above the tree line, 33–49 ft (10–15 m) in height.

The platform nest is a bulky, almost globular, collection of decaying leaves, mud, moss, and stems. Grass fibers and mud are used to saddle the nest to the branch. Placement varies, but is typically on a horizontal or slightly sloping branch, 1.2–3.9 in (3–10 cm) wide, and 3–23 ft (1–7 m) above ground. It may or may not have lateral support, but is always under a closed canopy and adjacent to water. Ground nesting is rare. The two to three eggs are smooth and slightly glossy, pinkish buff in color, with a scattering of purplish brown spots at the large end. Incubation lasts 27–30 days.

Hatching may be staggered, with the second chick hatching 24–48 hours after the first. Chicks are downy with open eyes and a bright pinkish orange gape. Costa Rican chicks are pale brown, marbled with black, whereas those of Venezuela are cream with black markings. Chicks are attended and brooded almost constantly during the first week, being able to stand and flap wings by day seven. Fledging occurs at approximately 30 days, the chicks leaving the nest with adult-like feathers. Observations of captive pairs indicate that both sexes are able to breed at two years of age. The adults molt after breeding.

Conservation status

Although not threatened, the race *E. helias major* has been listed as declining, described as very rare to local in some areas. *E. helias meridionalis* of Peru may be at threat due to its limited range. The species is becoming fairly common in zoo collections, negating the need to deplete wild populations. Po-



Sunbittern (Eurypyga helias). (Illustration by Wendy Baker)



Sunbittern (*Eurypyga helias*) adult and chicks in the rainforest. (Photo by Michael Fogden. Bruce Coleman Inc. Reproduced by permission.)

tential threats to populations are similar to those of many species, including loss of habitat and manipulation of waterways via damming or channeling of rivers.

Significance to humans

Young are occasionally removed from the nest and tamed by locals for their fly- and spider-catching abilities. Reported to live 25–30 years in captivity, but more commonly 15. There are no longevity records for wild birds. Hunting has been reported, but is not thought to constitute a threat due to the difficulty in finding the species and the abundance of more common game birds.



A sunbittern (*Eurypyga helias*) spreads its feathers at a stream in Venezuela. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)

Family: Sunbitterns Vol. 9: Birds II

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Pamela D. Lewis

Trumpeters (Psophiidae)

Class Aves

Order Gruiformes

Suborder Grues

Family Psophiidae

Thumbnail description

Trumpeters are long-necked, hunch-backed, small-headed, short-tailed, dark-plumaged, chicken-sized birds with a short, sharp bill, long legs, and an elevated hind toe; they roam the floor of South American rainforests and are named for their deep, booming territorial call

Size

17-21 in (43-53 cm); 2.2 lb (1 kg)

Number of genera, species

1 genus; 3 species

Habitat

Tropical forest with an ample supply of fruit trees

Conservation status

Not threatened



Distribution

Northern South America, mainly in the Amazon basin

Evolution and systematics

Trumpeters share many similar traits with other birds in the order Gruiformes (rails, cranes, moorhens, and gallinules), but the three trumpeter species are grouped within their own separate family (Psophiidae). Scientists still debate as to which of the other families in the order Gruiformes include their closest relatives. Some argue they are most similar to rails and cranes, based on similar anatomy. DNA analysis by Sibley and Ahlquist suggest trumpeters are more closely aligned with cranes, limpkins, and finfoots, along with seriemas, kagu, sunbitterns, and bustards.

Primates, such as spider monkeys, are a key part of the trumpeters' evolution. Trumpeters depend on monkeys and other animals to provide their food supply. Since trumpeters are not strong fliers, they forage on the forest floor relying on monkeys and larger birds to shake loose pieces of fruit and drop them to the ground.

Trumpeters, which travel in groups, evolved with a rare social structure known as cooperative polyandry. In this system, one dominant female mates with several dominant males, but all members of the group share in raising and feed-

ing the young. Researchers suggest trumpeters adapted with this system because they must defend large territories in order to gather enough food during the dry season. To patrol these large boundaries, the trumpeters need to attract several adult males. As a result, more than one male is allowed to mate with the dominant female in each group. Since predators prevent half of all trumpeter chicks from making it to adulthood, the group parenting approach may help increase their odds of survival.

Physical characteristics

Trumpeters are about the size of a domestic chicken and have long necks, hunched backs, small heads, and short tails. They have large, dark eyes and a short, sharp bill, which they use to pry open fruit. At first glance, trumpeters look somewhat stocky but they have slender bodies that appear larger as a result of their wings that are slightly arched at the sides. Adult male and female trumpeters have a similar appearance, but the males are heavier.

All trumpeters have mostly dark plumage. The three species can be distinguished by the color of the inner wing

Family: Trumpeters Vol. 9: Birds II



A pale-winged trumpeter (*Psophia leucoptera*) spreads its wings. (Photo by Doug Wechsler/VIREO. Reproduced by permission.)

plumage. This creates a contrasting patch on the bird's back when its wings are folded. The common trumpeter (*Psophia crepitans*) has gray inner wings. The dark-winged trumpeter (*P. viridis*) has green inner plumage and the pale-winged trumpeter (*P. leucoptera*) has contrasting white feathers. Like the cranes and rails, trumpeters have an elevated hind toe. Their long legs help them run quickly.

Juveniles hatch with brown and black striped plumage. This camouflage pattern helps them match their surroundings on the forest floor. Chicks begin to grow adult-looking plumage after about six weeks.

As their name indicates, trumpeters are noisy birds. They have several types of calls, but the most distinctive is their territorial call. It has been compared to the sound a person makes when blowing into an empty bottle. The call is not exactly like a trumpet, but it has a repetitive, low-pitched, drumming sound heard mostly at night.

Distribution

Trumpeters occur in Venezuela, Colombia, Ecuador, the Guianas, Peru, Bolivia, and Brazil. The Amazon River and its tributaries have played an important role in determining where various trumpeter species live. For example, the common trumpeter lives north of the Amazon. The pale-winged trumpeter can be found south of the Amazon and west of the Madeira; while the dark-winged trumpeter is distributed south of the Amazon and east of the Madeira.

Habitat

Trumpeters live on the ground in tropical rainforests. They prefer forests with a relatively open forest floor so they can more easily forage and run away from predators when necessary. Typical trumpeter habitat can range from dense, forested areas to swamps.

A good variety of mature fruit trees is a key requirement for trumpeter habitat. While they gather the fallen fruit from the ground, they also use trees for roosting at night. They prefer areas with a thick canopy to provide protection and cover while roosting and nesting. Trumpeters also seek trees with hollow cavities for nest-building sites.

Behavior

Before they begin searching for food, trumpeters spend some time socializing with other members of their territorial group. Scientists have observed them paying respects to the dominant adults, by crouching and spreading their wings to show they are subordinate. The dominant bird often will give a slight flick of the wings to acknowledge the gesture.

Preening is another way trumpeters socialize. One bird will lower its head and walk up to another to request this service. Usually, the first bird will return the favor. Dominant birds will preen subordinates and vice versa, so the hierarchical social structure does not seem to make a difference in preening.

Trumpeters also like to feed other members of their group. They use a special call and submissive displays to beg for food. If food is plentiful and they do not have to spend the entire day foraging, trumpeters also will engage in playful fights with each other. They flap their wings and kick in a mock attack. Researchers also have seen lone trumpeters playfully attack objects on the ground, such as a rock or leaf.

After a period of socializing, trumpeters set off in groups of three to a dozen birds to search for food. They walk along the forest floor, turning over leaves to look for insects and fallen fruit. During seasons when fruit is harder to find, trumpeters may have to cover a large territory to find enough food for the group.

While foraging, trumpeters often encounter a rival group that has infringed on their territory. As soon as they sense the intruders, the defending group will quickly run toward them without making a sound. When they catch the other birds, the trumpeters will blast them with their loud, distinctive territorial call. A fight typically ensues as the defenders jump into the air and kick their rivals, flapping their wings and pecking. The birds continue giving the territorial call until the intruders are driven back across the boundary line.

After they return from foraging and the sun sets, trumpeters roost in tree branches 30 ft (9 m) off the ground. After dark, the group continues to assert its boundaries by giving the territorial call every few hours.

In some cases, trumpeters interact with other animal species as well. For example, one scientist observed a palewinged trumpeter grooming parasites from the back of a Brazilian tapir in the Amazon rainforest.

Feeding ecology and diet

Fruits make up the majority of the trumpeter's diet. They prefer soft fruits without a thick rind. Most of the fruits they eat are either found on low-growing plants or have been knocked to the ground by monkeys.

Insects also provide an important trumpeter food source. Foraging trumpeters often use their bills to probe the forest floor for beetles, ants, termites, and other insects, as well as their eggs and larvae. Trumpeters have also been known to eat an occasional small snake.

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Reproductive biology

Trumpeters make attractive research subjects for scientists who are interested in their rare breeding system, known as cooperative polyandry. In this system, one dominant female mates with three dominant males, and the entire territorial group helps to raise and feed the young.

Courtship begins before the start of the rainy season, when food is most abundant for the emerging chicks. Two months before they begin breeding, a pair of trumpeters start searching for a suitable nest site. They prefer existing tree cavities high above the ground that have been abandoned by another bird or animal. To prepare the nest, the birds pack down a layer of wood and sticks gathered from the forest floor. At this time, the dominant male makes a ritual of feeding the dominant female.

When breeding season begins, the dominant males in the group compete with each other for the chance to copulate with the dominant female. When mating, the female presents her hind parts to solicit the male as he walks behind her in a circle.

On average, the female lays three white eggs. The dominant male and female share most of the incubation, but the subordinate males also spend some time on the nest. The eggs hatch after 27 days.

Chicks emerge covered with dark, striped down feathers. They depend on the adult birds to feed them for the first three weeks, then gradually begin to forage on their own. Since the chicks are not strong enough to fly at first, they roost closer to the ground at night. This makes them vulnerable to snakes, raptors, and other predators.

Conservation status

Trumpeters typically need large, uninterrupted tracts of land to find enough food to feed their territorial groups. But their rainforest habitat is rapidly shrinking, leaving their future in question. Trumpeters occur in the highest numbers in large, protected wildlife reserves. Scientists are concerned because trumpeters are not easy to breed in captivity. Also, the primates they depend upon for food availability are losing ground due to hunting and habitat loss. That, in turn, could create problems for trumpeters. Currently, however, trumpeters are not threatened or endangered.

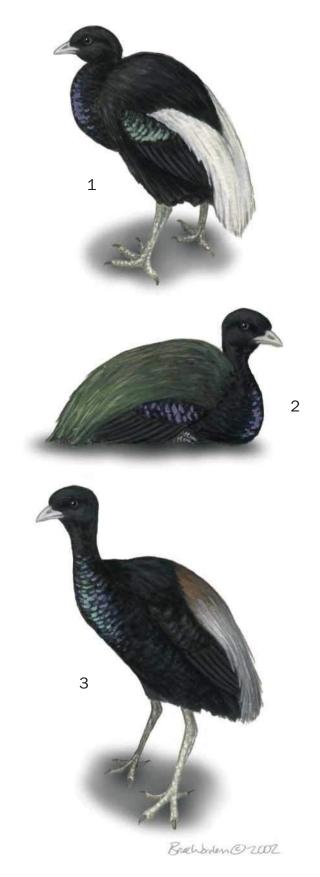


A common trumpeter (*Psophia crepitans*) chick. (Photo by J. Alvarez A./VIREO. Reproduced by permission.)

Significance to humans

Humans in many different regions have given nicknames to trumpeters. For example, in Surinam, they are called "Kamee-kamee," which means camel's back. The Tupi Indians call them "Jacamims," or bird with small head. Some native Brazilian people consider trumpeters to be their spiritual ancestors.

Trumpeters are said to make good pets, and often are used to protect chicken coops and alert their owners when snakes appear. Trumpeters are heavily hunted for food in some parts of their range. Hunters stun them by shining lights into their eyes while they roost at night. Since trumpeters are loyal to other members of their group, they often will stay close if another bird is injured, making them easy targets for hunters.



1. Pale-winged trumpeter (*Psophia leucoptera*); 2. Dark-winged trumpeter (*Psophia viridis*); 3. Common trumpeter (*Psophia crepitans*). (Illustration by Bruce Worden)

Vol. 9: Birds II Family: Trumpeters

Species accounts

Common trumpeter

Psophia crepitans

TAXONOMY

Psophia crepitans Linnaeus, 1758, Cayenne. Two subspecies.

OTHER COMMON NAMES

English: Gray-winged trumpeter; German: Graurücken-Trompetervogel; Spanish: Trompetero Aligrís.

PHYSICAL CHARACTERISTICS

18–20 in (45–52 cm); 2–3 lb (1–1.5 kg). Dark plumage with gray inner wings that form a light patch on the back. Long neck and legs, hunchback appearance. Juveniles are dark gray with cream underparts and reddish stripes.

DISTRIBUTION

North of the Amazon in northwestern Brazil, parts of Colombia, Ecuador, Peru, Venezuela, and the Guianas.

HABITAT

Dense tropical rainforest.

BEHAVIOR

Very social bird that uses a complex set of calls to communicate. Travels in groups of three to 12.

Psophia crepitans ■ Resident

FEEDING ECOLOGY AND DIET

Forages mostly on fruit knocked to the forest floor by primates. Insects, such as beetles, ants, and termites also are part of the diet.

REPRODUCTIVE BIOLOGY

Uses a rare breeding system, cooperative polyandry, in which a dominant female mates with three dominant males and the other adults in the group help feed and care for the chicks. Nests in hollow tree cavity. Lays a clutch of three eggs. Incubation is 28 days.

CONSERVATION STATUS

Not threatened, but population is shrinking due to loss of habitat and hunting.

SIGNIFICANCE TO HUMANS

None known. ◆

Pale-winged trumpeter

Psophia leucoptera

TAXONOMY

Psophia leucoptera Spix, 1825, Rio Madeira, Brazil. Two subspecies.



Family: Trumpeters Vol. 9: Birds II

OTHER COMMON NAMES

English: White-winged trumpeter; German: Weissflügel-Trompetervogel; Spanish: Trompetero Aliblanco.

PHYSICAL CHARACTERISTICS

18–20 in (45–52 cm); 2–3 lb (1–1.5 kg). Adults have dark plumage with contrasting white wing tips, which form a light patch on the back. Long neck and legs, hunchback appearance. Juveniles are reddish with cream underparts and white stripes.

DISTRIBUTION

South of the Amazon and west of the Madeira through parts of Brazil, Peru, and Bolivia.

HABITAT

Dense tropical rainforest.

BEHAVIOR

Very social bird that uses a complex set of calls to communicate. Travels in groups of three to 12.

FEEDING ECOLOGY AND DIET

Forages mostly on fruit knocked to the forest floor by primates. Insects, such as beetles, ants, and termites also are part of the diet.

REPRODUCTIVE BIOLOGY

Uses a rare breeding system, cooperative polyandry, in which a dominant female mates with three dominant males and the other adults in the group help feed and care for the chicks. Nests in hollow tree cavity. Lays a clutch of three eggs. Incubation is 23–29 days.

CONSERVATION STATUS

Not threatened, but population is shrinking due to loss of habitat and hunting.

SIGNIFICANCE TO HUMANS

None known. ◆

Dark-winged trumpeter

Psophia viridis

TAXONOMY

Psophia viridis Spix, 1825, Parintins. Three subspecies.

OTHER COMMON NAMES

English: Green-winged trumpeter; German: Grünflügel-Trompetervogel; Spanish: Trompetero Aliverde.

PHYSICAL CHARACTERISTICS

18–20 in (45–52 cm); 2–3 lb (1–1.5 kg). Adults have dark plumage with dark green wing tips, which form a green patch on the back. Long neck and legs, hunchback appearance. Juveniles are reddish with cream underparts and white stripes.

DISTRIBUTION

South of the Amazon and east of the Madeira in central Brazil.



HABITAT

Dense tropical rainforest.

BEHAVIOR

Very social bird that uses a complex set of calls to communicate. Travels in groups of three to 12.

FEEDING ECOLOGY AND DIET

Forages mostly on fruit knocked to the forest floor by primates. Insects, such as beetles, ants, and termites also are part of the diet.

REPRODUCTIVE BIOLOGY

Uses a rare breeding system, cooperative polyandry, in which a dominant female mates with three dominant males and the other adults in the group help feed and care for the chicks. Nests in hollow tree cavity. Lays a clutch of approximately five eggs. Incubation is 27 days.

CONSERVATION STATUS

Not threatened, but population is shrinking due to loss of habitat and hunting.

SIGNIFICANCE TO HUMANS

None known. ◆

Vol. 9: Birds II Family: Trumpeters

Resources

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Organizations

Neotropical Bird Club. c/o The Lodge, Sandy, Bedfordshire SG19 2DL United Kingdom. E-mail: secretary @neotropicalbirdclub.org Web site: http://www.neotropicalbirdclub.org>

Melissa Knopper

Seriemas (Cariamidae)

Class Aves

Order Gruiformes

Suborder Cariamae

Family Cariamidae

Thumbnail description

Long legs, tail and neck; short, decurved, hawklike bill; streaky and barred ashy brown plumage that is soft and loose; wispy, tufted crest on head; long feathers on neck; wings short; toes short and semipalmate (limited or reduced webbing between toes); sexes alike

Size

28–35 in (70–90 cm) in length; 2.6–3.3 lb (1.2–1.5 kg) in weight

Number of genera, species

2 genera; 2 species

Habitat

Grassland, open forest, thorny scrub, savanna-

Conservation status

Not threatened



Distribution

Central and eastern South America

Evolution and systematics

The family of seriemas is an ancient and poorly understood group surrounded by debate regarding taxonomic placement. Birds of this family were previously placed with the secretary bird (Sagittarius serpentarius), which occupies a similar niche in Africa. Based on fossil records, the most likely ancestors are the phorusrhacoids, which were giant, flightless predators of the Tertiary. Today, seriemas are placed within the order Gruiformes (cranes and rails) and are usually grouped closely with the bustards (family Otididae). The closest living relative may be the kagu (Rhynochetus jubatus) of New Caledonia, which shares the presence of a nuchal (an area at the back of the skull) crest, as well as similar displays and vocalizations, but evidence is tentative so far.

Physical characteristics

Both species have similar builds, with elongated bodies; long legs and tails; long necks; and short, rounded wings. The hawk-like bill is stout and hooked at the end. Plumage is ashy brown, finely barred on the upperparts, boldly barred on the flight feathers. The underparts are pale and the abdomen white. Sexes are similar in appearance.

Distribution

Brazil south to Argentina. Ranges of these species may overlap from southern Bolivia through the Paraguayan Chaco to Argentina.

Habitat

Grasslands, open forest, and thorny scrub.

Behavior

Seriemas spend most of the day on the ground, roosting in trees at night. Wary and alert, the birds tend to run rather than fly when startled, with speeds up to 37 mph (60 kph). Dust baths and sunbathing have been observed. Heard more commonly than seen, the birds' loud dog-like yelping may carry for several miles (kilometers). Use of perches, including

Family: Seriemas Vol. 9: Birds II



A red-legged seriema (*Cariama cristata*) bends its long legs. (Photo by Doug Wechsler/VIREO. Reproduced by permission.)

trees and termite mounds, help the song travel farther. Duets between pairs are common. The young are capable of singing by two to three weeks of age, then capable of assisting the parents in defending the territory. Disputes may lead to intense vocalization and kicking.

Feeding ecology and diet

Typically foraging alone or in pairs, seriemas stalk their prey deliberately. Groups of three or more are likely to be comprised of parents with young. Seriemas are diurnal hunters with an omnivorous diet that includes insects, small mammals, snakes, lizards, snails, worms, fruits, and vegetable matter. Small prey, such as rodents, is usually pulverized—by slamming onto nearby rocks or the ground—before being swallowed whole. Larger prey, including snakes, may be torn to pieces before feeding. Seriemas are unable to distinguish venomous from nonvenomous snakes and are not immune to venom.

Reproductive biology

Breeding typically occurs between September and May, corresponding with the rainy season. Courtship includes strutting and leaping by the male, as well as displays revealing the hidden pattern of the wings and tail. Seriemas are solitary nesters, remaining distant from other pairs. The nest is comprised of a large platform of sticks and twigs lined with clay or cattle dung. Built in about 30 days by both sexes, it is placed in a tree 3–30 ft (1–9 m) above ground. Nearby branches may allow the adults to jump their way to the nest. Two to three eggs are laid, and these are white to cream with brownish and purplish spots and streaks. The female is the primary incubator for 24–30 days. The downy brown young are able to jump out of the nest and follow the parents at 14 days, although adult weight will not be reached for five months.

Conservation status

Not threatened, although both species occur at fairly low densities throughout their ranges. Potential threats include hunting pressure and destruction of habitat through agricultural development.

Significance to humans

Seriemas are thought to kill large numbers of venomous snakes, although snakes actually make up only a small portion of their diet. Used by some farmers to guard chickens, they warn with a loud alarm call if predators approach. Birds may live up to 30 years in captivity.



1. Black-legged seriema (Chunga burmeisteri); 2. Red-legged seriema (Cariama cristata). (Illustration by Marguette Dongvillo)

Family: Seriemas Vol. 9: Birds II

Species accounts

Red-legged seriema

Cariama cristata

TAXONOMY

Palamedea cristata Linnaeus, 1766, Brazil.

OTHER COMMON NAMES

English: Crested seriema; French: Cariama huppé; German: Rotfußseriema; Spanish: cariama, siriema, Chuña Pattiroja.

PHYSICAL CHARACTERISTICS

Red legs and bill, yellow iris surrounded by pale blue bare skin, and a black subterminal bar on the white-tipped tail. Plumage of the neck and underparts is soft and somewhat loose. Long feathers on the hindneck form the nuchal crest, whereas the distinctive frontal crest is formed by permanently raised, stiffened feathers, 3–4 in (7–10 cm) in length, arising from the base of the bill. Sexes similar, but males slightly larger. Juveniles similar, but the bill and legs are blackish, and the markings of the head, neck, and back are more evident.

DISTRIBUTION

More widespread. Inhabits large parts of central and eastern Brazil, Paraguay, eastern and southeastern Bolivia, Uruguay and northeastern Argentina. Elevations up to 6,600 ft (2,000 m).



HABITAT

Primarily savanna-like areas; also open scrub and woodland edges.

BEHAVIOR

Generally nonmigratory, but temperature-related movement recorded. Rarely fly and spend most of the time on the ground, except for roosting in low trees or bushes. The birds are fast on the ground and can outrun predators. Considered diurnal. Dust bathing is practiced, as well as sunbathing, during which birds of this species lie on their sides, sometimes appearing as if dead. Call is similar to a yelping puppy and can be heard several miles away. Call is usually given in the morning and between pairs, often as a duet between the two birds, to define territory. At the beginning of the call, the head is held straight, but toward the end, the neck is held back so the head nearly touches the bird's back.

FEEDING ECOLOGY AND DIET

Omnivorous diet including small mammals, insects, snakes, worms, frogs, birds, lizards, snails, fruit, and vegetable matter. May eat eggs or chicks of other species. Slams large prey on rocks to pulverize to make it easier to swallow. The arrangement of their toes prevents them from catching prey with their feet. Forage in small groups or pairs.

REPRODUCTIVE BIOLOGY

Nests are in bushes or low trees from ground level to 10 ft (3 m) up in a tree; sticks are used for building material with mud and leaves for the lining. Both sexes build the nest, which generally takes a month. The male's courtship display involves showing off flight feathers by stretching them to one side and strutting before the female with head down and crest raised. Seriemas are considered monogamous. Clutches usually consist of two white eggs with irregular brown streaks. Incubation lasts for 25–28 days with both parents involved. Chicks fledge in a month.

CONSERVATION STATUS

Not threatened, though uncommon in far southern parts of Brazil; rare and possibly vanishing in Uruguay. A population in northeast Argentina appears to be pressured by hunting and destruction of habitat. Has begun to colonize deforested, grassy areas of Amazonian Brazil.

SIGNIFICANCE TO HUMANS

Occasionally offered for sale by illegal traders in parts of Brazil. Farmers often use them as watchdogs for their domestic fowl because of their call. ◆

Black-legged seriema

Chunga burmeisteri

TAXONOMY

Dicholophus burmeisteri Hartlaub, 1860, Argentina.

OTHER COMMON NAMES

English: Lesser seriema, Burmeister's seriema; French: Cariama de Burmeister; German: Schwarzfußseriema; Spanish: Chuña Patinegra. Vol. 9: Birds II Family: Seriemas



PHYSICAL CHARACTERISTICS

Sexes similar. Blackish legs and bill, red iris, two broad black bars before a narrowly tipped tail. Frontal feathers are hair-like at the tip, but frontal crest is not distinctive. Juveniles are similar to adults, but with distinct barring of the head, foreneck and breast, and white spots along the back and wing coverts.

DISTRIBUTION

East and southeast Bolivia, Paraguay, northwest Argentina.

HARITAT

Lowland open, dry wooded areas, grasslands, and thorny scrub.

REHAVIOR

More sedentary than red-legged seriema. Unable to distinguish between venomous and nonvenomous snakes, which can lead to a birds death. Call is loud yelping and has been compared to that of a yelping puppy. Call can be heard several miles away and is usually given early in the morning, most often to define territory between pairs and is often heard as a duet between the two birds.

FEEDING ECOLOGY AND DIET

Omnivorous diet including snakes, lizards, frogs, birds, small vertebrates, insects, fruit, and vegetable matter. May be found near livestock, eating insects stirred up during passage. Birds slam large prey on rocks to pulverize. Forages in pairs or small groups.

REPRODUCTIVE BIOLOGY

Nests are compact, made of sticks, and are built anywhere from ground level up to 10 ft (3 m) in a tree. Little else is documented on this species; however, they are likely similar to red-legged seriema.

CONSERVATION STATUS

Not threatened. Listed as still fairly common in Argentina, but documentation elsewhere is poor. May be more likely to be threatened in the future due to the smaller range.

SIGNIFICANCE TO HUMANS

Although egg-collecting and hunting are uncommon, the species has been hunted by natives of the Paraguayan Chaco. Farmers also place the species with chickens to signal the alarm when intruders approach, and to kill snakes.

Resources

Books

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Pamela D. Lewis

Bustards (Otididae)

Class Aves

Order Gruiformes

Suborder Otidides

Family Otidae

Thumbnail description

Medium size to very large terrestrial birds, with long legs and necks and fairly short straight bills

Size

15.75-47.25 in (40-120 cm); 1-42.2 lb (0.45-19 kg)

Number of genera, species

11 genera; 26 species

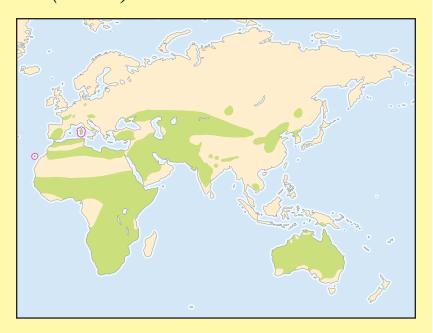
Habitat

Level or gently undulating grasslands, steppes, semideserts, and open savanna woodlands

Conservation status

Endangered: 3 species; Vulnerable: 1 species;

Near Threatened: 6 species



Distribution

Africa, southern Europe, south and Southeast Asia, New Guinea and Australia

Evolution and systematics

Bustards are linked ancestrally to cranes and their relatives (Gruiformes). Genetic studies place them in their own suborder, Otidides, whose divergence from the Gruides is estimated at 70 million years ago. Although conspicuous courtship displays imply a link with cranes, the evolutionary isolation of bustards finds manifestation in various morphological anomalies. These include the absence of a hind toe and preen gland, hexagonal rather than transverse tarsal scutellation, and unique dense powder-down.

Taxonomic relationships within the family are contested. The large bustards are grouped in *Otis*, *Neotis*, and *Ardeotis*, and these are possibly related to the smaller *Chlamydotis* and *Tetrax*. Diminutive *Tetrax*, long combined with the far larger *Otis* by taxonomists, might be related to *Sypheotides*, to which it more closely equates in terms of size, flight-feather modification, and display. Some recent appraisals combine 14 relatively small species within the genus *Eupodotis*, but an alternative treatment retains only five species in this grouping, separating the remainder into *Afrotis*, *Lissotis*, *Lophotis*, *Houbaropsis*, and *Sypheotides*.

Physical characteristics

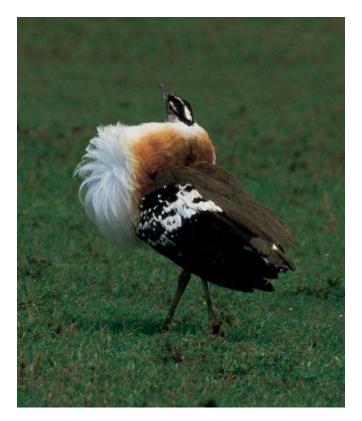
Bustards combine stout bodies carried horizontally with long legs and necks, the latter supporting flat-crowned heads and short, straight bills. As a result of an exclusively terrestrial lifestyle, they have no hind toe. They tend to escape danger by flying, and consequently their feet are relatively small, and their wings are large and strong. Mature male *Otis* and *Ardeotis* bustards regularly reach over 3.3 ft (1 m) in height, and as some approach 44 lb (20 kg), they are among the heaviest of flying birds. In these genera, females tend to be two-thirds the height and one-third the weight of their respective males. In smaller bustard species, the difference in size between the sexes is less pronounced.

Bustard plumage is largely cryptic: the upperparts are brown or finely barred, so that a crouching bird is camouflaged. The underparts are often white in open-country species, and sometimes black in species that inhabit taller vegetation (counter-shading being less of a consideration). Many species have patches of white and black in the wing that are concealed when standing or sitting but conspicuous in flight. Males are generally brighter or more strikingly patterned than females, at least in the breeding season, but sexes are similar in *Eupodotis*. In *Otis*, *Ardeotis*, *Neotis*, *Chalmydotis*, *Lissotis*, and *Houbaropsis*, males develop filamentous plumes that are used in courtship displays. The most elaborate are in *Chlamydotis* (elongated erectile piebald plumes on breast, neck, and crown), *Otis* (white moustachial plumes), and *Sypheotides* (long bare-shafted, spatulate-tipped cheek feathers).

Distribution

Bustards are confined to the Old World. A glance at patterns of bustard diversity suggests that they originated in Africa, where 21 species occur. Sixteen of these are purely Afrotropical, and another two only fractionally enter the

Family: Bustards Vol. 9: Birds II



Courtship display of a Jackson's bustard (*Neotis denhami*) in Kenya. (Photo by Erwin and Peggy Bauer. Bruce Coleman Inc. Reproduced by permission.)

North African portion of the Palearctic region. Within Africa, there are two distinct centers of speciation. One is in East Africa, between the Horn and the Nile, the other is in southern Africa south of the Zambezi. Of four species with chiefly Palearctic distributions, two are widespread in Europe and Asia, with portions of their ranges in North Africa. One is entirely North African; another is almost entirely Asian, extending from Egypt and the Middle East to China (these two forms, the Houbara bustard *Chlamydotis undulata* and Macqueen's bustard *C. macqueenii*, are often treated as conspecific). Three more species are Oriental (all centered on the Indian subcontinent, one with an outlying population in Indochina), and one species is Australasian, occurring in Australia and southern New Guinea.

Habitat

Bustards inhabit temperate and tropical semideserts, grassy plains, and open low-stature woodland. The majority (19 species) are most commonly associated with flat or gently undulating open landscapes, generally with vegetation sufficiently low to allow them a view over long distances. Many African bustards (*Eupodotis*, *Lophotis*, and *Lissotis*) tolerate varying degrees of wooded cover, including acacia woodland and thorny thickets, and the floricans (*Sypheotides* and *Houbaropsis*) are regularly found in tall grassland. A huge area of habitat suitable for bustards has been converted to cultivation,

especially in Europe and the Indian subcontinent. Fortunately, many species tolerate nonintensively farmed land.

Behavior

Most bustards are found walking slowly across open terrain. Several species are at least partially gregarious. The great bustard (*Otis tarda*) has been recorded in groups of over 50, and nonbreeding aggregations of the little bustard (*Tetrax tetrax*) can number in the thousands. The desert-adapted forms, such as *Chlamydotis*, are probably the most solitary. A few species gather at loose leks. Foraging bustards are regularly found near herds of grazing herbivores. Presumably they benefit from reductions in predation pressure or elevations in foraging success, as they hunt insects disturbed by the mammals.

It is unlikely that any bustard species is entirely sedentary, and many are clearly nomadic or migratory. Those that breed in Asia undertake long distance migrations to escape harsh winters. The lesser florican (*Sypheotides indica*) performs regular migrations in response to rainfall in India, and the same is true of several African species.

Feeding ecology and diet

Bustards are omnivorous and opportunistic. Most species have a diet predominately of vegetable matter. They eat fresh shoots, flowers, and leaves of herbaceous plants; excavate for soft roots and bulbs; and take fruit and seeds when available. In cultivated areas they consume a variety of crops. Insects are also an important food, at least seasonally. The timing of breeding tends to synchronize chick emergence with maximum insect abundance. Although beetles and grasshoppers are the main invertebrate prey items, many other arthropods



The black-bellied bustard's (*Lissotis melanogaster*) coloring helps to camouflage it in its environment. (Photo by Len Rue Jr. Bruce Coleman Inc. Reproduced by permission.)

Vol. 9: Birds II Family: Bustards



Two male kori bustards (Ardeotis kori) fighting on the Serengeti plain, Tanzania. (Photo by Davis Hosking. Photo Researchers, Inc. Reproduced by permission.)

are taken if available. Bustards also consume small vertebrates such as reptiles and rodents, particularly those killed or injured in bush fires or traffic. Bustards can thrive without water for long periods, but drink freely when water is available.

Reproductive biology

The breeding season tends to coincide with periods of high rainfall. At its outset, males of many species perform magnificent displays, often from traditionally favored locations. In general, pair bonds between male and female bustards appear to be absent, as females visit displaying males and then leave to incubate the eggs and raise the chicks alone. Sexual maturation is slowest and sexual dimorphism most pronounced in species with dispersed leks or solitary territorial males: males take up to six years to reach full size and possess plumage ornamentation absent in females.

The displaying great bustard selects an elevated site and then inflates his gular sac and raises his tail, exposing white undertail-coverts. The inner secondaries are then twisted over and fanned so that, at the height of his splendid performance, having apparently turned himself inside out, the gleam of white plumage is visible several miles away. The kori bustard (*Ardeotis kori*) grossly inflates his neck plumage, cocks his tail, and emits a low booming call. Many smaller bustards, particularly those that inhabit taller vegetation, incorporate vertical display leaps or short flights into courtship behavior so that they are visible from a distance.

The nest is a bare scrape into which one to six (usually two to four) eggs are laid. Incubation is 20–22 days in the little bustard, 24–25 days in the great bustard, and presumably between these extremes in all other species. Incubation starts with the first egg, leading to asynchronous hatching. The precocial young (hatched covered with down and open eyes) can usually walk after a few hours.

Conservation status

In the face of agricultural intensification, pesticide use, hunting, and disturbance, bustard populations are falling and their distributions shrinking. Four species are currently considered Threatened: the widespread great bustard and all three bustards from the Oriental region. Six more bustards are treated as Near Threatened: little, Denham's (Neotis denhami), Nubian (N. nuba), Houbara, little brown (Eupodotis humilis), and blue bustard (E. caerulescens). [This assessment treats Houbara and Macqueen's bustards as conspecific.] All remaining large species are suffering declines and extinction at the local level. The most threatened species are the two floricans and the great Indian bustard (Ardeotis nigriceps). They are confined to India and Indochina, where heavy hunting pressure and degradation of suitable habitat has savagely reduced their populations.

Although small numbers of each of these species breed and survive within protected areas, their future hangs in the balance. In general, bustards are at greater risk than many animals because populations in all but the very largest reserves Family: Bustards Vol. 9: Birds II

are not viable. Low population densities, and their nomadic or migratory lifestyles, mean that current protected area networks do not comfortably meet their needs.

Significance to humans

Bustards bring economic and ecological benefits. Depredation of insect plagues and other crop pests by bustards improves agricultural productivity, and they are likely to play an important role in seed dispersal. In return, most species have suffered grievously at the hands of man. A heavy toll is exacted in many

regions by hunting, to the point that Asian populations face a serious threat of extinction. The most significant method is the use by Arabian dignitaries of trained falcons to hunt bustards. The modern version of "traditional" entourages, equipped with teams of falcons and the latest technology, trawl across Middle Eastern deserts for the Macqueen's bustard. With numbers falling, the falconers have expanded their activities throughout North Africa, partly shifting their attention to Arabian (*Ardeotis arabs*) and Nubian bustards. A similar scale of persecution is reported from Cambodia, where Bengal floricans (*Houbaropsis bengalensis*) are a favorite source of food.



1. Blue bustard (*Eupodotis caerulescens*); 2. Little bustard (*Tetrax tetrax*); 3. White-quilled bustard (*Afrotis afraoides*); 4. Bengal florican (*Houbaropsis bengalensis*); 5. Houbara bustard (*Chlamydotis undulata*); 6. Great bustard (*Otis tarda*); 7. Great Indian bustard (*Ardeotis nigriceps*). (Illustration by Bruce Worden)

Family: Bustards Vol. 9: Birds II

Species accounts

Great bustard

Otis tarda

TAXONOMY

Otis tarda Linnaeus, 1758, Poland. Two subspecies recognized.

OTHER COMMON NAMES

French: Grande outarde; German: Großtrappe; Spanish: Avutarda Euroasiática.

PHYSICAL CHARACTERISTICS

Male: 41 in (105 cm), 13–40 lb (5.8–18 kg); female: 30 in (75 cm), 7–12 lb (3.3–5.3 kg). Back and tail barred black and gold; white underneath. Female and nonbreeding male head and neck are pale blue-gray; breeding male has white and russet on neck and whitish chin barbs.

DISTRIBUTION

O. t. tarda: northern Morocco and Iberia, Germany, Hungary, southern Ukraine; also breeds Turkey, western Iran, and southwestern Russia, through Kazakhstan to Kyrgyzstan, wintering from southern Turkey and Syria through southern Azerbaijan and northern Iran to Uzbekistan and Tadjikistan; O. t. dybowski: southeastern Russia, Mongolia, and northern China.

HABITAT

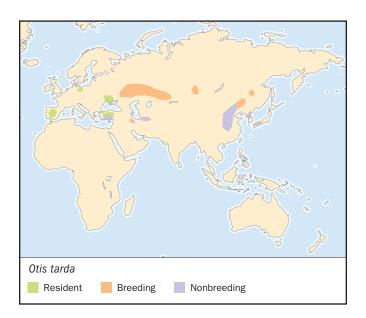
Level or gently undulating open short-grass plains, generally favoring undisturbed areas.

BEHAVIOR

Usually lives in nonterritorial sex-segregated groups, these sometimes large in winter. In breeding season dominant males display spectacularly on dispersed leks. Migratory in part of range.

FEEDING ECOLOGY AND DIET

Plant material and invertebrates, occasionally amphibians, reptiles, or young birds.



REPRODUCTIVE BIOLOGY

Two to three eggs laid in bare scrape, where incubated by female for about 25 days; fledging period 30–35 days. First breeding occurs at 5–6 years in males and 2–3 years in females.

CONSERVATION STATUS

Vulnerable. Populations have declined and fragmented. Main threats are agricultural intensification, disturbance, pesticide use, and hunting.

SIGNIFICANCE TO HUMANS

Appears in European heraldic imagery and insignia; now the figurehead of a major grassland conservation program in Iberia. ◆

Great Indian bustard

Ardeotis nigriceps

Otis nigriceps Vigors, 1831, Himalayas. Monotypic.

OTHER COMMON NAMES

English: Indian bustard; French: Outarde à tête noire; German: Hindutrappe; Spanish: Avutarda India. Monotypic.

PHYSICAL CHARACTERISTICS

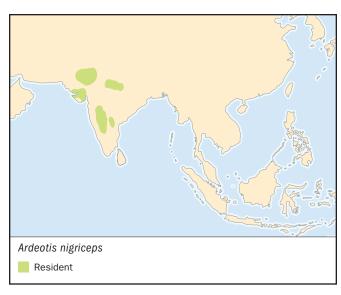
Male: 47 in (120 cm), 18–32 lb (8–14.5 kg); female: 35 in (90 cm), 7.8–15 lb (3.5–6.75 kg). Extensive black crown; head, neck, and breast white with fine dark gray barring and indistinct black breast band. Back and wings brown with fine dark vermiculations. Black panel on wing spotted with white.

DISTRIBUTION

Western and central India.

HABITAT

Rolling grassland with some shrubby vegetation, or sandy semidesert. Visits cultivation.



Vol. 9: Birds II Family: Bustards

BEHAVIOR

Solitary or in small groups. Males display on well-separated territories in the breeding season; no pair bonds.

FEEDING ECOLOGY AND DIET

Consumes grains, shoots, and berries in season, as well as arthropods, small reptiles, and mammals.

REPRODUCTIVE BIOLOGY

One egg (sometimes two) incubated for about 27 days in bare scrape by female only; fledging period 35–40 days.

CONSERVATION STATUS

Endangered. Probably fewer than 1,000 birds survive. Irrigation of semideserts, agricultural intensification, disturbance, and hunting continue to press this species toward extinction.

SIGNIFICANCE TO HUMANS

Symbol of the Bombay Natural History Society, India's largest wildlife and conservation organization. ◆

Houbara bustard

Chlamydotis undulata

TAXONOMY

Psophia undulata Jacquin, 1784. Three subspecies.

OTHER COMMON NAMES

English: Ruffed bustard; French: Outarde houbara; German: Kragentrappe; Spanish: Avutarda Hubara.

PHYSICAL CHARACTERISTICS

Male: 25.5–29.5 in (65–75 cm), 4–7 lb (1.8–3.2 kg); female: 21.5–25.5 in (55–65 cm), 2.7–3.8 lb (1.2–1.7 kg). Buff crown

Chlamydotis undulata

■ Resident

with white erectile feathers along center. Pale grayish buff head and neck with black erectile plumes down side of neck to breast. Back pale sandy buff, mottled and lined with darker brown. Female has reduced neck plumes, otherwise similar.

DISTRIBUTION

C. u. fuertaventurae: eastern Canary islands; C. u. undulata: Morocco to north central Egypt (not eastern Nile Valley or Sinai).

HABITAT

Arid semidesert with tussock grass, sandy grassland, and stony plains with scattered low shrubs; regularly on cultivation in nonbreeding season.

BEHAVIOR

Essentially solitary and nonmigratory (but locally nomadic). Males display in breeding season; no pair bonds.

FEEDING ECOLOGY AND DIET

Vegetable matter, insects, and small reptiles.

REPRODUCTIVE BIOLOGY

Main breeding season March and April. Clutch usually 2–3 eggs, laid in bare scrape and incubated for 24–28 days by female; fledging period about 35 days.

CONSERVATION STATUS

Expanded species (including *macqueenii*) considered Near Threatened. Although *undulata* is less severely hunted than its Asiatic cousin, numbers are probably much lower overall, and hunting pressure increasing. Population of race *fuertaventurae*: about 700 individuals.

SIGNIFICANCE TO HUMANS

Favored quarry of Arab dignitaries who hunt with falcons and guns. lacktriangle

Blue bustard

Eupodotis caerulescens

TAXONOMY

Otis caerulescens Vieillot, 1820, "Kaffraria" = eastern Cape Province. Monotypic.

OTHER COMMON NAMES

English: Blue korhaan; French: Outarde plombée; German: Blautrappe; Spanish: Sisón Azulado.

PHYSICAL CHARACTERISTICS

21.5 in (55 cm); 2.5–3.5 lb (1.1–1.6 kg). Blue-gray neck and underparts.

DISTRIBUTION

Eastern and central South Africa and Lesotho.

HABITAT

High rolling grasslands and croplands, usually above 4,900 ft (1,500 m).

BEHAVIOR

Pairs or small groups of up to six appear to be sedentary and group territorial, the young staying with adults for up to two years.

FEEDING ECOLOGY AND DIET

Plant matter, invertebrates, and small reptiles. Visits recently burned grasslands and plowed fields.

Family: Bustards Vol. 9: Birds II





Main breeding period October–November, 1–3 eggs laid on bare scrape in grassland, incubated for 24–28 days. Mature offspring from last brood probably cooperate in breeding attempts.

CONSERVATION STATUS

Near Threatened. Declining in some areas through agricultural intensification, but population is thought to exceed 10,000 individuals.

SIGNIFICANCE TO HUMANS

None known. ◆

White-quilled bustard

Afrotis afraoides

TAXONOMY

Otis afraides A. Smith, 1831, flats near Orange River. Three subspecies.

OTHER COMMON NAMES

English: White-quilled korhaan; French: Outarde à miroir blanc; German: Weißflügeltrappe; Spanish: Sisón Negro Aliclaro.

PHYSICAL CHARACTERISTICS

19.7 in (50 cm); 1.5 lb (0.7 kg). Black neck and underparts, with gold and brown barred spot on crown, white collar behind neck, and white ear-coverts. Wings and back barred dark brown on whitish; white on primaries is conspicuous in flight.

DISTRIBUTION

A. a. etoschae: northwestern Namibia and northern Botswana; A. a. damarensis: Namibia and central Botswana; A. a. afraoides: southeastern Botswana through northern and northeastern South Africa to Lesotho.



HABITAT

Flat grassland with sward of 19.7–39.4 in (50–100 cm), semi-desert scrub, grassy dunes, and arid savanna. Tolerates heavily grazed areas.

BEHAVIOR

Generally solitary; males display on territories using stylized flights accompanied by loud calling.

FEEDING ECOLOGY AND DIET

Variety of plant and animal material, including insects, seeds, flowers, and leaves.

REPRODUCTIVE BIOLOGY

Breeds almost throughout year, but mainly September to March. Lays one, sometimes two, eggs on bare ground. Incubation period 19–21 days in captivity.

CONSERVATION STATUS

Not threatened. Common in most of range.

SIGNIFICANCE TO HUMANS

None known. ◆

Bengal florican

Houbaropsis bengalensis

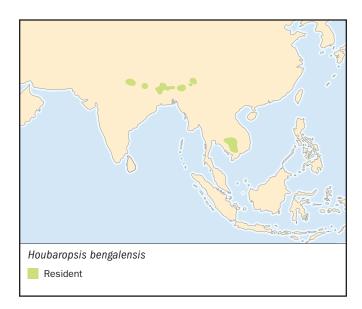
TAXONOMY

Otis bengalensis Gmelin, 1789, Bengal. Sometimes merged with *Eupodotis*. Two subspecies.

OTHER COMMON NAMES

French: Outarde du Bengale; German: Barttrappe; Spanish: Sisón Bengali.

Vol. 9: Birds II Family: Bustards



PHYSICAL CHARACTERISTICS

Male: 25 in (64 cm), 2.8–3.8 lb (1.25–1.7 kg); female: 27 in (68 cm), 3.8–5 lb (1.7–2.25 kg). Back and tail buffy brown, vermiculated with black pattern. Male has head, neck, and underparts black. Female has buffy head and underparts.

DISTRIBUTION

H. b. bengalensis: along border of southern Nepal and India, east to lowlands of Assam; H. b. blandini: central and southern Cambodia, southern Vietnam.

HABITAT

Flat grasslands, often with scattered shrubs, or in recently burned patches. Visits cultivation.

BEHAVIOR

Both races dispersive, *b. blandini* probably with regular short distance migration. On breeding grounds, males make display flights from traditional sites.

FEEDING ECOLOGY AND DIET

Mainly vegetable matter in the nonbreeding season, invertebrates in the breeding season.

REPRODUCTIVE BIOLOGY

One to two eggs laid in March to June (India) on bare scrape where incubated for 25–28 days. No pair bond; female responsible for all incubation and chick rearing.

CONSERVATION STATUS

Endangered. Total population thought to be around 500 individuals in India/Nepal, but unquantified Indochinese population possibly contains several thousand birds. Conversion of grasslands and heavy hunting in some areas are the main threats.

SIGNIFICANCE TO HUMANS

Important food source in Cambodia. ◆

Little bustard

Tetrax tetrax

TAXONOMY

Otis tetrax Linnaeus, 1758, France. Monotypic.

OTHER COMMON NAMES

French: Outarde canepetière; German: Zwergtrappe; Spanish: Sisón Común.

PHYSICAL CHARACTERISTICS

17 in (43 cm); male: 1.7–2.2 lb (0.8–1 kg); female: 1.5–2 lb (0.7–0.95 g). Upperparts buffy brown, lightly vermiculated with black; tail white mottled with three bars. Breeding male has blue-gray face, black neck and breast, with white V at foreneck and white band across breast, and white undersides. Female has buff face, neck, and breast, with streaking and barring on breast. Nonbreeding male is similar to female.

DISTRIBUTION

Western Mediterranean basin, Turkey, Ukraine, and southwestern Russia through Kazakhstan and Kyrgyzstan, extreme northwestern China and extreme northern Iran. Eastern populations winter to Iran, Azerbaijan, and Afghanistan.

HABITAT

Flat or rolling short-grass plains, stony semideserts, pasture, and fallow land.

BEHAVIOR

Highly gregarious in mixed-sex groups outside breeding season. Males give crepuscular jumping display in breeding season.

FEEDING ECOLOGY AND DIET

Invertebrates and plant material, the former predominate in summer, the latter in winter.

REPRODUCTIVE BIOLOGY

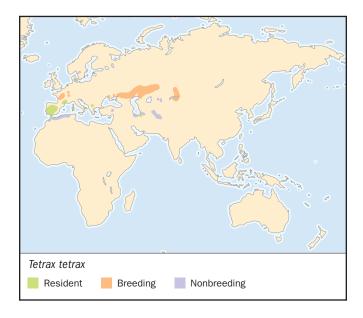
Two to six eggs laid February to June in bare scrape, usually in grassy cover; incubated by female 20–22 days, remaining with her until first autumn.

CONSERVATION STATUS

Near Threatened. Although over 100,000 individuals probably survive, there has been a massive decline almost throughout its range, particularly in the east where habitat modification continues, and hunting is not controlled.

SIGNIFICANCE TO HUMANS

Favorite food item and target of hunters in many countries. •



Family: Bustards Vol. 9: Birds II

Resources

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Joseph Andrew Tobias, PhD

Charadriiformes

(Gulls, terns, plovers, and other shorebirds)

Class Aves

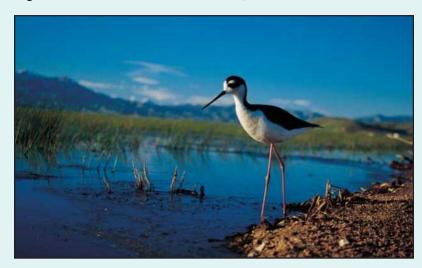
Order Charadriiformes

Number of families 13 families

Number of genera, species 91 genera,

approximately 343 species

Photo: A black-necked stilt (*Himantopus mexicanus*) at Camas Prairie Centennial Marsh Wildlife Management Area in Idaho. (Photo by Michael Wickes. Bruce Coleman Inc. Reproduced by permission.)



Introduction

The Charadriiformes represent one of the largest avian orders and exhibit an astounding diversity in morphology, behavior, and life histories. Species range in size from 0.06-4.4 lb (25 g-2 kg), with considerable variation in such characteristics as body form, leg length, and bill design. Further, the habits of these birds vary from gregarious to solitary and migratory to sedentary. Reflecting the diversity of this taxonomic group, the Charadriiformes have a global distribution and occur in a variety of environments. As a result of all these factors, generalizations across the group are problematic. However, member species do share a number of common characteristics. Chief among these is a marked preference for inland water and marine habitats. In addition, many species are gregarious and congregate during all or various phases of the annual cycle. The Charadriiformes are generally grouped into three major suborders consisting of shorebirds or waders (Charadrii); gulls, skimmers, jaegers, skuas, and terns (Lari); and auks (Alcae).

Evolution and systematics

The Charadriiformes are an ancient assemblage, with fossil evidence dating as far back as the Eocene epoch, over 36 million years ago. Storrs, Olson, and Feduccia proposed that a group of "transitional" shorebirds represent the basal lineage for all neognaths, the major group of extant birds. A premise of their theory was that ancestral Charadriiformes were one of the few avian groups to survive the massive extinction event of the late Cretaceous period, the same event that marked the disappearance of the dinosaurs. These prehistoric birds are believed to have displayed combined features of modern shorebirds, ducks, and other waterbirds. Since the Cretaceous period, the Charadriiformes have undergone an extensive adaptive radiation that resulted in their

diversity of form and function. For centuries, naturalists and taxonomists have struggled with the classification and evolutionary relationships of the different Charadriiformes. Efforts to determine their affinities have relied on an array of morphological, behavioral, biochemical, and molecular evidence and resulted in a myriad of groupings. It is clear that no single trait dictates inclusion or binds this diverse order together. Currently, the Charadriiformes are recognized as a cohesive group based on an assortment of characters. For example, morphological traits common to most members include a schizognathous palate, rump feathers with an aftershaft, a bilobed and tufted uropygial gland, and similarities in syrinx and leg tendons. An alternative taxonomy resulted from the complete avian phylogeny constructed in the 1990s by Sibley and Ahlquist. This effort was based on DNA/DNA hybridization studies and the authors maintained the association of species found in the charadriiform grouping; however, some species were lumped in the collective order Ciconiiformes, along with various other waterbirds. Although considered an important contribution, their methodology has received considerable criticism that has prevented wide acceptance. Undoubtedly, continued research efforts and the advent of increasingly sophisticated analytical methods will result in the further refinement of the Charadriiformes classification. In particular, analyses of mitochondrial and nuclear DNA promise to provide some of the most complete and persuasive information.

General ecology

The Charadriiformes occur in a wide range of waterassociated habitats at inland, nearshore, coastal, island, and pelagic areas. These habitats are generally extremely productive and provide a rich source of food for breeding, migrating, and wintering birds. However, some of the most Order: Charadriiformes Vol. 9: Birds II



Horned puffin (*Fratercula corniculata*) on Pribilof Islands, Alaska. (Photo by Art Wolfe. Photo Researchers, Inc. Reproduced by permission.)

productive sites also occur in regions where harsh conditions prevail during various times of the year. As a result, the Charadriiformes exhibit various morphological and behavioral adaptations related to survival and the ability to exploit these environments. Fundamental to most Charadriiformes is the issue of osmoregulation, meaning the maintenance of an appropriate balance of body water and salts in a saline environment. This is harder to achieve for those species that inhabit regions with few freshwater sources. However, the Charadriiformes have highly specialized supra-orbital salt glands that provide an effective means of excreting excess salt. Another strategy to exploit resources in regions that are inhospitable at various times is to migrate. Although some species are sedentary, the Charadriiformes generally exhibit a wide range of annual movement patterns. In particular, shorebirds and terns display some of the most remarkable migratory feats. For example, the Arctic tern (Sterna paradisaea) annually migrates over distances of more than 18,000 mi (28,962 km) between Arctic breeding grounds and wintering areas in extreme southern latitudes. The Pacific golden plover (Pluvialis fulva) completes a nonstop journey of more than 2,200 miles (3,540 km) between Hawaii and Alaska in less than two days.

The Charadriiformes display considerable variation in mating and social habits. Most species are monogamous and in many cases maintain pair bonds in successive breeding seasons. Adherence to a monogamous system, particularly in the Alcae and Lari, is possibly related to the requirements of nest defense and bi-parental care of young. In contrast, polyandrous and polygynous behavior occurs in a number of the shorebirds (Charadrii). Examples include the phalaropes (genus *Phalaropus*; family Scolopacidae), jacanas (family Jacanidae), and some sandpipers (family Scolopacidae). Another fascinating aspect of Charadriiform social systems is the gregarious nature of many species during various phases of the annual cycle. This is most pronounced in the colonial nest-

ing habits of gulls and terns (family Laridae), and alcids (family Alcidae). Colonies range in size from hundreds of birds to hundreds of thousands of birds. Additionally, a small number of shorebirds, such as the banded stilt (*Cladorhynchus leucocephalus*) of Australia, are semi-colonial or colonial breeders. Outside the breeding period, many species also occur in large flocks on migration and at wintering sites. For example, it is estimated that over five million shorebirds stop at the Copper River Delta in Alaska each spring.

Nest construction in most Charadriiformes is relatively crude. In fact, many of the cliff nesting seabirds (e.g. Alcae) lay eggs directly on rock ledges with no nesting material. Shorebird nests generally consist of a shallow scrape lined with small pebbles and bits of vegetation. Perhaps the most unusual nesting habits of the Charadriiformes are found in some murrelets (genus Brachyramphus) and some sandpipers (Scolopacidae) that build nests in trees or reuse nests constructed by songbirds. Clutch size ranges from 1-4 eggs with an incubation period of three or more weeks. Shorebird chicks are precocial and leave nests shortly after hatching, while many of the seabird chicks (Alcae and Lari) remain at or near nests for extended periods. The diversity of Charadriiformes is exemplified by their range of diets and foraging strategies. Diet ranges from animal to vegetable matter and in some cases is highly specialized. For instance, many species are piscivorous. Of these, the terns are skilled fliers with relatively long, narrow wings and a slight build. Foraging individuals plunge into the water from above to deftly catch fish near the surface. In comparison, the alcids are stockier marine birds, with short wings well adapted for use when swimming underwater in pursuit of prey. Also, their bills are narrow and sharp-tipped with ridged edges for holding onto fish. The skimmers (genus Rhynchops), are primarily tropical birds with a bill design that is unique among birds. In this group, the lower mandible extends further than the truncated upper mandible. When foraging, birds skim low over the water and use their specialized bill to grab fish from near the surface of the water. Another important food among the Charadriiformes is aquatic and terrestrial invertebrates. The group that has evolved the greatest diversity of foraging strategies associated with an invertebrate diet is the shorebirds, which exhibit a wide array of bill and leg morphology. For instance, the plovers are relatively short, stocky birds of upland and shallow wetland habitats. In most cases, these birds are generalist, visual foragers with short bills that are used to pick small invertebrates from the surface of the substrate. In contrast, the sandpipers and other scolopacids forage almost entirely in wetland habitats of coastal and inland areas and often use tactile cues to capture prey. Their bills vary in length and in some cases are highly sensitive, with the ability to detect prey items that live in mudflats and other soft sediments. A number of the alcids are plankton feeders with short, wide bills and strong, flexible tongues to aid in handling prey. Also, these birds have a modified gular pouch that is used for storing and carrying food to their young. In addition to animal matter, many Charadriiformes are omnivorous with a diet that includes varying amounts of vegetable matter. The sheathbills (family Chionidae) are generalists of extreme southern latitudes. During some parts of the year, particularly when other food sources are scarce, a significant portion of their diet consists Vol. 9: Birds II Order: Charadriiformes

of algae. Species following this diet include the enigmatic plains-wanderer (*Pedionomus torquatus*) and seedsnipes (genera *Thinocorus* and *Attagis*). More than 50% of the plains-wanderer diet consists of seeds and in spite of their name, most seedsnipes subsist almost entirely on buds, leaf tips, and small green leaves.

Conservation status

Whereas a number of charadriiform species have expanded their range and increased in numbers, the vast majority face an uncertain future and in some cases have experienced severe declines. A total of 34 different species are considered vulnerable, endangered, or critically endangered by the international community. For example, the black stilt (Himantopus novazealandiae), once common in New Zealand, now numbers less than 100 birds and ranks as one of the most endangered species in the world. It is clear that the greatest threats facing the Charadriiformes and other avian groups arise from the effects of expanding human populations. Complicating matters, there are various aspects of charadriiform ecology that increase the vulnerability of the group. In particular, the productive waters of coastal and inland habitats attract not only large numbers of birds, but also the activities of humans. These areas are increasingly the focus of development and exploitation of resources, such as fish and petroleum. In addition, the tendency for many Charadriiformes to congregate during all or various phases of the annual cycle increases the potential impacts of various threats, such as habitat loss and catastrophic events. In some cases, exposure to such forces is not a recent



Fairy tern couple at French Frigate Shoals, Hawaiian Islands National Wildlife Refuge. (Photo by Frans Lanting. Photo Researchers, Inc. Reproduced by permission.)

event. Historically, many charadriiform species were harvested by humans for meat, feathers, oil, and eggs. Often, this consumption was part of subsistence hunting with limited impacts on the persistence of bird populations. However, expanding human populations and advances in exploration and technologies progressively led to dramatically increased harvests of some species. Large flocks of sandpipers were easy targets for hunters during migrations and at wintering areas, with reports of wagons filled and barrels packed with birds for market. It is thought that such persecution led directly to the demise and probable extinction of the Eskimo curlew (*Nume*-



Herring gulls (Larus argentatus) stealing fish. (Photo by David T. Overcash. Bruce Coleman Inc. Reproduced by permission.)

Order: Charadriiformes Vol. 9: Birds II



Ruddy turnstones (*Arenaria interpres*) during spring migration in Churchill, Manitoba, Canada. (Photo by Bob & Clara Calhoun. Bruce Coleman Inc. Reproduced by permission.)

nius borealis). Harvests of colonial nesting sea birds (e.g., Alcids) have been equally dramatic. Explorers, whalers, fishermen, and traders often stopped at seabird colonies to replenish stores by harvesting large numbers of birds and eggs. Over time, the ability to market this resource led to even greater takes. A noted example involves the great auk (Pinguinus impennis) that was driven to extinction in the mid-1800s. A growing body of research and expanded monitoring efforts has resulted in a greater understanding of the impacts of harvests on bird populations. Knowledge of dramatic declines has led to increased protection through legislation and the regulation of hunts. Even so, in some regions harvests continue at unsustainable levels. For example, an estimated 300,000–400,000 thick-billed murres (Uria lomvia) were killed in Greenland in 1988-89. The widespread loss and alteration of interior and coastal wetland habitats has been implicated in the decline of numerous species. For example, in North America, the mountain plover (Charadrius montanus), the piping plover (Charadrius melodus), and the snowy plover (Charadrius alexandrinus) have all experienced significant range contraction and population declines as a result of the degradation of interior upland, wetland, and riverine systems. In various coastal areas, there is also the constant danger of catastrophic oil spills. The progressive increase in the world harvests of fish and other marine resources has also led to increased interactions of fisheries and marine birds. Troublesome negative effects on birds include entrapment in fishing gear, prey depletion, and disturbance. Other major conservation issues include the introduction of non-native species (particularly at seabird colonies), disturbance from human recreational activities, and the potential effects of climate change.

Suborder Charadrii

Shorebirds, also referred to as waders, are the largest and most diverse group of Charadriiformes with 11 families and 216 species. This includes the thick-knees (Burhinidae); plovers (Charadriidae); sheathbills (Chionidae); crab plovers (Dromadidae); coursers and pratincoles (Glareolidae); oystercatchers (Haematopidae); jacanas (Jacanidae); stilts and avocets (Recurvirostridae); painted snipes (Rostratulidae); phalaropes, snipes, and sandpipers (Scolopacidae); and seedsnipes (Thinocoridae). These birds occur in a wide range of environments including coastal and inland wetlands, grasslands, and even deserts.

Suborder Lari

The single-family Lari suborder consists of the gulls, terns, skimmers, jaegers, and skuas (Laridae). The skimmers and terns are primarily piscivorous and occur in marine and freshwater habitats. Skuas and jaegers are found at nearshore, coastal, and pelagic areas. These aggressive birds are known for their kleptoparasitic and predatory habits, in many cases preying on the young of other seabirds. The gulls are generalist foragers, occurring in a range of inland, marine, and coastal habitats.

Suborder Alcae

Also consisting of a single family, the auks (Alcidae) are restricted to marine environments of the Northern Hemisphere. In these regions, the auks fill the niche of the penguins found in southern latitudes. Auks are short-winged birds that

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are specialized for diving to capture fish and feed on plankton. A majority are colonial nesters, often nesting on cliffs at rocky coastal areas. In some cases, breeding colonies number in the tens to hundreds of thousands. A notable exception are the murrelets, some of which nest in trees and may occur many miles (kilometers) inland.

Resources

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Peter Martin Sanzenbacher, MS

Jacanas (Jacanidae)

Class Aves

Order Charadriiformes Suborder Charadrii

Family Jacanidae

Thumbnail description

Medium-sized waterbirds with elongated legs and extremely long toes, which they use to walk on floating aquatic plants

Size

6-23 in (15-58 cm); 1.4-9.7 oz (40-275 g)

Number of genera, species

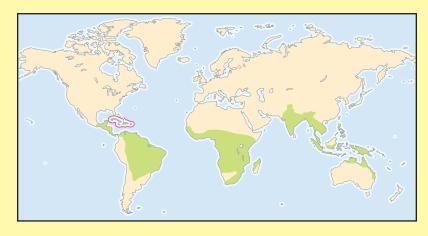
6 genera; 8 species

Habitat

Inland lakes, ponds, and marshes with floating vegetation; also flooded farm fields and wet grassy areas

Conservation status

Not threatened



Distribution

Tropical and subtropical regions in Central America, South America, Africa, India, Australia, and Asia

Evolution and systematics

Grouped with gulls and shorebirds, jacanas belong to the same suborder (Charadrii) as similar small, long-legged birds found near water, such as sandpipers, plovers, and snipes.

Since jacanas have similarities in appearance and behavior to rails, some researchers have suggested that they are related to Gruiformes, but recent studies call this theory into question. Instead, scientists believe jacanas are more closely related to sandpipers and painted snipes. In all, eight species of jacanas are grouped within six genera.

Studies have shown the Charadriiformes separated from the Gruiformes in the late Cretaceous period. While jacanas appeared more recently, little fossil evidence has been found. A DNA analysis found two geographically distinct taxa for all six genera of jacanas, including the painted snipe. They included the New World *jacana* and Asian *bydrophasianus* in one group and the African *microparra* and Australian *irediparra* in the other. Scientists suggested this pattern resulted from the extinction of intervening African and Asian taxa.

Scientists are still studying the evolutionary reason for another unusual characteristic of jacanas: they are polyandrous (females mate with more than one male). Jacanas also exhibit sex-role reversal. Males tend the nest and care for chicks while the larger, more aggressive females defend the territory from predators. Researchers have theorized that jacanas may have evolved with this unorthodox system to compensate for a high rate of egg and chick loss, which typically is greater than 50% due to their unstable aquatic habitat and attacks by water snakes, turtles, and larger birds. If females can spend less time

sitting on the nest and more time mating with multiple partners, scientists argue, they can lay more eggs and contribute to the overall success of the species.

Physical characteristics

Lesser jacanas have neotenous plumage, downy chicks, carpal spurs, cornified leading edge of radii, and frontal shields, wattles, or combs.

Of all the waterbirds, jacanas have the longest toes and claws, which can reach 4 in (10.2 cm) long in some species. Jacanas evolved with these slender feet to help them better adapt to their watery environment. They can easily skip across lily pads and other floating plants to search for food, build nests, and evade predators.

Like their close relatives the plovers, some jacanas have a metacarpal spur jutting out from the bend in their wing. They use these sharp, bony weapons to threaten rivals and predators during fights.

Also called "lily trotters," the most dramatic jacana feature is oversized feet, which help them to balance on lily pads. They sometimes appear to walk on water, which is why the jacana is also called the "Jesus bird" in some areas.

Jacanas are medium-sized birds with long, slender necks. The largest species is the pheasant-tailed jacana (*Hydrophasianus chirurgus*). This foot-long bird grows resplendent tail feathers, which can reach 20 in (50.8 cm) in length. The smallest species in the family is the 6 in (15.2 cm) lesser jacana (*Microparra capensis*). Female jacanas are 60% heavier than males.

Family: Jacanas Vol. 9: Birds II



An African jacana (*Actophilornis africanus*) nest with eggs in Botswana. (Photo by Virginia Weinland. Photo Researchers, Inc. Reproduced by permission.)

Jacanas appear rather plain, with black or reddish-brown plumage, but when they spread their wings they are very dramatic birds. Jacanas often flash their contrasting flight feathers to startle predators. The flight feathers may be contrastingly colored, depending on the species. In the northern jacana, for example, wing tips are bright yellow. Most jacanas also have a colorful frontal shield. Male and female jacanas have the same coloration. With the exception of the northern and lesser species, jacanas lose all of their flight feathers concurrently during the annual molt, making them temporarily flightless.

Young jacanas have brown plumage with white underparts. They assume adult characteristics after about a year. Newly fledged jacanas have a smaller forehead shield.

Jacanas may not have melodious calls, but they are very vocal, especially when breeding and caring for young. Ornithologists have described the northern and pheasant-tailed jacanas' calls as a cat-like mewing sound, which can turn into a more strident cry during times of stress or crisis. Males and females give the same calls, but males have higher voices and vocalize more often.

Distribution

Jacanas are widely distributed across the tropical areas of the world, including Central and South America, Africa, Asia, Australia, and Madagascar.

The American representative of this family is the northern jacana (*Jacana spinosa*), whose popular and scientific names are derived from a Tupi Indian expression. There are nine subspecies of *Jacana spinosa*, distributed from Mexico to Argentina.

The African jacana, or lily trotter (Actophilornis africanus) and the lesser jacana (Microparra capensis) are found south of

the Sahara in Africa, along with the Malagasy jacana (*Actophilornis albinucha*), which is close to the African jacana. There are two species in India; one of these, the pheasant-tailed jacana (*Hydrophasianus chirurgus*), is conspicuous because of a long tail, wings that are dazzling white in flight, and golden-yellow neckband. Its breeding area reaches as far as China and Afghanistan. The comb-crested jacana, (*Irediparra gallinacea*), has three subspecies with a distribution from Borneo to Australia.

Habitat

Water is the key requirement for jacana habitat. They also need thick mats of floating aquatic vegetation for shelter, nesting material, and food supplies. Freshwater marshes are the preferred habitat, although they have been known to feed in flooded pastures, rice fields, ephemeral ponds, and sometimes in emergent marsh vegetation.

Jacanas can be found from sea level to 8,000 feet (2,438 m). They prefer lowland ponds and marshes with an unobstructed view of the water. Jacanas rarely, if ever, occur in forested areas.

Behavior

From the time they hatch, jacanas can swim and dive. They use this ability to escape predators when they are young and during the molting period when the adult bird loses its flight feathers.

Despite their size, jacanas are very inconspicuous birds. Adults and chicks are adept at hiding in aquatic vegetation.

Jacanas usually are found in pairs, grouped in clusters of territories. Each female mates with and defends the territory of one to four or more males at a time, and each territory can be as large as half a football field. For example, territories for bronze-wing jacanas range in size from 40–347 acres (16.5–139 hectares). The northern jacana's territory ranges in size from 0.25–1.7 acres (0.1–0.69 hectares). Unattached female rivals often will approach a mated pair and challenge the dominant female in an attempt to take over her territory. If the rival female is successful, she may kill chicks produced by the previous pair so that she can begin mating with the male.

Male and female partners work together to defend their territory. If a predator enters their boundaries the male, who sits on the nest, will call to the female. The female will come close and, if necessary, physically attack an intruder or rival female. The conflict usually begins with a territorial display. The female spreads her feathers, with wings slightly down and forward, to display sharp wing spurs. If the predator comes closer, the female may strike with wing spurs or jab with the bill.

Males have a complex range of calls to signal danger to their offspring. When they hear these sounds, chicks move closer to the male. He gathers them under his wings to protect them, or encourages them to hide under water plants. Many juvenile jacanas have evolved with special breathing holes at the end of their bills. This allows them to dive underwater to safety, with only the tips of their bills emerging

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from the surface. When the male signals that it is safe, they come out of hiding. Observers have noted this "snorkeling" behavior in young wattled jacanas, northern jacanas, and pheasant-tailed jacanas. At other times, the male may fake a broken wing to lure a predator away from chicks.

In rare cases, jacanas will develop a symbiotic relationship with other animals in their environment. For example, a researcher in the Congo observed an African jacana standing on a hippopotamus, grooming its back. Jacanas also clean ticks from capybaras.

Jacanas generally do not migrate, but the pheasant-tailed jacana is a partial migrant. Jacanas remain in the same place as long as they have suitable habitat. If drought conditions cause a pond to dry up, however, they may move to an area with a better supply of aquatic plant material. When they are not breeding, jacanas may flock together by the hundreds.

Feeding ecology and diet

Jacanas' primary food source is insects, which they find by perching on floating water lily leaves with their heads down and turning leaves over with their toes. Invertebrates such as aquatic moth larvae are another source of food. They seem to prefer small, floating organisms to flying insects. Jacanas occasionally eat small fish, but this is rare.

Jacanas use their bills to forage for seeds and insects caught in the fibrous roots of water lilies. They also may run their bills along the stems of marsh grasses to collect and eat other types of seeds.

Female jacanas help build and defend the nest of offspring, but only males are responsible for feeding the chicks.

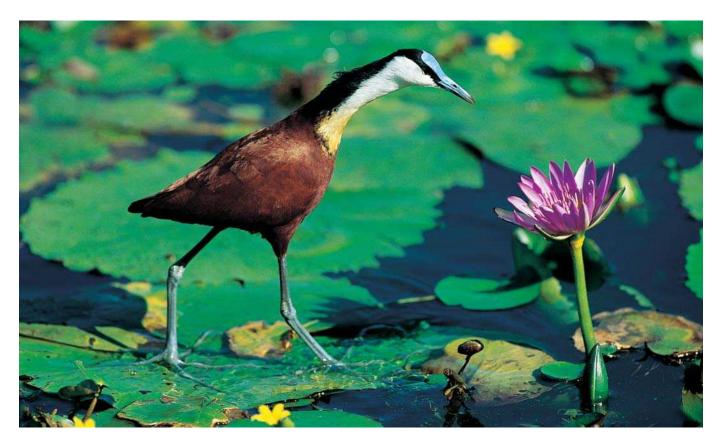
Reproductive biology

During the rainy season, when nesting material and food are in ample supply, jacanas will begin actively breeding. Unlike other bird families, jacana females dominate the process.

Once a female initiates courtship, a male starts building several nest sites. The more aggressive female will choose which nest to use for laying eggs, or she may choose an entirely different site in the male's territory and the male will have to build a new nest. Jacana nests are not elaborate; they consist of water lily leaves and other plant material heaped on top of a thick mat of floating vegetation.

Courtship begins when the female approaches an eligible male. The two birds may flash their wings and call to each other. As a sign that a pheasant-tailed jacana female is ready to mate, she may grow larger and develop more distinctive tail feathers. When a female takes over a rival female's territory, she often displays her dominance by pecking at the male's neck and back. The male signals submissiveness by crouching and lowering his head.

Because females are busy guarding harems of four or five males, the males sit on the nest and incubate eggs. Studies



An African jacana (Actophilornis africanus) walks on lilypads to feed on insects in a lily flower in South Africa. (Photo by Nigel Dennis. Photo Researchers, Inc. Reproduced by permission.)

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have shown that female jacanas, who mate with several partners simultaneously, often will lay eggs from several different males in one clutch. In other words, a male may spend days caring for eggs and offspring that are not his own.

Female jacanas typically produce four small eggs that are glossy brown and covered with speckles. To better warm the eggs, males have evolved with incubation patches (special areas of increased circulation) on their chests. After a long incubation period of 22–28 days, chicks emerge from their shells. At first they are covered with downy plumage that has a striped camouflage design. Like their parents, they are born with extremely large feet.

In addition to incubating the eggs, males are primary caregivers. As soon as the chicks hatch, the male teaches them to forage for plants and insects while paddling around the lily pads. The male sends the chicks out to search for food, then calls them back to check on them. Ornithologist Alfred Hoffman, who studied Chinese pheasant-tailed jacanas in the 1940s, described the male jacana as a devoted father: "First he plants himself with his legs spread, then lowers his body a little by bending his legs and raising his wings slightly, and with them he protects the chicks as they snuggle up to him. Such a comforting rest period of about five to 10 minutes breaks up the strenuous wanderings in search of food."

Despite the male's vigilant parenting skills and the female's vigorous defense of boundaries, juvenile jacanas face low odds of survival. More than 50% never make it out of the nest. Of those that survive, fewer than 50% reach adulthood. In some species, such as the African jacana, the failure rate is as high

as 90%. The jacana's most common predator is the purple gallinule (*Porphyrula martinica*, family Rallidae), which often robs eggs from the nest. Floods, water snakes, otters, and turtles also pose a threat.

Conservation status

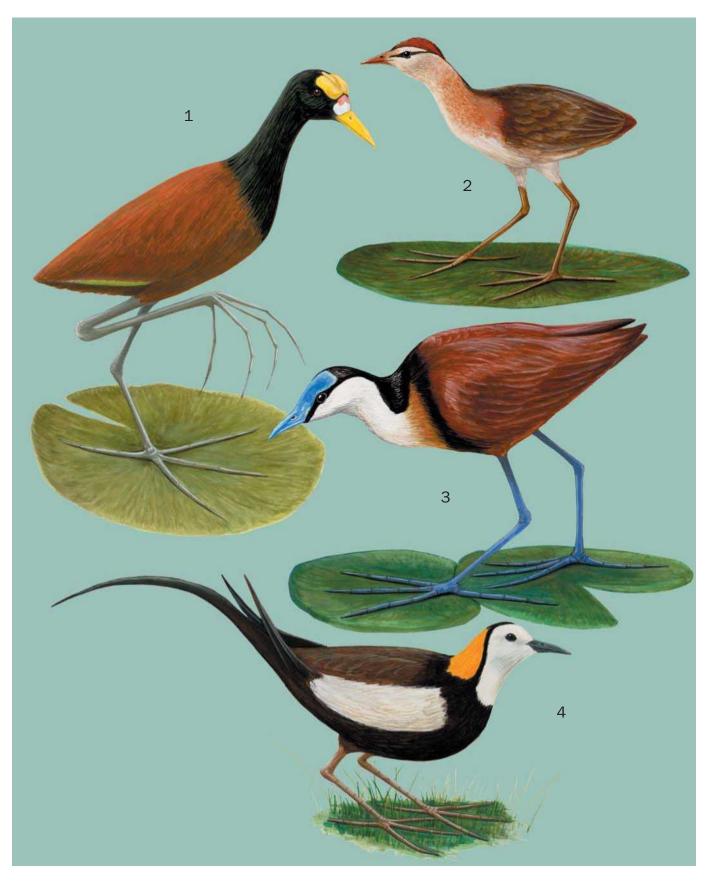
Currently, there are no threatened species. Jacanas depend on wetlands for survival, but in many parts of the world their habitat is being drained to make way for housing and commercial development or agriculture.

In Taiwan, local conservationists took steps to create a new habitat for a group of pheasant-tailed jacanas threatened by a high-speed rail project under construction in their territory.

Some studies show that pesticides may pose a danger to jacanas. In one area, near a coffee plantation in Costa Rica, researchers noted that pesticide exposure may have caused a decrease in egg-laying activity.

Significance to humans

Jacanas are not in danger of shooting or trapping anywhere in their range. Because most jacana species are well known to local fishermen and suffer relatively little persecution, they are often tame and confiding. In much of the world they are found on artificial water bodies, often fairly close to human habitation.



1. Northern jacana (*Jacana spinosa*); 2. Lesser jacana (*Microparra capensis*); 3. African jacana (*Actophilornis africanus*); 4. Pheasant-tailed jacana (*Hydrophasianus chirurgus*). (Illustration by Dan Erickson)

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Species accounts

Northern jacana

Jacana spinosa

TAXONOMY

Jacana spinosa Linnaeus, 1758, western Panama. Three subspecies.

OTHER COMMON NAMES

English: American jacana; French: Jacana du Mexique; German: Gelbstirn-Blatthühnchen; Spanish: Jacana Centroamericana.

PHYSICAL CHARACTERISTICS

6.7–9 in (17–23 cm). Females are 60% heavier than males. Adults have reddish-brown plumage with contrasting greenish-yellow wing feathers and a yellow forehead shield. Juveniles are light brown and white.

DISTRIBUTION

Year-round resident in Mexico, from Gulf of Mexico south, including Yucutan peninsula and Cozumel, Central America, and West Indies; also occasionally appears in southern Texas, north to Austin and west of San Antonio, where it used to breed.

HABITAT

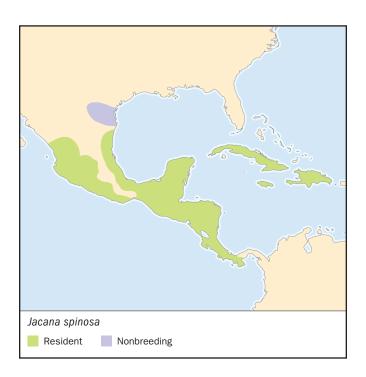
Marshes, ponds, and lakes with floating aquatic vegetation; also rivers, flooded pastures, and wet meadows. Breeds in both permanent and seasonal wetlands.

BEHAVIOR

Males and females actively defend territories with vocal calls. Females will engage in fights with intruders.

FEEDING ECOLOGY AND DIET

Prefers a variety of aquatic plants and insects; except for water lily seeds, ingestion of plant material may be incidental.



REPRODUCTIVE BIOLOGY

Breeds during rainy season if a permanent marshland is available. Females are polyandrous and mate with up to four males and guard their territories. Males incubate eggs and care for chicks. Males build nests of leaves and plants on floating vegetation. Females lay four glossy brown speckled eggs. Incubation is 22–28 days. Breeding success is less than 50%.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Pheasant-tailed jacana

Hydrophasianus chirurgus

TAXONOMY

Chirurgus Scopoli, 1786, Luzon, Philippines. Monotypic.

OTHER COMMON NAMES

English: Chinese water pheasant; French: Jacana àlongue queue; German: Wasserfasan; Spanish: Jacana Colilarga.

PHYSICAL CHARACTERISTICS

11–12.2 in (28–31 cm); 4.8–8 oz (126–231 g). Largest species in the jacana family. Dark plumage with contrasting white wing tips and yellow neckband. Long, dramatic tail feathers in breeding male.

DISTRIBUTION

Pakistan, India, Nepal, Sri Lanka, Myanmar to southeast China, to southeast Asia, Java, and the Philippines.



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HABITAT

Marshes, ponds, and lakes with floating aquatic vegetation. Uses emergent vegetation more in winter.

BEHAVIOR

Uses elongated toes to walk on floating vegetation; only flies short distances. Spends much of its time sunning, preening, and foraging for food when not defending its nest.

FEEDING ECOLOGY AND DIET

Prefers insects and invertebrates.

REPRODUCTIVE BIOLOGY

Breeds during rainy season. Females are polyandrous and mate with up to four males and guard their territories. Males incubate eggs and care for chicks. Males build nests of leaves and plants on floating vegetation. Females lay four glossy brown speckled eggs. Incubation is 22–28 days. Breeding success is less than 50%.

CONSERVATION STATUS

Some populations have been threatened in China and Taiwan by habitat loss due to drained wetlands and high-speed rail projects.

SIGNIFICANCE TO HUMANS

None known. ◆

Lesser jacana

Microparra capensis

TAXONOMY

Parra capensis Smith, 1839, Algoa Bay, South Africa. Monotypic.

OTHER COMMON NAMES

English: Lesser African jacana, lesser lily trotter; French: Jacana nain; German: Zwergblatthühnchen; Spanish: Jacana Chica.

PHYSICAL CHARACTERISTICS

6 in (15 cm); 1.4 oz (41 g). Smallest species in the jacana family. Brown plumage with white underparts. Adults resemble juveniles of other jacana species.

DISTRIBUTION

Tropical Africa, including parts of Mali, Sudan, Ethiopia, Uganda, Kenya, Zambia, Zimbabwe, Mozambique, South Africa, Angola, and Namibia.

HABITAT

Marshes, ponds, and lakes with floating aquatic vegetation. Also shallow water, often in emergent vegetation (sparse sedge and grass).

BEHAVIOR

Males and females actively defend territories with vocal calls. Females will engage in fights with intruders.

FEEDING ECOLOGY AND DIET

Primarily insects. Swims like a phalarope.

REPRODUCTIVE BIOLOGY

This is the only monogamous species, with both males and females sharing equally in nest incubation and caring for chicks.

CONSERVATION STATUS

Not threatened.



SIGNIFICANCE TO HUMANS

None known. ◆

African jacana

Actophilornis africanus

TAXONOMY

Parra africana Gmelin, 1789, Ethiopia. Monotypic.

OTHER COMMON NAMES

English: Lily trotter; French: Jacana àpoitrine dorée; German: Blaustim-blatthühnchen; Spanish: Jacana Africana.

PHYSICAL CHARACTERISTICS

9-12.2 in (23–31 cm); 4-9 oz (137–261 g). Brown with white and black areas. Blue forehead shield.

DISTRIBUTION

Tropical Africa, including wetlands of sub-Saharan Africa. Rarely found in forests or dry areas.

HABITAT

Marshes, ponds, and lakes with floating aquatic vegetation, including both permanent and seasonal sites. Also uses tall vegetation near shore for shelter.

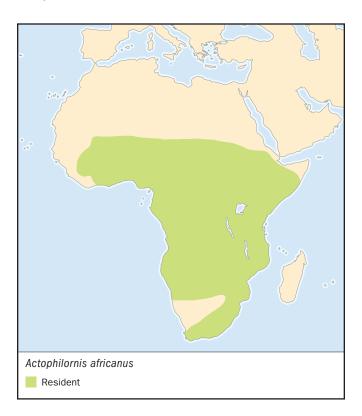
BEHAVIOR

Males and females actively defend territories with vocal calls. Females will engage in fights with intruders.

FEEDING ECOLOGY AND DIET

Eats a wide range of aquatic plant seeds and invertebrates.

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REPRODUCTIVE BIOLOGY

Breeds during rainy season. Females are polyandrous mate with up to four males and guard their territories. Males incubate eggs and care for chicks. Males build nests of leaves and plants on floating vegetation. Females lay four glossy brown, speckled eggs. Incubation is 22–28 days. Breeding success is less than 50%.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

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Wiesner, Pat. "A Strong Case of Role Reversal." *BioScience* 42, no. 4 (April 1992): 327.

Organizations

Neotropical Bird Club. c/o The Lodge, Sandy, Bedfordshire SG19 2DL United Kingdom. E-mail: secretary @neotropicalbirdclub.org Web site: http://www.neotropicalbirdclub.org

Melissa Knopper

Painted snipes

(Rostratulidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Rostratulidae

Thumbnail description

Medium-sized, chunky waders with relatively long bills, rounded wings, and brighter, more intricately patterned plumage than true snipes, to which they bear only a passing resemblance

Size

7.4-10.9 in (19-28 cm); 2.3-7.0 oz (65-200 g)

Number of genera, species

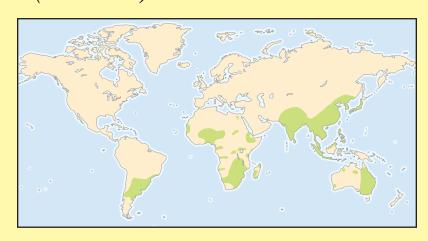
2 genera; 2 species

Habitat

Lowland wetlands, including grassland, marshes, and agricultural areas (e.g., ricefields)

Conservation status

The Australian taxa, *R. australis*, for which species status has been proposed, may require listing as Endangered



Distribution

Sub-Saharan Africa, Madagascar, South and East Asia, Indonesia, the Philippines, Australia, and southern South America

Evolution and systematics

In the 1980s, DNA-DNA hybridization studies suggested that painted snipes are most closely related to jacanas (Jacanidae), while other near relatives appear to include the phalaropes (Phalaropodinae) and some members of the sandpipers (Scolopacidae). The superficial resemblance of painted snipes to true snipes (Gallinago), from which their English name derives, is considered to have no taxonomic importance. Certain skeletal and anatomical features of the painted snipes recall the Rallidae (rails) or Gruidae (cranes), as well as woodcocks (Scolopax) and seedsnipes (Thinocoridae). Jehl's 1968 proposal that painted snipes be grouped with jacanas in the superfamily Jacanoidea, most closely aligned to another such family containing the crab plover (Dromas ardeola), with all other shorebirds belonging to a third superfamily, has gained widespread support in subsequent literature. Lack of fossil material prevents an understanding of the evolutionary history of painted snipes.

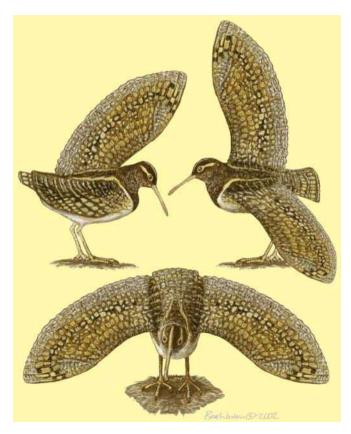
Traditionally, the Rostratulidae have been considered to represent two species in the monotypic genera *Rostratula* (greater painted snipe) and *Nycticryphes* (South American painted snipe). However, research in 2000 recommends that the Australian form of greater painted snipe (*Rostratula australis*) be elevated to species status based on its longer wing, shorter bill and legs, and coloration. Australian greater painted snipe males have boldly spotted (not barred) wingcoverts and a paler gray tail, and females possess a mainly dark chocolate-brown (rather than rufous) head and neck and discrete, round tail spots. In addition, there appears to be clear

differences in vocalizations between the two forms. Female *R. australis* almost never give the low booming advertising call that is so distinctive of nominate *R. benghalensis*. The authors of the new study, Lane and Rogers, speculate that Australian birds may lack the trachea and esophagus modifications that permit female *R. benghalensis* to make such calls.

Physical characteristics

The South American painted snipe (Nycticryphes semicollaris) is the smaller of the two/three species, measuring 7.4–9.0 in (19–23 cm) and weighing 2.3–3.0 oz (65–86 g). Like greater painted snipes (Rostratula bengalensis), its legs are strong and the toes are elongated. The bill is powerful and curves sharply downward at the tip (which has earned it the name "bicotorto," or crooked beak, in Brazil). The tip also broadens like a spatula and acquires a slight reddish tone. The head and neck are dark reddish brown with a conspicuous cream-colored crown stripe and a bright white spot at the base of the necksides. The wings are black-brown, marked by large snowwhite round spots, and the abdomen is white. Males and females are hardly distinguishable, but the latter tend to be slightly larger and possess marginally brighter plumage. In contrast, greater painted snipes exhibit a marked difference in the coloration of the sexes. Females are considerably larger and more brilliantly patterned than males. The head and neck of females are a rich chestnut brown, whereas those of males are spotted and inconspicuous. Females have bronze-green wings and upperparts that are finely barred in black (which

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Painted snipe displays. (Illustration by Bruce Worden)

look rather uniform at a distance), and males have ashy-gray upperparts that are extensively barred and spotted with golden buff, especially on the wing-coverts. Both genders have a striking pale eye patch that is elongated at the rear and a pale crown stripe and mantle V; these parts are bright white in females and golden in males. Juvenile South American painted snipes look similar to adults, but the spotting on their upperparts is reduced and cream-colored. Juvenile greater painted snipes resemble adult males but have grayer wings and reduced, paler spotting.

Distribution

Greater painted snipes are distributed widely through Africa, South and Southeast Asia, the Philippines, Indonesia, and eastern Australia. South American painted snipes are restricted to the southern third of South America.

Habitat

Lowland wetlands, including swamps, reedbeds, ricefields, man-made wetlands with sufficient cover, damp grassland, and cover along streams and rivers are all used by painted snipes. The South American species occasionally occupies more open habitats and is more restricted to true lowland habitats. Vagrant or migrant greater painted snipes are occasionally recorded at high altitudes (e.g., in the Himalayas or Tibetan Plateau). Habitat use by greater painted snipes is more closely governed by rainfall, especially in Africa where

they will relocate to recently flooded areas, and they are usually absent from regions of lower rainfall.

Behavior

Painted snipes usually occur alone or in pairs, although exceptional groups of up to 100 greater painted snipes have been reported. These aggregations may be the result of localized populations being forced into a small area of remaining wetland as its surroundings dry out. Both species perform short-distance movements in response to changing water levels, but in Australia the nonbreeding areas are completely unknown; there is one record from New Zealand at this season.

Unlike South American painted snipes, where there is apparently no sexual role reversal, it is the female greater painted snipe that advertises for a mate. A number of displays have been described, and females take a lead in courtship by uttering prolonged series of low hooting notes, either from the ground or in a woodcock-like rolling flight. The calls are reminiscent of a hiccup or the noise made by blowing across an empty bottle. Such displays are principally given at twilight. The female has a convoluted trachea that is folded and measures twice the length of the neck; this configuration permits her to make strong calls.

Feeding ecology and diet

Painted snipes are omnivorous and eat small invertebrates, such as snails, earthworms, crustaceans, and insect larvae, as well as seeds of many grasses and cultivated grain. They probe soft mud or stand in shallow water and use a scything action of the bill to sift food. In greater painted snipes, much feeding occurs at twilight or at night.

Reproductive biology

The breeding biology of both species, particularly that of the South American species, is poorly studied. South Ameri-



A greater painted snipe (*Rostratula benghalensis*) leaves the water. (Photo by M. Strange/VIREO. Reproduced by permission.)

Vol. 9: Birds II Family: Painted snipes

can painted snipes are monogamous and breed in loose colonies, with five or six nests found in 2.5–3.7 acres (1.0–1.5 ha). Greater painted snipes usually adopt a polyandrous mating system (females copulate with up to four males), although nests are often solitary. Both species construct shallow cups of reeds and grasses in waterlogged areas well-concealed by dense vegetation. Occasionally they build nests in more open wetlands. The male greater painted snipe's rather cryptic plumage serves as a defense, and he takes responsibility for nest-building, incubation, and chick-care duties. The division of parental duties (if any) are unknown in the South American painted snipe, as are incubation and fledging periods. Greater painted snipes lay two to five (usually four) eggs, and South American painted snipes lay two (rarely three) eggs. The chicks are precocial and nidifugous in greater painted snipes, being brooded for the first few days of life by the male. Young males become sexually mature at one year, whereas females probably are not sexually mature until they are two years old.

Conservation status

Neither of the traditionally recognized species is classified as being threatened, but should the Australian form *R. australis*

be treated at species level, as has been proposed, it could warrant listing as Vulnerable, perhaps even as Endangered, under IUCN criteria. Declines have been particularly pronounced in the southeast, its traditional stronghold, and in the southwest of its range. Prolonged periods of drought may have caused locally significant population declines of greater painted snipes, while the destruction and alteration of native grasslands, especially in Argentina, are presumably causing similar losses in the South American species. Very few comparative data are available, and both species are still numerous in many areas.

Significance to humans

Like true snipes, painted snipes have long been regarded as part of the sportsman's bag. However, while South American painted snipes are highly prized in Argentina and Chile for their taste, the slow escape flight of greater painted snipes means that more competent marksmen often consider such sport too easy. Neither species is held in captivity with any frequency, although some studies have been made of greater painted snipes based on birds in collections or zoos.

Family: Painted snipes Vol. 9: Birds II

Species accounts

Greater painted snipe

Rostratula benghalensis

SUBFAMILY

Rostratulinae

TAXONOMY

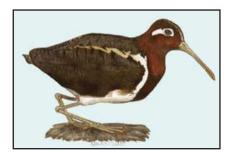
Rostratula benghalensis Linnaeus, 1758, Asia. A study published in 2000 recommended that R. australis demanded species-level recognition. Two subspecies.

OTHER COMMON NAMES

English: Painted snipe, African painted snipe; French: Rhynchée peinte; German: Goldschnepfe; Spanish: Aguatero Bengalí.

PHYSICAL CHARACTERISTICS

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Rostratula benghalensis

spotted upperparts. Both sexes have largely white underparts, pale eye patches, a crown stripe, and a mantle V. Juvenile largely resembles adult male.

DISTRIBUTION

Madagascar and Sub-Saharan Africa, with the exception of the Congo Basin. To the east, it also occurs through South and Southeast Asia, north to Japan and extreme southeast Russia, east through the Philippines and Indonesia. The form *australis*

Rostratula benghalensis

Resident Breeding

occurs in south Australia, Victoria, New South Wales, and parts of Queensland, with sporadic records from elsewhere in north Australia and west Australia.

HABITAT

Lowland wetlands, including human-made and human-modified areas.

BEHAVIOR

Solitary or in small groups. Chiefly crepuscular (active at twilight) and partially nocturnal.

FEEDING ECOLOGY AND DIET

Omnivorous, probing mud or wading in shallow water in search of insects, crustaceans, seeds, etc.

REPRODUCTIVE BIOLOGY

Polyanadrous or monogamous. Nests are usually solitary. Breeds year-round, chiefly following rains in Africa. Generally lays four eggs in shallow cup nest, concealed in marshy areas. Incubation, by male, 15–21 days, but fledging period unknown. Chicks precocial and leave the nest a short time after hatching; usually cared for by male alone.

CONSERVATION STATUS

Widespread, can range from uncommon to frequent, but often locally common. Formerly widely hunted, especially in European colonies. Declining in some areas due to wetland drainage and drought conditions. Australian population of serious conservation concern and may require IUCN listing as either Vulnerable or Endangered.

SIGNIFICANCE TO HUMANS

Principally known to sport hunters, but apparently of little significance to local human populations. ◆

South American painted snipe

Nycticryphes semicollaris

SUBFAMILY

Nycticryphinae

TAXONOMY

Nycticryphes semicollaris Vieillot, 1816, Paraguay. Monotypic.

OTHER COMMON NAMES

English: American painted snipe; French: Rhynchée de Saint-Hilaire; German: Weißflecken-Goldschnepfe; Spanish: Aguatero Americano.



Nycticryphes semicollaris

Vol. 9: Birds II Family: Painted snipes



PHYSICAL CHARACTERISTICS

7.4–9.0 in (19–23 cm); 2.3–3.0 oz (65–86 g). Both sexes have a dark reddish brown head and neck, dark grayish brown and black upperparts and wings, the latter spotted white, and

largely white underparts, pale eye patches, and a crown stripe. Females may tend to be larger and slightly brighter. Juvenile largely resembles adult.

DISTRIBUTION

Southern Brazil, Paraguay, and Uruguay to central Chile and central Argentina.

HARITAT

Lowland wetlands, including wet grasslands, estuaries, rivers and streams.

BEHAVIOR

Solitary or in small groups. Chiefly crepuscular and partialy nocturnal. Largely sedentary, with some seasonal movements dictated by rainfall.

FEEDING ECOLOGY AND DIET

Omnivorous, probing mud or wading in shallow water in search of insects, larvae, crustaceans, seeds, etc.

REPRODUCTIVE BIOLOGY

Monogamous. Nests semi-colonially. Breeds July through February, according to local conditions. Lays two or three eggs in shallow cup of grasses and reeds, often surrounded by water. Incubation and fledging periods unknown, but both sexes involved in chick care.

CONSERVATION STATUS

Widespread, but usually uncommon or localized. Very few precise data concerning populations, but probably known from rather few protected areas. Presumably declining, especially in northeast Argentina, due to wetland drainage and conversion of grasslands to agriculture and forestry.

SIGNIFICANCE TO HUMANS

Highly prized by hunters in Argentina and Chile for its tender, tasty flesh, and often shot in the breeding season (at least formerly). ◆

Resources

Books

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Guy M. Kirwan

Crab plovers

(Dromadidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Dromadidae

Thumbnail description

Medium-sized birds with long blue-gray legs, contrasting black-and-white plumage, and a large, all-black, heavy, dagger-like bill with an angled lower mandible

Size

Height 13.0–16.1 in (33–41 cm); 0.5–0.7 lb (230–325 g); wingspan 29.1–30.7 in (74–78 cm)

Number of genera, species

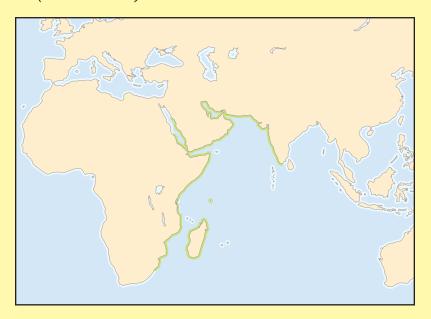
1 genus; 1 species

Habitat

Coastal dunes, intertidal mudflats, and coral reefs

Conservation status

Not threatened



Distribution

Maritime coast of east Africa, Persian Gulf, and Arabian Peninsula

Evolution and systematics

Crab plovers (*Dromas ardeola*) are classified as Charadriiformes. The species was named by Paykull in India, in 1805.
However, these birds are distinct enough that most taxonomists
consider them to be a monotypic family with uncertain affinities to other groups. For instance, the tarsal scutellation and unpatterned down of chicks indicate a grouping with the gulls
(family Laridae), whereas their burrow-nesting habits suggest a
close relationship with the auks (family Alcidae). In general, the
most widely accepted classification is to group crab plovers
within the shorebirds or waders of the suborder Charadrii.

The Charadrii comprise a large and diverse group. Based on plumage and initial appearance, crab plovers closely resemble avocets (family Recurvirostridae), yet there are greater similarities in skeletal characteristics and external morphology with thick-knees (family Burhinidae) and coursers and pratincoles (family Glareolidae). DNA-DNA hybridization work of Sibley and Ahlquist (1990) support grouping crab plovers within the Glareolidae and divergence of crab plovers from other shorebirds during the Oligocene, approximately 35 million years ago. However, the methodology of this work has received sufficient criticism to cast doubt on results. A more detailed examination of the origin of crab plovers and its taxonomic affinities must await results from detailed comparisons of mitochondrial and nuclear DNA.

Physical characteristics

Crab plovers are striking long-legged birds with blackand-white plumage and a large heavy bill. The distinct and powerful black bill is dagger-shaped and well-suited for stabbing and consuming crabs. Adult crab plovers have predominantly white plumage contrasting with a black mantle, primary and greater coverts, and primaries. The tail is palegray. In juvenile birds, the crown, hindneck, mantle, and lesser and median wing coverts are also gray. The legs are blue-gray with partially webbed feet and a well-developed first toe, potentially associated with digging nesting burrows. Sexes are similar in appearance but males have slightly longer and heavier bills.

Distribution

The distribution of crab plovers is restricted to maritime coastal areas of the Indian Ocean. Breeding occurs from Somalia and Madagascar east to areas of western India. The limited breeding distribution is partly a result of the need for areas with sandy substrate suitable for burrow construction in conjunction with sufficient foraging sites. During the non-breeding season, birds disperse and occupy sites that extend from South Africa east to Thailand, although most of the population winters in India, Kenya, Tanzania, and parts of the Arabian Peninsula.

Habitat

Crab plovers are a coastal marine species that occurs in desert and semi-desert regions. Generally, activities are restricted to areas within 0.6 mi (1 km) of the coast. Breeding colonies construct burrows in large expanses of coastal

Family: Crab plovers Vol. 9: Birds II



Crab plover (*Dromas ardeola*). (Illustration by Patricia Ferrer)

sand dunes or sandflats. Birds forage on exposed mudflats and shallow-water areas of the intertidal zone.

Behavior

Crab plovers are gregarious birds that congregate throughout the year at breeding colonies, foraging areas, and roost sites. Flock sizes at foraging sites are as large as hundreds of birds. At traditional roost sites birds may travel as far as 15.5 mi (25 km) to join flocks of up to a thousand individuals. In these groups, birds are noisy and emit a constant chatter of barking "ha-how" or "crow-ow-ow" calls. There are reports of flocks being audible from distances of 1 mi (1.5 km). Birds are most active at dawn and dusk in addition to nocturnal periods. This activity pattern is attributed to avoidance of the intense mid-day temperatures of regions they inhabit. Both migratory and sedentary populations.

Feeding ecology and diet

Crab plovers are specialized predators that forage on exposed mudflats and shallow intertidal areas. As their name implies, crabs are the major component of both adult and chick diets throughout the year. Crab plovers forage in noisy groups and walk or run after prey, stabbing it with their heavy bills. Smaller crabs are swallowed whole whereas larger prey are dismembered and then eaten. In addition, crab plovers also feed on various other crustaceans, fish, marine worms, and assorted invertebrates. Adults do not regurgitate food to young chicks but instead pass bits of mashed prey. Older chicks are given whole prey items.

Reproductive biology

Various aspects of crab plover reproduction are fascinating and in some cases unique. For instance, these birds nest during the hottest and driest times of the year (April to June) when temperatures in the shade can exceed 104°F (40°C). Presumably, the timing of nesting coincides with the period when crabs are plentiful enough to sustain young growing chicks. As a response to these extreme temperatures, crab plovers nest underground and are the only shorebird or wader (Charadrii) to construct burrows. These birds use their bills and feet to construct burrows in sandy substrates. The downward-sloping burrow tunnels are from 47.2–74.0 in (120–188 cm) long and also provide protection from potential nest predators.

Crab plovers are colonial nesters with burrows situated close together, resulting in a honeycomb effect at breeding sites. The mating system is not well understood but birds are presumed to be monogamous. As many as 10 birds have been observed at a single burrow, leading some investigators to suggest that crab plovers are communal. Complicating the situation is the suspicion that there are helpers at nests.

In contrast to the clutches of two to four eggs laid by other Charadrii, crab plovers lay a single white egg of approximately 0.1 lb (45 g). Relative to body mass, the egg of the crab plover is one of the largest laid by any bird species. Because crab plovers nest in burrows, the duration of both incubation and fledging periods are unknown. The role of the sexes in parental care is also not well understood, but of 10 adults pulled from burrows, all were female. Crab plover chicks are precocial and semi-nidifugous. Young birds remain at nest burrows for extended periods. During this time, adults pro-



Crab plovers (*Dromas ardeola*) forage in shallow water. (Photo by H. & J. Eriksen/VIREO. Reproduced by permission.)

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vide food for the young and may travel as far as 7.5 mi (12 km) roundtrip on single foraging trips.

Conservation status

Crab Plovers are not listed as threatened or endangered. Based on extrapolations from large-scale winter surveys, the global population is estimated at 43,000–50,000 individuals with the greatest numbers found in Tanzania (20,000–26,000 birds). Counts at nine known colonies sum to 4,000–5,000 pairs. Includes Iran: 1,500 pairs; United Arab Emirates: 300 pairs; Oman: 85 pairs; Saudi Arabia: 110 pairs. However, with only nine identified breeding colonies worldwide, the locations of most breeding sites remain unknown.

One cause for concern is that large concentrations of crab plovers occur near to oil production sites. Due to their small population size, low reproductive rate, and narrow habitat requirements, the species would take a long time to recover from a catastrophic event. Other potential threats are the destruction and degradation of mangrove and other coastal habitats from pollution and development. This fascinating species warrants further studies, as well as increased survey and monitoring efforts to ensure its continued persistence.

Significance to humans

Crab plovers occur in relatively remote and harsh areas such that they have little contact with humans. During the early 1900s, birds and eggs were exploited by people in Iraq as a food source, but the current status of this practice is unknown. Reports of egg collecting from other areas occurred as recently as the 1970s. Both known crab plover breeding colonies in the United Arab Emirates receive formal protection from the ruling family. •

Resources

Books

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Peter M. Sanzenbacher, MS

Oystercatchers

(Haematopodidae)

Class Aves

Order Charadriidae

Suborder Recurvirostrinae

Family Haematopodidae

Thumbnail description

Medium to large-sized, stocky waders with distinctive dark and light plumage, blunt-tipped dagger-like reddish bills, red to yellow eyes, and pink legs

Size

15.8–19.8 in (40–49 cm); 0.88–1.54 lb (400–700 g)

Number of genera, species

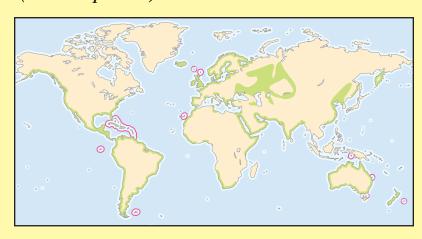
1 genus; 7 species

Habitat

Rocky and sandy shores, marshes, tidal mudflats, estuaries

Conservation status

Endangered: 1 species; Near Threatened: 1 species



Distribution

North America, Europe, Africa, East Asia, Australia, New Zealand

Evolution and systematics

The number of species within the genus *Haematopus* (oystercatchers) has been in dispute since its designation. Five species and seventeen subspecies were recognized through the 1970s. As of 2001, this list had been expanded to include as many as 14 species; 11, however, are generally accepted according to Sibley and Monroe. One of these, the Canary Islands oystercatcher (*Haematopus meadewaldoi*), has not been reported since the 1940s and is considered extinct.

The fossil record for oystercatchers is spotty. Morphological differences between New and Old World taxa, along with a distribution heavily tilted toward the Southern Hemisphere, suggest that the group originated in the paleocontinent of Gondwana and was split with the departure of the South American landmass. Two early Pliocene specimens have been reported in North America: the oldest fossil species, *H. sulcatus*, from the Bone Valley Formation (Palmetto Fauna), Florida, and a second record of *Haematopus* sp. from the Yorktown Formation at Lee Creek, North Carolina.

Physical characteristics

The similarities in appearance among oystercatcher species help explain the family's disputed taxonomy. Apart from differences in eye color between Old and New World taxa, all black oystercatcher taxa have completely dark plumage. Pied taxa in both regions have dark upperparts, head, neck, tail, and upper breast, white lower breast, belly, and uppertail coverts, and white bars on the upper wing. Variable oystercatchers (*H. unicolor*) are unique among waders in their poly-

morphism. Slightly fewer than three-quarters of variable oystercatchers are black and another 20% are pied. The rest fall somewhere in between and are known colloquially as "smudgies." Pied morphs tend to be smaller than their black counterparts, but in this aspect variable oystercatchers are once again unique; black morphs of this species are on average lighter than are pied morphs.

Oystercatcher females are heavier and have longer wings and bill than males. Otherwise, wing length is very similar among species. Immature oystercatchers have buffy margins on their dark feathers and duller colors on the eye rings, legs, and bill.

Elongated and thickest near the tip, the distinctive bill of an oystercatcher is often described as blade-like or daggerlike, an image intensified by its red or orange color. *Haematopus*, meaning "blood eye" in Greek, denotes the scarlet eye and eye ring found on Old World oystercatchers. New World taxa have yellow irises and orange-red or yellow eye rings.

Distribution

Oystercatchers inhabit coasts worldwide and lake shores inland in the Palearctic and New Zealand. Nine species occur in the Southern Hemisphere; none of these migrate significantly, although their ranges do overlap. Two species occur in Australia, New Zealand, and western South America, and three coincide in parts of southern South America. In both cases, black or polymorphic species specialize on rocky shores, whereas pied species stake out softer substrates or forage inland.

Family: Oystercatchers Vol. 9: Birds II



American oystercatchers (*Haematopus palliatus*) in flight. (Photo by T. Vezo/VIREO. Reproduced by permission.)

Oystercatcher ranges vary widely. American oystercatchers (*H. palliatus*) are found along the coasts of North and South America from Patagonia to the Gulf of California and Massachusetts, as well as the West Indies. Their Old World counterpart, Eurasian oystercatchers (*H. ostralegus*), range from western Europe, Scandinavia, western Russia (including the Black, Caspian, and Aral seas), and North Korea to winter habitats on the coasts of East Africa, Arabia, India, and eastern China. In contrast, Chatham Islands oystercatchers (*H. chathamensis*) are restricted to the Chatham Islands east of New Zealand.

Habitat

Oystercatchers primarily inhabit shorelines of every type, from rocky shores to beaches of sand, pebble, and shell. Salt marshes, estuaries, and coastal lagoons are also suitable habitat. A few species occur inland in areas of low vegetation or on agricultural land and pastures. Most oystercatchers found inland are soft-substrate specialists, drawn by freshwater bodies of all sizes. Two races of Eurasian oystercatchers breed inland in the Palearctic, some around the Black and Caspian Seas. South of the equator, inland breeders include Magellanic oystercatchers (*H. leucopodis*), the South Island race of the Eurasian oystercatcher (*H. o. finschi*), and, infrequently, the Australian pied oystercatcher (*H. longirostris*).

Habitat switching, particularly between the breeding and nonbreeding season, is the norm rather than the exception among oystercatchers. Pied taxa often return to rocky coasts in the winter, as in the case of Magellanic oystercatchers and American black oystercatchers (*H. bachmani*). Among all-black species, blackish oystercatchers (*H. ater*) exhibit similar behavior, whereas American oystercatchers seek out mudflats in winter. Eurasian oystercatchers, American black oystercatchers, and sooty oystercatchers (*H. fuliginosus*) tend to winter on softer substrates such as those associated with estuaries.

Behavior

Oystercatchers demonstrate strong fidelity to both mates and breeding sites. Migratory species such as Eurasian oystercatchers return to the same locations from year to year. Young return to breed close to where they were hatched, often from hundreds of miles away. All oystercatchers defend breeding territories, and some species exhibit year-round territoriality.

Other species, such as African black oystercatchers (*H. moquini*), form high-tide roosts to defend against predators and keep warm in cold climates. Foraging flocks most often have fewer than 50 members (black taxa seldom gather in groups of more than 10), but groups of over 1,000 inland breeders, such as Australian pied oystercatchers and some races of Eurasian oystercatchers, occasionally gather.

Only Eurasian oystercatchers are truly migratory, with three Palearctic races that fly as far as 30°s in winter. These birds may double their body mass in preparation for the journey. In their northern extents of their ranges, American oystercatchers and American black oystercatchers also move south in winter.

Oystercatcher calls are simple, sharp, and loud peeps, often starting out with a rapid, brief trill that becomes progressively longer.

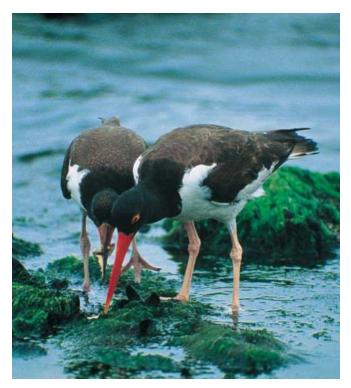
Feeding ecology and diet

Oystercatchers depend on a wide range of marine invertebrates for food. Bivalve mollusks of several species are dom-



A variable oystercatcher (*Haematopus unicolor*) at its nest. (Photo by B. Chudleigh/VIREO. Reproduced by permission.)

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A pair of American oystercatchers (*Haematopus palliatus*) feeding. (Photo by T. Vezo/VIREO. Reproduced by permission.)

inant prey items, but oystercatchers also eat crabs, chitons, sea urchins, whelks, snails, and an occasional fish. Variety is key; African black oystercatchers are known to eat at least 52 species. Arthropods are the main food source inland.

Oystercatchers exhibit an impressive range of techniques to overcome the often substantial defenses of their prey. When an oystercatcher finds a feeding mussel with its shell slightly open, the oystercatcher quickly stabs its bill inside to sever the muscle connecting the valves before cleaning out the flesh inside. (Oystercatchers have been known to drown with incoming tides after their bills became caught by shell-fish.) The bird's narrow bill fits through small openings, and a concentration of nerve endings near the tip help locate prey in muddy waters.

American oystercatchers infrequently hammer mussels against rocks to crack the shell, and American black oystercatchers will pry limpets off rocks to eat. Eurasian oystercatchers use their long bill to extract lugworms (*Arenicola marina*) from their U-shaped tubes in intertidal flats. Regardless of technique, oystercatchers can often catch prey faster than they can digest it.

Reproductive biology

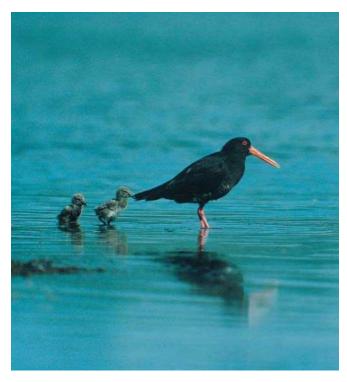
All oystercatchers are predominantly monogamous and breed in summer. During the "piping" courtship display, two birds utter a single piped note while walking, running, or flying closely parallel, turning often. This display may be joined by nearby pairs for a piping "tournament" and is also used as

a mate greeting or territorial display. Breeding Magellanic oystercatchers cock the tail skyward to reveal pure white undertail coverts.

Clutches can be one to four eggs but are most often two or three; rarely, Eurasian oystercatchers produce five eggs. Oystercatcher nests are scrapes on the ground that may be lined or unlined. First eggs are often undertended and lost (up to 40% among Eurasian oystercatchers), and parents incubate alternately and continuously for 24–39 days. The eggs are spotted gray with bluish or buffy tints, and blend in well on pebbly surfaces. Oystercatcher chicks are the same dull gray-brown as their surroundings and unique in being fully mobile within a day of hatching. Old World taxa have crowns marked conspicuously with black, while New World taxa (and the Magellanic oystercatchers) do not. Oystercatcher parents feed their chicks, who can run and hide from danger, until well after fledging, which is at least 60 days after hatching in the case of American oystercatchers. This strategy minimizes the risk of predation while maximizing the high growth rates of parent-fed young. Nevertheless, average rearing success is usually less than one chick per pair per year. Storms and predators pose the greatest risks to oystercatcher eggs and chicks, respectively.

Conservation status

As a whole, oystercatchers are doing well; as of 2001, only three species numbered less than 5,000 individuals. Introduced predators and human disturbance both take a significant toll on eggs and chicks. The total population of African



A variable oystercatcher (*Haematopus unicolor*) adult with chicks. (Photo by B. Chudleigh/VIREO. Reproduced by permission.)

Family: Oystercatchers Vol. 9: Birds II

black oystercatchers was estimated at 4,800 birds in the early 1980s, earning the species Lower risk/Near Threatened status. Coastal recreation, including off-road vehicles, disturbs or destroys nests or causes parents to flee, leaving eggs vulnerable to overheating or natural predation. Populations on near-shore islands, however, have stabilized or increased due to improved management. Chatham Island oystercatchers number only 100–150 individuals and are classified as Endangered. Limited to four small islands in New Zealand, the species appears to have increased significantly in the 1990s,

thanks to conservation efforts that include predator removal and artificial incubation. Fluctuating population levels, however, ensure the species' situation remains precarious.

Significance to humans

Aside from unsubstantiated reports of oystercatchers preying on commercial oyster beds and frequent comments on the birds' somewhat comical appearance, oystercatchers have no particular significance to humans.



1. Variable oystercatcher (*Haematopus unicolor*), pied morph; 2. Variable oystercatcher (*Haematopus unicolor*), black morph; 3. Variable oystercatcher (*Haematopus unicolor*), intermediate morph; 4. American oystercatcher (*Haematopus palliatus*); 5. African black oystercatcher (*Haematopus moquini*). (Illustration by Patricia Ferrer)

Family: Oystercatchers Vol. 9: Birds II

Species accounts

American oystercatcher

Haematopus palliatus

TAXONOMY

Haematopus palliatus Temminck, 1820, Venezuela. Two subspecies.

OTHER COMMON NAMES

English: American pied oystercatcher; French: Huîtrier d'Amérique; German: Braunmantel-austernfischer; Spanish: Ostrero pio Americano.

PHYSICAL CHARACTERISTICS

15.75–17.32 in (40–44 cm); male averages 1.25 lb (567 g), female 1.41 lb (638 g). Black head, neck, upper breast, tail, flight feathers; white belly and lower breast; orange-red bill and eyering; yellow eye. Only pied oystercatcher with brownish dorsal plumage. Juveniles have dark eyes, inconspicuous eye ring, dark tip on bill, and the upperparts are fringed with buff.

DISTRIBUTION

Coastal Americas from Gulf of California to Chile, southern Argentina to Massachusetts, West Indies. *H. p. galapagensis* occurs only in Galapagos Islands.



HABITAT

Sandy, shell, and pebble beaches, salt marshes, rocky shores.

BEHAVIOR

Territorial, sometimes moves to mudflats in winter.

FEEDING ECOLOGY AND DIET

Takes snails, oysters, crabs, mussels, and clams using a variety of techniques. On rocky shores in Panama feeds almost entirely on mollusks.

REPRODUCTIVE BIOLOGY

Breeds only at the coast. Known to hybridize with blackish oystercatchers in South America and American black oystercatchers in western Mexico and Gulf of California (the latter resulting in disputed race *H. p. frazari*). Chick plumage consists of drab upperparts, white underparts, and dark stripes on sides and back. Breeding occurs during a two-month breeding season over range, ranging from February to October.

CONSERVATION STATUS

With a total population of about 5,000 birds, generally not considered globally threatened, but sometimes considered Near Threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

African black oystercatcher

Haematopus moquini

TAXONOMY

Haematopus moquini Bonaparte, 1856, Cape of Good Hope. Monotypic.

OTHER COMMON NAMES

English: African oystercatcher, black oystercatcher; French: Huîtrier de moquin; German: Schwarzer austernfischer; Spanish: Ostrero negro Africano.

PHYSICAL CHARACTERISTICS

16.54-17.72 in (42–45 cm); 1.28-1.67 lb (582–757 g), females 1.42-1.76 lb (646–800 g). Dark overall with vermilion bill and eye ring, red eye, and pink legs. Females have noticeably longer bills.

DISTRIBUTION

Coastal southern Africa from northern Namibia to Cape of Good Hope and east to Natal.

HABITAT

Sandy and rocky shores, offshore islands, occasionally estuaries and coastal lagoons.

BEHAVIOR

Territorial, relying on camouflage on dark rocky substrates. Sedentary adults rarely disperse as far as juveniles; most often less than 100 mi (160 km) in any case.

FEEDING ECOLOGY AND DIET

Eats limpets, mussels, whelks, and polychaetes in rocky areas, wider range of prey on sandy substrates but favors sand mussels.

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REPRODUCTIVE BIOLOGY

Usually breeds on offshore islands and sandy beaches, laying one to two eggs between October and April. Eggs are greenish or buff with dark brown spots. Eggs and young are vulnerable to terrestrial mammalian predators, although young are well camouflaged. The chick plumage is gray with black stripes on back and sides.

CONSERVATION STATUS

Considered Near Threatened as of 2001, with a total population of about 5,000 birds. Major threats are introduced mammalian predators on island populations, followed by human disturbance on sandy beaches.

SIGNIFICANCE TO HUMANS

None known. ◆

Variable oystercatcher

Haematopus unicolor

TAXONOMY

Haematopus unicolor J.R. Forster 1844, New Zealand. Pied morph occasionally considered separate species (H. reischeki) or race.

OTHER COMMON NAMES

English: New Zealand black oystercatcher, New Zealand sooty oystercatcher, northern oystercatcher; French: Huîtrier variable; German: Neuseeländischer austernfischer; Spanish: Ostrero Variable. •

PHYSICAL CHARACTERISTICS

18.50–19.29 in (47–49 cm); male averages 1.49 lb (678 g), female 1.59 lb (724 g). Only oystercatcher species with black and

pied morph. Dominant morph is black overall with red eye, bill, and eye ring; pied morph has white breast, belly, back, and small wingbar. Frequent intermediate morphs are larger overall and are called "smudgies."

DISTRIBUTION

Coast and islands of New Zealand.

HABITAT

Rocky and sandy shores.

BEHAVIOR

Territorial and sedentary, occasionally flock in harbor and estuaries.

FEEDING ECOLOGY AND DIET

Feeds on sandy beaches and rocky shores. Varied diet includes crabs, gastropods, bivalves, and polychaetes.

REPRODUCTIVE BIOLOGY

Frequent interbreeding between morphs. Breeds from December through January (occasionally as early as September) on dunes and sandy beaches. Clutches are most often three eggs incubated for 25–32 days. Chicks of black morph have dark underparts and crown, while those of pied morph have white breasts and grayish-brown upperparts.

CONSERVATION STATUS

Not considered threatened, even though total population is estimated at 3,900 birds. Threats include human disturbance and mammalian predation, but several populations were increasing in 1980s and 1990s, especially on North Island where over two-thirds of variable oystercatchers reside.

SIGNIFICANCE TO HUMANS

None known. ◆



Family: Oystercatchers Vol. 9: Birds II

Resources

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Julian Smith, MS

Stilts and avocets

(Recurvirostridae)

Class Aves

Order Charadriformes

Suborder Charadrii

Family Recurvirostridae

Thumbnail description

Tall, slim, long-legged shorebirds with striking black-and-white plumage, long, thin, often upturned bills and a loud strident call

Size

14-20 in (35-51 cm); 5.8-16.2 oz (166-461 g)

Number of genera, species

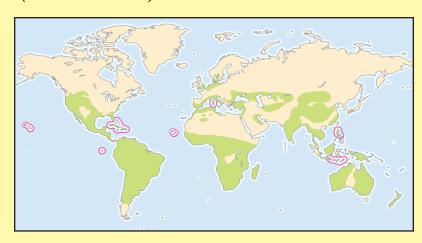
4 genera, 8 species

Habitat

Extensive shallow wetlands with abundant invertebrate prey

Conservation status

Critically Endangered: 1 species; Endangered: 1 subspecies



Distribution

Cosmopolitan, found in most tropical and temperate regions, greatest diversity in Australian region

Evolution and systematics

Researchers tend to agree on the closest relatives of this family of elegant shorebirds; morphological, behavioral, and DNA evidence all suggest that the Recurvirostridae shares a common ancestry with the oystercatchers (Haematopodidae) and the lapwings and plovers (Charadriidae). This treatment splits the Recurvirostridae into two subfamilies; the Recurvirostrinae, comprising 3 genera (*Himantopus*, *Cladorhynchus*, *Recurvirostra*) and 7 species, and the Ibidorhynchinae, comprising a single genus and species (*Ibidorbyncha struthersii*).

While there is consensus regarding the family's relatives, the species-level relationships within the Recurvirostridae remain controversial, especially among the stilts. The genus *Himantopus* is recognized as having from one to six species, although most authors recognize two species; the black stilt (*Himantopus novaezelandiae*) and the black-winged stilt (*Himantopus himantopus*), and 3–5 races or subspecies of the black-winged stilt. The subspecies can be separated by plumage and biometrics, but subspecific distinction is often not discrete, there being a continuum of variation among the recognized races. Further research is required to resolve these species-level relationships.

Evolutionary origins of the recurvirostrids are thought to begin with an ancestor of the stilts and ibisbills that evolved on the shores of the ancient sea of Tethys, in the center of today's Eurasia. During the Mesozoic, as the Tethys gradually disappeared and the mountains of central Asia began to form, the ibisbill lineage may have established itself in these new mountain habitats, while the stilt lineage remained associated with the sea.

Physical characteristics

Proportionally, the stilts and avocets are the longest legged shorebirds and their legs range from crimson to blue to gray. All of the recurvirostrids have distinctive bills, and, as suggested by the genus' Latin name, are upcurved in avocets, especially in the females. The ibisbill's bill is also decurved and bright crimson in color, the stilts tend to have straight or only slightly curved bills. The blue or crimson legs and colored or curved bills combined with their black, white, and sometimes orange plumage, make the recurvirostrids conspicuous, unmistakable birds.

The ibisbill's plumage is perhaps the most striking of the recurvirostrids, with banded and barred black and white plumage. While bold, it camouflages the nesting bird remarkably well. The stilts and avocets are also dressed in patterns of black-and-white, and three species have areas of reddish-brown plumage. The black-winged stilt, the juvenile black stilt and the Andean avocet are generally black on their upperparts and white beneath. The banded stilt and other avocets are mostly white with black markings on the shoulders and wings. As with the ibisbill, breeding and non-breeding plumages are similar, the exception is the reddish-orange plumage of the American avocet (*Recurvirostra americana*) which is only present in the breeding season. Except for the black stilt, the juvenal plumages resemble adults', though often duller in contrast.

Overall, the stilts and avocets are long-legged, elegant birds, varying little in size. Stilts' body size ranges from 13.7–16.9 in (35–43 cm) and 5.8–9.1 oz (166–260g), and are slightly smaller than avocets whose body size ranges from 15.7–20 in (40–51 cm) and 7.9–16.2 oz (225–461 g). The ibisbill appears the most compact and sturdily built, 15.3–16.1 in (39–41 cm) and 9.5–11.2 oz (270–320 g).

Family: Stilts and avocets Vol. 9: Birds II



A black-necked stilt (*Himantopus mexicanus*) at its nest. (Photo by Bob & Clara Calhoun. Bruce Coleman Inc. Reproduced by permission.)

Distribution

The stilts and avocets have a worldwide distribution, and are generally found in temperate and subtropical zones. The black-winged stilt is the most widespread and found in shallow wetlands of temperate and tropical regions around the world, the black and banded stilt have more limited distributions.

The avocets are found throughout temperate and subtropical Eurasia, Africa, and the Americas. Two members of the family are confined to colder, montane climates; the ibisbill in central Asia, and the Andean avocet (*Recurvirostra andina*) inhabits lakes of the high Andes.

Habitat

Extensive, shallow wetlands with high densities of small, invertebrate prey is the ideal habitat for stilts and avocets. The ibisbill has narrower requirements; it inhabits only rocky, slow-moving rivers. The avocets and banded stilt favor saline environments, though they often come inland to breed. The greatest variety of wetlands are used by the *Himantopus* stilts, which occur in habitats across a range of salinity, altitude, and water speed. Conversely, the Andean avocet remains at high altitude, saline lakes throughout the year. Opportunistic in habitat selection, stilts and avocets increasingly take advantage of man-made wetlands such as dams, irrigation sites, and sewer ponds.

Behavior

Except for the ibisbill and the black stilt, members of this family are gregarious and will feed in flocks of up to several

thousand birds. Recurvirostrids feed mainly during the day, although some stilts will forage at night, especially in coastal areas where feeding activity may follow tidal cycles. When lounging, these birds gather on waterbanks in dense flocks, sit on the ground, or stand on one leg with the bill tucked under the wing, they also roost standing in the water. The ibisbill is more of a loner, although it is sometimes seen in pairs or small groups of seven or eight birds and flocks of up to 25 birds have been reported.

Except for the ibisbill, recuruirostrids nest in colonies, intermingling with other shorebirds. They are especially noisy birds when breeding, the commonest call being a bark or yelp, given as an alarm. Some species have a variety of vocalizations including different alarm calls, parental calls, and copulation calls. Ibisbills have three main calls, which have more notes than that of stilts and avocets.

Outside of the breeding season, ibisbills are quiet, keeping to themselves. They only migrate altitudinally, usually staying within their breeding range. The northern populations of the black-winged stilt, pied avocet, and American avocet migrate between temperate and subtropical regions. Some Southern Hemisphere members of this family move inland to breed, and all will move depending on the seasonal availability of wetlands.

Feeding ecology and diet

Stilts and avocets feed on a diversity of aquatic invertebrates, primarily small crustaceans and larval insects, but also some worms and mollusks (in *Himantopus*); small fishes and some plant matter (especially in *Himantopus*) is also included in the diet. All species exhibit a range of feeding techniques,



American avocet (*Recurvirostra americana*) adult and chicks. (Photo by David Weintraub. Photo Researchers, Inc. Reproduced by permission.)

Vol. 9: Birds II Family: Stilts and avocets



Banded stilts (Cladorhynchus leucocephalus) in Australia. (Photo by M.P. Kahl. Photo Researchers, Inc. Reproduced by permission.)

the most common method is to directly peck food items. Avocets often "scythe" for food, sweeping the bill at a low angle through water or soft mud. The upcurved bill is filled with folds of thin layers of tissue (lamellae) that filter out small food items caught when scything; the bird then flicks the food into its mouth with its fleshy tongue. The banded stilts' bill also contains lamellae; lamellae are absent in *Himantopus*. Other feeding strategies of the stilts and avocets include plunging the entire head under water and probing for food, and snatching at flying insects.

The ibisbill has three basic feeding strategies; pecking, probing for food while waist deep in the water, and raking. Raking involves tipping its head to the side and raking its bill through pebbles in the stream-bed, dislodging small aquatic animals that it then snatches up. All recurvirostrids are able to quickly change feeding style in response to changing weather, water temperatures, water levels, and prey species present.

Reproductive biology

For data available, it appears that recurvirostrids are monogramous, although not necessarily over a whole breeding season. Stilts and avocets are generally colonial nesters, sometimes at such great densities in avocets that nests are abandoned. "Dip-shake-preen" male courtship displays are followed by copulation, and some species engage in an en-

dearing post-copulation behavior in which the birds cross bills and walk together, the male with his wing over the back of the female. Usually three or four eggs are laid, and both parents incubate and care for the downy young.

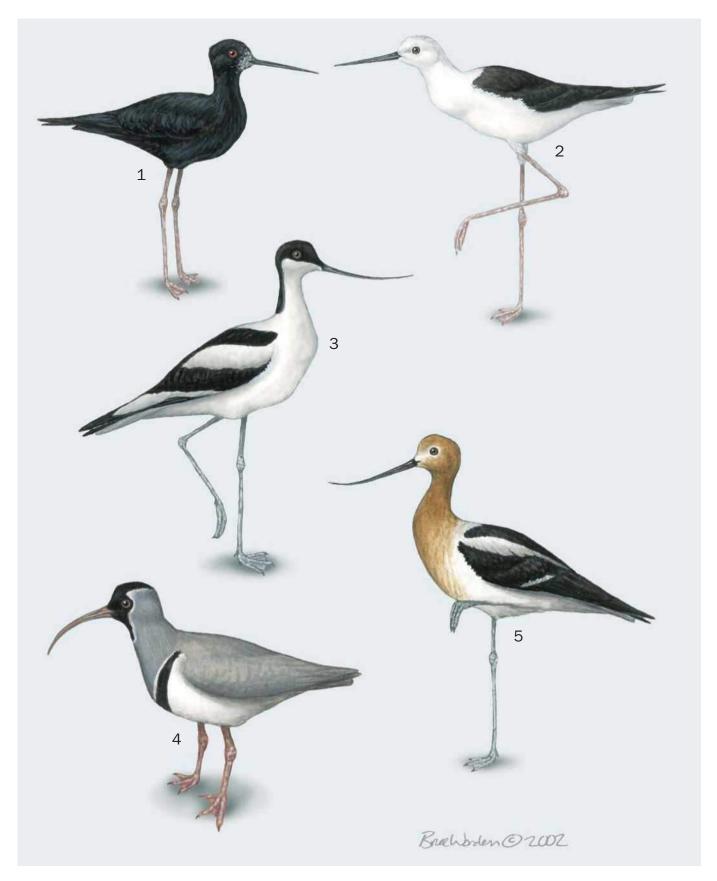
Breeding pairs of ibisbills establish territories of 295–3,280 ft (90–1,000 m) along a river in march or early April. Both parents incubate the two eggs and rarely leave the nest unattended for more than one to two minutes. Chicks are distinctive with inordinately long toes and an already slightly upcurved bill 0.7 in (18 mm) long. Both adults feed and guard the young. When disturbed with chicks, adults fly directly at intruders, emitting a loud piping call. Adults will also fake injury to draw intruders away from chicks.

Conservation status

Most recurvirostrids have large, stable populations. Destruction of habitat by humans poses the greatest threat. Captive breeding programs have been established for the black stilt and the Hawaiian subspecies of the black-winged stilt, both of which are endangered.

Significance to humans

Most recurvirostrids enjoy a high positive profile and there are varying efforts to protect these birds and their habitat.



1. Black stilt (*Himantopus novaezelandiae*); 2. Black-winged stilt (*Himantopus himantopus*); 3. Pied avocet (*Recurvirostra avosetta*); 4. Ibisbill (*Ibidorhyncha struthersii*); 5. American avocet (*Recurvirostra americana*). (Illustration by Bruce Worden)

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Species accounts

Ibisbill

Ibidorhyncha struthersii

SUBFAMILY

Ibidorhynchinae

TAXONOMY

Ibidorhyncha struthersii Vigors, 1832, Himalayas. Taxonomy still unresolved, often placed in own monotypic family.

OTHER COMMON NAMES

French: Bec-d'ibis tibétain; German: Ibisschnabel; Spanish: Picoibis.

PHYSICAL CHARACTERISTICS

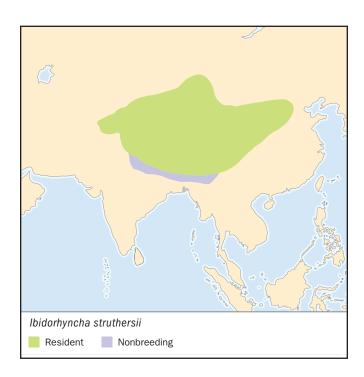
15.6–16.4 in (39–41cm); 0.59–0.7 lb (270–320 g), bill 2.6–3.2 in (68–82 mm). Distinctive wader with long, decurved, crimson bill and striking plumage. Dark brown or black face with white margin towards neck. Neck and upper back bluish gray, lower back brownish gray and white belly with broad black band. Legs grayish purple. Female and male similar, female marginally larger with slightly longer bill. Juvenile browner with less clearly marked plumage and paler coloring, bill dark pinkish gray. Unlike stilts and avocets, salt glands are nearly absent in ibisbill.

DISTRIBUTION

Southeastern Kazakhstan, south to Kashmir and east through northwestern China, Tibet, and northeastern India to eastern central and northern central China. Mainly in major mountain systems of central Asia.

HABITAT

Flat, stony, rivers at high altitudes (1,640-14,435 ft [500-4,400 m]), may occur as low as 330 ft (100 m) in winter.



BEHAVIOR

Territorial, solitary breeders, may roost together outside of breeding season. Rarely fly unless disturbed.

FEEDING ECOLOGY AND DIET

Feeds during the day, usually singly. Feeds by pecking, probing, or raking bill through gravel, often forages breast deep in water. Specializes on insect larvae, occasionally eats small fish.

REPRODUCTIVE BIOLOGY

Monogamous and territorial, incubation by both sexes. Generally lays four eggs in April or May in a shallow, sometimes pebble-lined pit in ground. Eggs usually greenish-gray with brown speckles, chicks hatch mid-May through late June and led away from nest by female as soon as they dry, brooded up to 23 days. Can fly when 45–50 days old.

CONSERVATION STATUS

Not threatened, range is extensive an in areas with few humans. However, ibisbills are adapted to rather restricted habitat, so could be vulnerable to habitat destruction from industrial mining of gravel from river-beds and building of hydro-electric plants. Nest trampling by sheep, predation by foxes and disturbance by humans can also be a problem. Species not known to have been kept in captivity, as of 2001 no captive-breeding programs are in operation.

SIGNIFICANCE TO HUMANS

None known. ◆

Black-winged stilt

Himantopus himantopus

SUBFAMILY

Recurvirostrinae

TAXONOMY

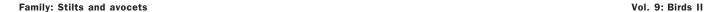
Charadrius himantopus Linnaeus, 1758, southern Europe. Forms superspecies with black stilt (*Himantopus novaezelandiae*), sometimes considered conspecific. Races can be split into three groups ("nominate" race, "pied" race, and "black-necked" race) and 2–5 separate species recognized.

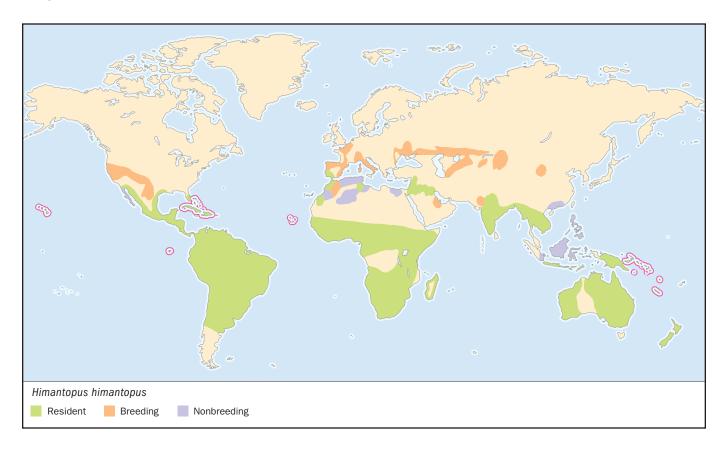
OTHER COMMON NAMES

English: Common stilt; French: Échasse blanche; German: Stelzenläufer; Spanish: Cigüeñuela Común.

PHYSICAL CHARACTERISTICS

13.7–15.7 in (35–40 cm), 5.8–7.2 oz (166–205 g). All have extraordinarily long, pink legs and long black, straight or slightly upcurved bills. Male's back and wings black, sometimes with greenish sheen, white below, gray banding on white tail. Upper parts of female dullish brown. Juvenile resembles adult female. Races differ in head and hindneck plumage color, from mainly white to continuous black. Sexual dimorphism is more evident in some races.





DISTRIBUTION

H. h. himantopus Linnaeus, 1758, France and Iberia south to sub-Saharan Africa and Madagascar, east to central Asia and northern central China, Indochina, Taiwan, and Indian subcontinent. H. h. leucocephalus Gould 1837, Java east to New Guinea, south to Australia and New Zealand; winters north to Philippines, Greater Sundas, and Sulawesi. H. h. knudseni Stejneger, 1887, Hawaiian Islands. H. h. mexicanus P.L.S. Mäller, western and southern United States to Central America, West Indies, to southwestern Peru, eastern Ecuador, and northeastern Brazil. H. h. melanurus Vieillot, 1817, northern Chile and eastern central Peru through Bolivia and Paraguay to southeastern Brazil, and south to south central Argentina.

HABITAT

Temperate and tropical shallow wetlands. Usually breeds in freshwater, including lake edges, marshes, swamps, river-beds and flooded fields, also found in coastal salt marshes.

BEHAVIOR

Gregarious, may feed in flocks of several thousand birds. Alarmed birds often head-bob. Call is a sharp monosyllabic "yep" or "kek." Sometimes performs a high-leaping display with a "floating" descent, the significance of this performance isn't clear. "Mob-display" also observed, whereby a few birds come together and behave in a mildly aggressive fashion for no apparent reason.

FEEDING ECOLOGY AND DIET

Diet strongly seasonal depending on habitat. Preys on various aquatic invertebrates including insects, small mollusks, crustaceans, and worms, as well as small fish and their eggs, and tadpoles. Active forager, employs a variety of methods to cap-

ture prey. Well-adapted to nocturnal vision, these birds will feed on windy, moonless nights.

REPRODUCTIVE BIOLOGY

Usually breeds in colonies of two to 50 pairs. Timing of breeding quite variable over range. Nests often widely spaced on ground or among grasses, sometimes a well-lined, floating mass of water weeds. Incubation of four eggs 22–26 days, by both sexes. Fledging 28–37 days.

CONSERVATION STATUS

Not globally threatened but controversial taxonomy calls for monitoring at subspecific level. Hawaiian subspecies *knudseni* is endangered, survival depends on predator control and protection of nesting habitat. As of 2001 only 1,800 birds. Nominate race was in decline in the 1800s, but has rebounded with population estimates now at minimum of 21,000 pairs.

SIGNIFICANCE TO HUMANS

None known. ◆

Black stilt

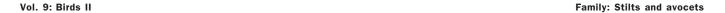
Himantopus novaezelandiae

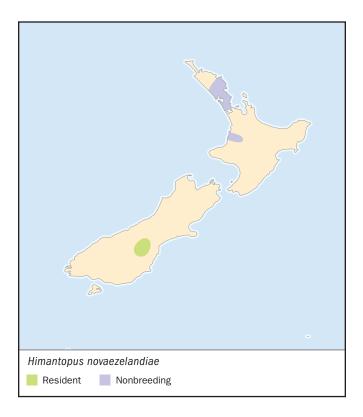
SUBFAMILY

Recurvirostrinae

TAXONOMY

Himantopus novæ-zelandiæ Gould, 1841, Port Nicholson, North Island, New Zealand. Forms superspecies with *H. bimantopus* sometimes considered conspecific. Monotypic.





OTHER COMMON NAMES

French: Échasse noire; German: Schwarzer Stelzenläufer; Spanish: Cigüeñuela Negra.

PHYSICAL CHARACTERISTICS

14.5–15.7 in (37–40 cm); 7.7 oz (220 g). Long pink legs, distinctive plumage; all black with greenish gloss on back and wings. Shorter legs and longer bill than *H. bimantopus*. Female similar to male, usually shorter legs. Non-breeding adult has grayish white chin and forehead. Juvenile has black wings and back, white below, develops grayish black markings on white areas first winter. Plumage of hybrids with *H. b. leucocephalus* variable, often with black collar and black markings on belly and breast.

DISTRIBUTION

New Zealand, was widespread but now restricted to MacKenzie Basin central South Island, small numbers winter in North Island.

HABITAT

Ponds, lakeshores, river-beds and swamps of MacKenzie Basin. Some visit coastal estuaries and lagoons outside of the breeding season.

BEHAVIOR

Defends some sort of territory all year, an exception in the Recurvirostrids. Outside of the breeding season more gregarious, though it will still defend feeding territories.

FEEDING ECOLOGY AND DIET

On riverbed breeding grounds feeds primarily on aquatic insect larvae and small fish. In stiller waters eats various aquatic insects, worms, and mollusks. Probes with bill beneath stones for food, and employs the scything method which is commonly used at night and especially effective with worms.

REPRODUCTIVE BIOLOGY

Seasonal breeder, usually September–January. Lays four eggs in a well-lined nest bowl, near water, usually solitary and will defend territory. Incubation 24–26 days, by both sexes. Fledging 41–55 days, first breeding at two years. In wild many eggs and chicks are eaten by introduced predators.

CONSERVATION STATUS

Critically Endangered. Habitat loss, predation on eggs after introduction of carnivorous animals to island, and interbreeding with *H. bimantopus* all contribute to decline. Population crashed in late 1950s from 1,000 birds to fewer than 100, where it remains today. Captive-breeding, anti-predator, and habitat restoration programs began in the 1980s have had some success in reducing population decline.

SIGNIFICANCE TO HUMANS

None known. ◆

American avocet

Recurvirostra americana

SUBFAMILY

Recurvirostrinae

TAXONOMY

Recurvirostra americana Gmelin, 1789, North America. Monotypic.

OTHER COMMON NAMES

French: Avocette d'Amérique; German: Braunhals-Säbelschnäbler; Spanish: Avoceta Americana, Piqocurvo.

PHYSICAL CHARACTERISTICS

16.1–2.0 in (41–51 cm); 10.6–16.2 oz (302–461 g). Large, striking birds legs bluish, strongly upcurved black bill. The only avocet with annual color change, the head, neck, and breast change from gray to orange-brown in breeding season. Wings and back black, contrasting with white on wing coverts. Sexes similar in plumage, male often larger, bill shorter and more strongly recurved in female. Juvenile resembles adult but crown pale brown with dull chestnut nape and hindneck.

DISTRIBUTION

Southeastern British Columbia east to southwestern Ontario, south to northern Baja California east to central Texas, eastern United States, and central Mexico. Winters from California and south, Texas through Mexico to Guatemala and irregularly to northern Honduras, southeastern United States and Bahamas to Cuba.

HABITAT

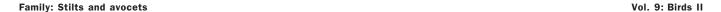
Specializes in using ephemeral wetlands of arid western United States, breeds around sparsely vegetated saline lakes and ponds, in large numbers at marshes of Great Salt Lake, Tulare Basin of California and across northern Great Basin. Outside of breeding season occurs in freshwater habitats and coastal lagoons and estuaries.

BEHAVIOR

After flock arrives at breeding grounds, transition from flocking to territoriality. Territory defended by male and female. "Upright posture," where the bird faces its opponent with neck extended vertically, is used to threaten other birds.

FEEDING ECOLOGY AND DIET

Mostly feeds on aquatic invertebrates while wading or swimming, also crustaceans, worms, small fish, and seeds. Scything





is hallmark method, but also pecks, plunges, and snatches. Will forage in dense flocks.

REPRODUCTIVE BIOLOGY

Monogamous, though pair bond doesn't usually extend past one season. Semi-colonial nesting, nest is a grass-lined depression in soil. Usually four eggs, incubation 22–29 days by both sexes. Both adults care for chicks, fledging four to five weeks.

CONSERVATION STATUS

Not threatened. Before 1900s shooting and trapping led to population declines, particularly on the Atlantic coast. Many wetlands used by American avocets in western United States have been contaminated with selenium as a result of irrigation and other human activities, loss of wetland habitat has led to population declines. Operators of selenium-contaminated ponds in California's Tulare Basin now required to provide mitigation habitat for breeding recurvirostrids, and species response has been favorable.

SIGNIFICANCE TO HUMANS

Considerend a game bird in early 1900s in California. ◆

Pied avocet

Recurvirostra avosetta

SUBFAMILY

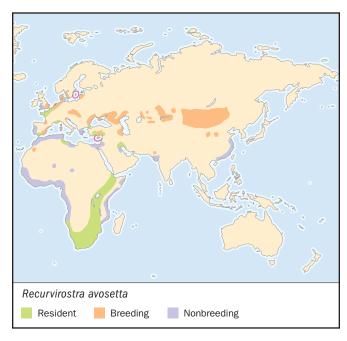
Recurvirostrinae

TAXONOMY

Recurvirostra avosetta Linneaus, 1758, Italy. Monotypic.

OTHER COMMON NAMES

English: (Eurasian) avocet; French: Avocette élégante; German: Säbelschnäbler; Spanish: Avoceta Común.



PHYSICAL CHARACTERISTICS

16.5–17.7 in (42–45 cm); 7.9–14 oz (225–397 g). Distinctive, black, strongly upcurved bill and long-blue gray legs. Plumage white with black forehead, crown to beneath eyes and nape and upper hindneck. At rest has three black bands on mantle and wings. Female bill shorter with stronger curve. Juvenile resembles adult but black plumage tinged brown and white upperparts have brown or gray mottling.

DISTRIBUTION

Europe through western and central Asia to southeastern Siberia and northeastern China, through northern Africa to eastern and southern Africa. Winters from western Europe and Africa through Middle East to northwestern India and southeastern China.

HABITAT

Breeds in dry and sparsely-vegetated flat, open areas, usually shallow saline lakes, lagoons and estuaries, up to 9,840 ft (3,000 m). Outside of breeding season found in muddy tidal flats, rarely at freshwater lakes and rivers.

BEHAVIOR

Gregarious, engages in elaborate mating ceremony. Adults give "broken wing" display to distract predators from young. Makes frequent clear flutish calls of "kluit, kluit."

FEEDING ECOLOGY AND DIET

Mostly feeds by picking, also scything, takes variety of aquatic invertebrates. Winter diet dominated by worms, will feed by sight on the siphons of mollusks. Sometimes feeds communally.

REPRODUCTIVE BIOLOGY

Breeds April through August, nests in large colonies. Nest is a grass-lined depression in open ground or short vegetation. Lays three to five eggs, brownish with dark spots or blotches. Incubation 23–25 days, by both sexes, fledging 35–42 days. Conspecific nest parasitism documented, parasitic eggs laid earlier in the season into nests of other pied avocets. Known to have lived over 24 years in the wild.

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CONSERVATION STATUS

Not threatened. Has rebounded from range contraction in northwestern Europe in 1800s, number of breeding pairs in Europe estimated at 31,000–56,000 with greatest numbers in Denmark, Netherlands and Spain. Less opportunistic than other recurvirostrids, this is cause for concern as pressure on wetland habitat increases due to lack of protection and contamination from pollutants including selenium.

SIGNIFICANCE TO HUMANS

During successful conservation effort of early 1900s in Europe, the pied avocet was adopted as the Royal Society for the Protection of Birds' symbol, and the image is strongly associated with ornithological conservation. •

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Rachel Ehrenberg, MS

Thick-knees

(Burbinidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Burhinidae

Thumbnail description

Medium-sized, long-legged, terrestrial birds with highly developed vocalizations, striking patterns on the spread wing, and stout, pointed bills for catching, manipulating, and breaking up tough prev

Size

12.5–23 in (32–59 cm); 0.65–2.4 lb (0.293–1.13 kg)

Number of genera, species

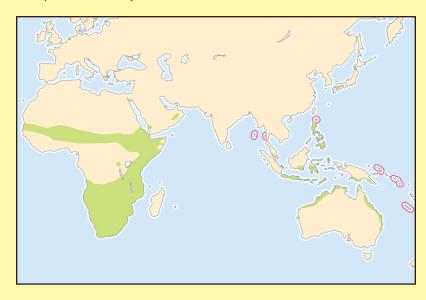
2 genera; 9 species

Habitat

Semi-arid to arid areas with low or sparse vegetation, watersides including rivers and sea coasts

Conservation status

No species endangered or vulnerable; Near Threatened: 3 species



Distribution

South, southeast, and southwest Asia, southern and western Europe, Australia, Africa, the Middle East, and central and northern South America

Evolution and systematics

Taxonomically, thick-knees sit uneasily between the stilts (Recurvirostridae) and the coursers and pratincoles (Glareolidae) in most systematic lists; they also have some characteristics akin to the bustards (Otididae). The bustard-like appearance, which is reflected in old, local names for some species and in past classification in the Gruiformes, is likely to be a result of convergent evolution. In their ground-breaking checklist, Burt Monroe and Charles Sibley listed thick-knees after the Chionidae (sheathbills) and before the Charadriidae.

Two species in the genus *Esacus* are generically separable from the seven species in the genus *Burhinus*. The two *Esacus* species are larger than the others, and both have particularly large, heavy bills and similar diets and habitats. In the past they have themselves been separated into two genera, based largely on bill structure and plumage pattern. In the Peters 1934–1986 taxonomy, the two species are broken into two genera: *Esacus* and *Orthoramphus*, each with one species.

Variation within species is limited, although 19 subspecies are recognized. Division into subspecies is based on small differences in size and color, especially in the widespread species such as the stone-curlew (*B. oedicnemus*) of Europe, North Africa, and Asia.

Physical characteristics

All thick-knees are long-legged and have three short, thick toes and a pointed bill. The two *Esacus* species have a pow-

erful bill with a markedly upswept lower mandible. All thick-knees have a round head on a slim, waisted neck, a broad, bulky body, and long tails that are narrow and tapered when closed and held pointing slightly downwards. Strikingly large, round eyes, a pale bill base, and various combinations of stripes above, through, and below each eye create bold plumage patterns. The head stripes tend to be more eye-catching at long range, but the piercing eye is most arresting up close. A wide iris contracts greatly in poor light to open a very large pupil but makes a vivid yellow or amber disk in bright sun.

Plumages are pale and sandy brown with white undersides; most thick-knees have a dark-edged, pale panel across the folded wing. Wing patterns are streaked, spotted, or plain, but in flight all reveal black-and-white patterns above and below the wings and tail. Sexes are almost alike and juvenal plumages are similar to those of adults. Downy chicks' complex patterns mimic stony, sandy ground.

Distribution

Most *Burbinus* species are Old World birds; two are Neotropical. The double-striped thick-knee (*B. bistriatus*) is found in central and northern South America from Mexico to Brazil, whereas the Peruvian thick-knee (*B. superciliaris*) occupies a Pacific coastal strip from southern Ecuador through Peru. In Europe, Africa, and Asia, distribution of thick-knees is much wider, ranging from as far north as

Family: Thick-knees Vol. 9: Birds II



Bush stone-curlew (*Burhinus magnirostris*) threat behavior. (Illustration by Michelle Meneghini)

Britain in the case of the stone-curlew (B. oedicnemus) to the southern tip of South Africa (the spotted dikkop [B. capensis]), and from the Canary Islands off northwest Africa east to Southeast Asia and Australia, where the bush thick-knee (B. grallarius) is common. The great thick-knee (E. recurvirostris) ranges from Iran east to China, and the beach thick-knee (E. magnirostris) is found more southerly, from Malaysia and the Philippines to coastal Australia.

Habitat

Several species have adapted to agricultural development in open, flat landscapes, but they often lose eggs and chicks to agricultural operations and to trampling by livestock, and feeding opportunities are reduced as extensive agriculture is intensified. Original habitats of double-striped and Peruvian thick-knees, the stone-curlew, and the bush thickknee are bushy to open grassy landscapes, bordering on semi-arid in hotter areas, with exposed sandy soil. Stonecurlews in Britain once occupied coastal shingle ridges but disappeared from this habitat as human activity increased. The African spotted dikkop inhabits quite arid places away from water, as well as open savanna woodland. The water dikkop (B. vermiculatus) of southern Africa and the Senegal thick-knee (B. senegalensis) from farther north in Africa are typically waterside birds, although they usually live close to rivers that run through semi-arid or even desert countryside. Groups of Senegal thick-knees are often seen on sandbanks beside the Nile against a backdrop of the golden cliffs of the Egyptian desert. Senegal thick-knees nest on flat roofs in big cities such as Cairo, water dikkops may be found on village playing fields, and double-striped thick-knees gather close to ranches and are frequent victims of road traffic at night.

Behavior

The *Burbinus* thick-knees become active at dusk, having stayed quiet and immobile by day. They call loudly as night approaches, with far-carrying, strident, or fluty calls. As pairs fly to feeding places their bold wing patterns show well in fading light. Stone-curlews breed in isolation or in loose groups where limited habitat concentrates a few pairs. They are mostly solitary except when gathering to molt just before autumn migration. Senegal thick-knees and water dikkops, however, are found in small, close groups. In midday heat, they frequently find deep shade beneath bushes and are difficult to find. Senegal thick-knees make the air ring with their eerie calls around city roofscapes after dark. Bush thick-knees melt into the background with their cryptic coloration on open ground with scattered dead branches and fallen leaves.

Great thick-knees tend to avoid open sand and resort to rocks, stony banks, and muddy places along rivers or around large lakes; they are mostly active by night. Beach thick-knees are mostly seen by day, but it is not clear when they are most active



A Eurasian thick-knee (*Burhinus oedicnemus*) with its eggs. (Photo by J. Cancalosi/VIREO. Reproduced by permission.)

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All thick-knees are terrestrial birds and perch no higher than on a fallen log or rock (except for the rooftop-perching Senegal thick-knee). They fly low but strongly when moving between nesting, roosting, and feeding places or if disturbed; otherwise, they are ground-dwelling birds. Courtship and territorial aggression are ground activities with loud calls, presumably because their nocturnal nature precludes extensive display flights. If undisturbed, a thick-knee may rest on its tarsi, or stand with its body markedly sloping, tail down, head withdrawn into the shoulders, but a long-striding, feeding bird has a special elegance, if a somewhat furtive character.

Feeding ecology and diet

Thick-knees walk slowly, looking for prey on the ground. Large beetles and birds' eggs are slow-moving or immobile prey that are easily approached. When a thick-knee spots food, it tilts forward to pick up the item in its bill. Thick-knees use their sharp bill tip to hammer large prey and to break it up if necessary before it is swallowed.

The beach thick-knee eats crabs and uses its massive, powerful bill to break them into manageable pieces. Otherwise, preferred foods are similar across species: the Senegal thick-knee eats beetles, crickets, grasshoppers, crustaceans, mollusks, worms, frogs, and a few small rodents, while the stone-curlew also eats earwigs, snails, slugs, lizards, frogs, and even shoots of low-growing plants. Much food is associated with animal dung, and stone-curlews fly up to two miles at dusk to suitable pastures where sheep graze or pigs forage. Grass becomes too long and dense for stone-curlews if it is not grazed, and some nature reserves specially managed for stone-curlews are fenced to concentrate and protect dense populations of rabbits that keep vegetation very short.

Reproductive biology

Northern species nest in late spring whereas tropical species breed whenever the opportunity arises, which is often related more to river and lake levels than to time of year. Stone-curlews are monogamous and pair for life, and other species may do the same. Stone-curlews that winter in southern Europe or Africa arrive in spring in the United Kingdom already paired, reinforcing strong pair bonds by ritual displays. The black-and-white patterns of wings and tail probably form an important part of nocturnal or crepuscular displays, but there appears to be little in the way of posturing or aggression. While feeding, pairs keep in close contact by regular calling.

Nests are mere scrapes in soft earth, selected by the pair as they bow together towards the preferred spot. The male finally pinpoints the site and the female shuffles onto it to scrape earth away with her feet. Small twigs, pebbles, and bits of detritus are scattered around the scrape, but several others may be created in this way before a final choice is made.

The beach thick-knee lays one egg; all other species lay two, occasionally three, in a clutch. Eggs are pale with brownish spots and streaks in a camouflage pattern. Senegal thick-knees and spotted dikkops surround the eggs with twigs, stones, and animal droppings. Incubation, by both parents,



A great thick-knee (*Esacus recurvirostris*) stands in the water. (Photo by H. & J. Eriksen/VIREO. Reproduced by permission.)

lasts from 24 to 27 days; empty eggshells are carried away by parent birds to prevent predators from locating the nest.

Newly-hatched chicks dry and leave the nest before they are a day old. They are fed by their parents for a short time but quickly learn to find food themselves, although they are still protected by their parents and are often brooded beneath a wing. If a predator threatens the young, adult thick-knees will display with fanned wings and tail, but they rarely feign injury to draw the intruder away. Sheep, which may trample eggs or chicks, are driven off by thick-knees with fanned wings and tail. The chicks make their first flight at around 42–50 days old. They do not normally breed until they are two or three years old.

Conservation status

Stone-curlew populations have declined in Europe and populations in the United Kingdom have recovered only with intensive efforts involving cooperation between conservationists and farmers. Farming operations are apt to destroy nests and intensification of farms, especially a reduction in the variety of crops and increased height and density of plants in spring, removes breeding opportunities. Security of the United Kingdom population may require annual efforts to protect individual pairs and nests, and the species would decline without such special consideration. Whether the United Kingdom populations are sustainable remains to be seen.

South American species have declined with increased disturbance and development, and the Peruvian thick-knee may now be in a precarious state. Recent assessments of its status are somewhat optimistic according to Ridgely and Greenfield. In Australia, bush thick-knees have suffered long-term

Family: Thick-knees Vol. 9: Birds II

declines in numbers and range because of habitat loss. Claims that fox predation, poisoned baits, shooting, and egg collecting have been the cause of the decline confuse the issue. The beach thick-knee is thinly scattered and its beach habitat is especially vulnerable to development and disturbance. The open ground occupied by most species is always likely to be subject to human disturbance and development and many habitats are considered "waste" by most people.

Significance to humans

Birds that are scarcely seen by day but make loud noises at night give rise to stories in simple rural communities. However, as people have become more dissociated from the land and its wildlife, awareness of the bird or even its voice has declined. Old names for stone-curlews, such as goggle-eyed plover, thick-kneed bustard, and Norfolk plover, suggest some familiarity with the species, but few people living in the twenty-first century would recognize such names. Bush thick-knees appear in folklore in Australia, with onomatopoeic names such as Weeloo and Willaroo, and they gave rise to suspicion and unease among early white settlers. The double-striped thick-knee, however, has at times been kept as a semi-domesticated bird to reduce insect infestations. It was welcome around farms and settlements.

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Species accounts

Spotted dikkop

Burhinus capensis

TAXONOMY

Oedicnemus capensis Lichtenstein, 1823, Cape of Good Hope. Four subspecies.

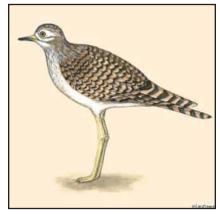
OTHER COMMON NAMES

English: Spotted thick-knee, Cape dikkop, Cape thick-knee; French: Oedicnème bistrié; German: Dominikanertriel; Spanish: Alcaraván Venezolano.

PHYSICAL

CHARACTERISTICS

16-17.5 in (37-44 cm) Most obviously spotted thick-knee, rich rusty-brown with bold black arrow-head spots, whiter below with fine streaks and white on the face, behind the eye, and on the throat. The bill base, eyes, and legs are rich yellow. This is an elongated species, long-winged and long-tailed.



Burhinus capensis

DISTRIBUTION

Found in a narrow sub-Saharan band from Senegal on the west coast to the Horn of Africa in the east, with a small, isolated population in Arabia; extends south, more widely and commonly, through East Africa to Zambia and in a broad zone across the south of the continent. The distribution reflects unsuitable areas of the Sahara in the north and the Congo basin forests in West Africa.

HABITAT

Semi-arid areas away from marshes and rivers, but sometimes more or less wooded in dry savannas or around clumps of trees and bushes near open grasslands; such cover is important in providing daytime shade and shelter. Sometimes found on playing fields, parkland, and near coastal beaches.

BEHAVIOR

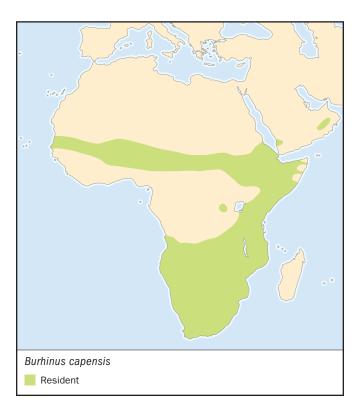
Seeks shade and cover by day; pairs or small groups remain quiet and still until dusk except on dull, cloudy days when they may feed.

FEEDING ECOLOGY AND DIET

Typical plover-like feeding action involves a steady forward walk and a swiveling, tilting motion to pick up food from the ground in the bill. Large insects are favored, but a number of crustaceans and frogs are eaten, as well as a limited amount of vegetable matter, mainly seeds. It feeds mostly at night and entirely on the ground.

REPRODUCTIVE BIOLOGY

Pairs are monogamous, probably established for several seasons, breeding in the dry season or at the beginning of seasons.



sonal rains. The nest is a simple hollow made on bare ground with the feet, sparsely lined with small pebbles, grass, leaves, and dried animal droppings. Lays two eggs (less often one or three) and incubation lasts 24 days; chicks fly at eight weeks.

CONSERVATION STATUS

Its ability to cope with human activity and limited alteration of open habitats allows the spotted dikkop to thrive in quite well-populated areas, so long as disturbance and persecution remain slight and housing or industrial development is absent. Generally quite numerous in suitable areas, one of the more common and most secure thick-knees.

SIGNIFICANCE TO HUMANS

Most African people take little or no specific notice of the spotted dikkop in areas where nocturnal noise from an assortment of birds and mammals is common. ◆

Beach thick-knee

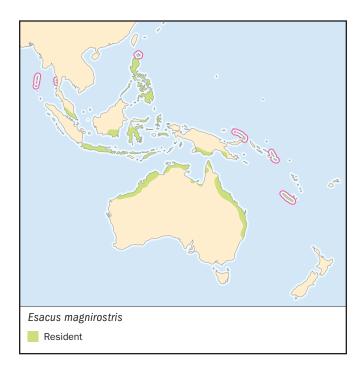
Esacus magnirostris

TAXONOMY

Edicnemus magnirostris Vieillot, 1818, Depuch Island, Western Australia. Monotypic.

OTHER COMMON NAMES

English: Beach stone curlew, beach curlew, Australian stoneplover; French: Oedicnème des récifs; German: Rifftriel; Spanish: Alcaraván Picogruesco Australiano. Family: Thick-knees Vol. 9: Birds II



PHYSICAL CHARACTERISTICS

21-22.5 in (53-57 cm) The largest thick-knee, massively built and thicklegged, with a long, strongly-upcurved bill. Plain graybrown above, marked with a blackish shoulder bordered below by a thin white line, above pale gray wing coverts; rusty patch under tail. Dark crown and black



Esacus magnirostris

cheek stripe separated by wide white stripe over eye; white lower cheek and throat patch. Bill largely black with small yellow base; eyes and legs yellow.

DISTRIBUTION

Scattered through the Andaman Islands to the Philippines, Indonesia, New Guinea, and many islands of the Southwest Pacific, and south to the north and northeast coasts of Australia

HABITAT

Found on island shores and mainland beaches, whether of sand, shingle, rocks, or mud, in wide open spaces or restricted to narrow beaches fringed by mangroves or rocks. Often feeds in intertidal areas and equally at home on windswept estuaries, sheltered river mouths, and exposed rocks.

BEHAVIOR

Usually found along the beach close to the water's edge, the beach thick-knee tends to fly off over the sea if disturbed before sweeping back to the shore. It may resort to undisturbed dunes and sand flats a little way inland, or even to the shores of shallow, coastal lagoons. It will rest on offshore reefs, and even enters quite tall and moderately dense mangroves.

FEEDING ECOLOGY AND DIET

The main food is crabs, where they are common, but other crustaceans may also be taken when crabs are scarce. Larger crabs are broken up before being swallowed. Typical feeding technique is a slow, quiet stalk, followed by a lunge or sudden fast run to snatch up prey, but the beach thick-knee will also probe mud and sand. It does not wade in water.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds at low density in isolated pairs, frequenting regular territories for many seasons. The nest, on a sandbank or spit, is a simple depression, occasionally ringed (but not lined) with bits of vegetation. Lays just one egg, which is incubated for 30 days; young develop slowly and fly after 12 weeks, but they remain with adults for up to a year.

CONSERVATION STATUS

Locally secure but in general faces increasing threats from disturbance as beaches are subject to human pressures, including tourist and hotel development, off-road vehicles on beaches, and other disruptive activities. Faces potentially large, locally catastrophic, but uncertain threats from rising sea levels with global climate change.

SIGNIFICANCE TO HUMANS

None known. ◆

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Rob Hume

Pratincoles and coursers

(Glareolidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Glareolidae

Thumbnail description

Small to medium-sized, rather slender, with long, pointed wings; bill short to moderately long, arched on culmen, sometimes colored red or yellow at base; legs long (coursers) or fairly short (most pratincoles); plumage usually quietly colored in brown, black, or white, except in Egyptian plover (*Pluvianus aegyptius*) which is boldly patterned in black, gray, and white

Size

6.7-11.4 in (17-29 cm); 1.3-6.1 oz (37-172 g)

Number of genera, species

6 genera; 16 species

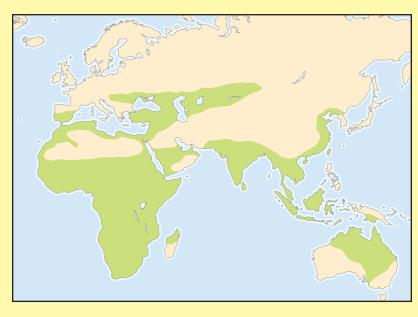
Habitat

Desert, steppe, savanna, open woodland, and

large rivers

Conservation status

Endangered: 1 species



Distribution

Africa, Eurasia, and Australia

Evolution and systematics

The oldest known fossil of the Glareolidae is *Paractiornis* from Lower Miocene deposits of North America, about 20 million years old. Fossils of the recent genus *Glareola* occur in the Middle Miocene of Europe, about 15 million years old. No fossil coursers have yet been found.

The coursers are structurally closer to other shorebirds. They are highly terrestrial and are probably ancestral to the pratincoles, which have diverged from the terrestrial condition to become specialized aerial feeders, often associated with large rivers. Coursers are more closely associated with arid habitats than are the pratincoles, again with the exception of the Australian pratincole (*Stiltia isabella*), which is mainly a bird of stony desert. The Egyptian plover is also exceptional in that it is a courser which inhabits the banks and sandbars of the larger rivers of Africa.

The closest relatives of the glareolids have long been a subject of discussion, but the latest evidence, based on DNA-DNA hybridization, suggests that they share a common ancestor with the aberrant crab plover (*Dromas ardeola*) and with the auks, gulls, and terns. These relationships are shown also by osteological and other evidence.

Physical characteristics

Glareolids have 15 cervical vertebrae; the middle toe is usually pectinate (but not in the Australian pratincole or in the

Egyptian plover). The pratincoles are slender, swallow-like birds with long wings and relatively short legs, except in the long-legged Australian pratincole, which also has exceptionally long wings and courser-like plumage, indicating a transitional evolutionary stage between the pratincoles and the coursers. The hind toe of pratincoles is reduced and elevated; the front three toes are moderately long. The genus Glareola is characterized by a forked tail. Pratincoles have a wide gape to facilitate catching flying insects on the wing. The coursers are somewhat stockier than the pratincoles and have relatively shorter wings, a square tail, short front toes, and no hind toe. They have very long legs, except for the Egyptian plover whose legs are rather shorter and scaled in two rows back and front. The Egyptian plover may represent a family of its own, the Pluvianidae, or it may be separable merely as a subfamily Pluvianinae.

Distribution

The Egyptian plover occurs on the major rivers of tropical Africa, mainly north of the equator and south of the Sahara. Coursers occur throughout Africa, including the Sahara, as well as across the Arabian Peninsula into the Indian subcontinent. Pratincoles have a similar distribution to that of the coursers, but extend into southern Europe and Asia. One species is found in Madagascar and another in Australasia.

Family: Pratincoles and coursers Vol. 9: Birds II



A collared pratincole (*Glareola pratincola*) at its nest with chick and egg. (Photo by H. & J. Eriksen/VIREO. Reproduced by permission.)

Habitat

Most pratincoles are associated with water in the form of large rivers or of inland pans. This is true even of the desert-dwelling Australian pratincole, which seldom nests more than a mile (1.6 km) from the nearest body of water. Some Eurasian pratincoles inhabit the region between short-grass steppes and desert, usually with surface water available in some form. The Egyptian plover is exceptional among coursers in that it occurs only on the larger tropical African rivers with sandbars. The remaining eight species of courser are all birds of dry habitats, from dry, thin forest to extreme desert.

Behavior

Pratincoles are almost invariably gregarious: flocks may number many hundreds of birds, especially in the non-breeding season and during migration. The steppe-nesting species of the Northern Hemisphere migrate from their breeding grounds to Africa or Australia where they gather on grasslands and shorelines to rest and feed. The river-nesting pratincoles are largely nomadic, moving away from rivers when high water covers the rocks and sandbanks on which they normally nest and roost. Although silent much of the time, pratincoles may become quite vocal when migrating or when disturbed at their breeding sites, uttering loud, sharp tern-like calls. They roost on the ground or on rocks in midstream, usually in flocks, with all of the birds facing into the wind.

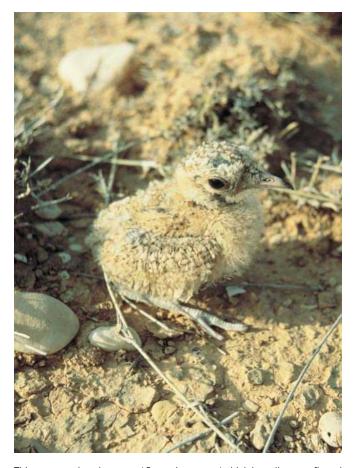
Coursers, as their name suggests, are great runners, hence their need for open ground. Most species prefer to run rather than to fly in the face of disturbance, but they fly extremely well when the need arises. Their plumage is usually highly cryptic, providing excellent camouflage, on which the birds rely for concealment. Coursers are seldom truly migratory, though some may have more or less seasonal movements. The species that inhabit the most arid environments are highly no-

madic, moving about as the food supply dictates, or departing from regions where rainfall has brought on too dense a stand of vegetation. Most species are largely solitary, but members of the genus *Cursorius* often form flocks of 5–10 birds, seldom more.

Coursers are largely silent when on the ground, but have distinctive, loud flight calls. They also have sharp alarm calls when disturbed near the nest. They tend to be rather shy as a rule, seldom allowing a close approach, then running rapidly away before taking flight if hard pressed. They are active both day and night, becoming crepuscular or partly nocturnal in hot weather, especially on moonlit nights.

Feeding ecology and diet

All glareolids are largely insectivorous, although coursers may occasionally eat small mollusks and seeds. Pratincoles catch much of their food on the wing, but often chase insects on the ground also. The Australian pratincole is particularly adept at feeding both in the air and on the ground, since it has long wings as well as long legs. Coursers are exclusively ground feeders, taking their food by a run and a peck, much as plovers do. Members of the genus *Cursorius* use their relatively long, decurved bills for digging in soft soil to unearth insects or seeds.



This cream-colored courser ($\it Cursorius \, cursor$) chick is well camouflaged in its surroundings. (Photo by A. Forbes-Watson/VIREO. Reproduced by permission.)

Reproductive biology

All glareolids nest on the ground without any nest, or in a shallow scrape in the soil. The clutch consists of two to four eggs in those species of pratincoles that nest in the Northern Hemisphere; elsewhere the clutch seldom exceeds two eggs. The double-banded courser (*Smutsornis africanus*) invariably lays only one egg. Glareolid eggs are cryptically colored—a whitish or cream ground color is more or less heavily marked with black, brown, and gray streaks, spots, and blotches. Pratincoles usually nest in more or less dense colonies, but sometimes solitarily. Coursers are always solitary nesters. The three-banded courser (*Rhinoptilus cinctus*) lays its two eggs in a fairly deep scrape and incubates them partly buried in soil. The Egyptian plover also incubates its eggs partially buried in sand, and it will cover them completely when disturbed at the nest.

Conservation status

Only Jerdon's courser (Rhinoptilus bitorquatus) of east-central India is listed as endangered. No other glareolid is

globally threatened. The rarity of Jerdon's courser is a result of habitat destruction and the bird's great sensitivity to human disturbance. At least two protected areas, the Sri Lankamalleswara Wildlife Sanctuary and the Sri Venkateswara National Park, have recently (1992) been established for the bird's protection, and other protected areas are planned.

Significance to humans

In parts of Africa and southeast Asia, coursers and pratincoles are sometimes hunted for food, and the eggs of the collared pratincole (*Glareola pratincola*) used to be collected commercially for food, to the extent that some breeding colonies in Hungary were wiped out. These eggs are still collected in large numbers, mainly for the illegal egg-collecting trade. Furthermore, the practice of gathering chamomile on the grassy steppes of Hungary destroys many clutches of pratincole eggs. Otherwise glareolids impinge little on human activities beyond their aesthetic value to birdwatchers who seek them out as additions to their lists of desirable birds seen.



1. Collared pratincole (*Glareola pratincola*); 2. Rock pratincole (*Glareola nuchalis*); 3. Egyptian plover (*Pluvianus aegyptius*); 4. Australian pratincole (*Stiltia isabella*); 5. Double-banded courser (*Smutsornis africanus*); 6. Gray pratincole (*Glareola cinerea*); 7. Burchell's courser (*Cursorius rufus*); 8. Three-banded courser (*Rhinoptilus cinctus*). (Illustration by Bruce Worden)

Species accounts

Collared pratincole

Glareola pratincola

SUBFAMILY

Glareolinae

TAXONOMY

Hirundo pratincola Linnaeus, 1766, Austria. Three subspecies recognized.

OTHER COMMON NAMES

English: Common pratincole, red-winged pratincole, locust bird, swallow-plover; French: Glaréole à collier; German: Rot-flügel Brachschwalbe; Spanish: Canastera Común.

PHYSICAL CHARACTERISTICS

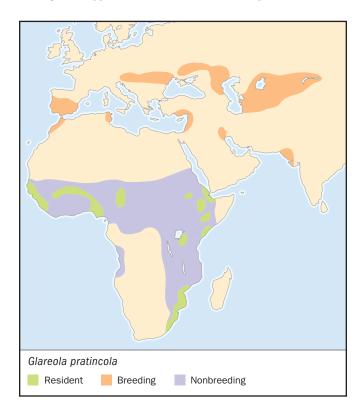
8.7–9.8 in (22–25 cm); 2.1–3.7 oz (60–104 g). Slender, shortlegged, long-winged; plumage mostly smoky grayish brown shading to white on belly. Throat yellowish buff surrounded by narrow black collar (absent when not breeding). Bill red at base and around gape. Underwing coverts dull rusty brown to chestnut.

DISTRIBUTION

The most widespread of the pratincoles. Breeding populations are scattered discontinuously throughout sub-Saharan Africa and Eurasia from Spain to Lake Balkhash in Kazakhstan. Non-breeding birds migrate to sub-Saharan Africa.

HABITAT

István Sterbetz describes the habitat as the zone between short-grass steppes and desert, as well as floodplains, dried es-



tuarine mud banks, and marine shore with semi-desert features.

BEHAVIOR

Collared pratincoles are highly gregarious at all times, even when breeding. They spend much time resting on the ground between bouts of aerial feeding. They tend to be vocal, especially in breeding colonies and on migration. Their flight is buoyant.

FEEDING ECOLOGY AND DIET

Catch flying insects on the wing and chase prey on the ground by running or by a short leap into the air. Food is mainly grasshoppers and beetles; during locust plagues, flocks of pratincoles devour large numbers of these insects.

REPRODUCTIVE BIOLOGY

Breeds in spring in the Northern Hemisphere, in the dry season in most of tropical Africa and in early summer in southern Africa; breeding is usually in loose colonies. The nest is a shallow scrape, sometimes lined with a few bits of earth or dry plant fragments. The clutch in Eurasia is usually three eggs, but only two in Africa. The eggs are whitish to cream, heavily blotched with black, gray, and brown. Both sexes incubate for 17–19 days, and feed the precocial chicks for at least a week. The young fly at the age of about a month.

CONSERVATION STATUS

Though not globally threatened, collared pratincoles have declined in numbers in Europe and parts of Africa as a result of pesticides, artificial fertilizers, habitat destruction, and disturbance, especially of breeding colonies. Breeding sites need protection.

SIGNIFICANCE TO HUMANS

Apart from the commercial collecting of eggs, the collared pratincole has little significance to humans. In the past it probably helped to control locust plagues, but the decline in numbers reduces the birds' impact in this regard. ◆

Rock pratincole

Glareola nuchalis

SUBFAMILY

Glareolinae

TAXONOMY

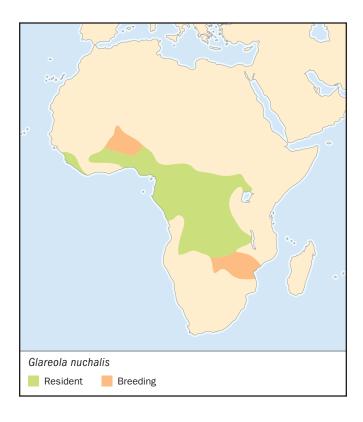
Glareola nuchalis G. R. Gray, 1849, Fifth Cataract of the Nile, Sudan. Two distinctive subspecies.

OTHER COMMON NAMES

English: Collared pratincole, white-collared pratincole, rufous-(or chestnut-) collared pratincole; French: Glaréole auréolée; German: Halsband-Brachschwalbe; Spanish: Canastera Sombría.

PHYSICAL CHARACTERISTICS

7.1–7.5 in (18–19 cm); 1.5–2.0 oz (43–58 g). Small, charcoal gray, paler below, with white collar (subspecies *nuchalis*) or rufous collar (subspecies *liberiae*) on hindneck; legs and base of bill bright red.



DISTRIBUTION

Tropical Africa.

HABITAT

Larger rivers with exposed rocks and sand bars.

BEHAVIOR

Usually in small flocks; perch on exposed rocks in midstream between bouts of aerial foraging. May also perch on riverside trees if rocks submerged. Migratory according to water levels, moving away from rivers that are flooded. Rather silent as a rule. May become tame around human habitations.

FEEDING ECOLOGY AND DIET

Forage both aerially and on rocks mostly at dawn and dusk, catching insects in flight or by running after them. May catch insects around street lights at night.

REPRODUCTIVE BIOLOGY

Nest singly or in small colonies on exposed rocks, laying two eggs in a hollow or crevice of bare rock. Both sexes incubate for about 20 days and feed the chicks for a further 20–30 days when they reach flying age.

CONSERVATION STATUS

Not threatened, but some stretches of river may be rendered unsuitable by damming and unseasonal release of water downstream. Rock pratincoles no longer occur in Sudan, where first collected, so numbers are probably declining.

SIGNIFICANCE TO HUMANS

None known. ◆

Gray pratincole

Glareola cinerea

SUBFAMILY

Glareolinae

TAXONOMY

Glareola cinerea Fraser, 1843, mouth of River Niger, Nigeria. Monotypic.

OTHER COMMON NAMES

English: Cream-colored pratincole; French: Glaréole grise; German: Graubrachschwalbe; Spanish: Canastera Gris.

PHYSICAL CHARACTERISTICS

7.1–7.9 in (18–20 cm). Small and pale overall; above pale gray with rufous hindneck; below white, washed ochre across breast. Legs and base of bill red.

DISTRIBUTION

Tropical West Africa from Mali to Congo (Zaire).

HABITAT

Large rivers with exposed sand banks; in flood season also coastal habitats, including mangrove swamps.

BEHAVIOR

Usually gregarious at all times. Forages on the wing and rests on sand banks.

FEEDING ECOLOGY AND DIET

Catches flying insects on the wing and also chases insects and spiders by running on ground.

REPRODUCTIVE BIOLOGY

Nests colonially on sand banks, laying one or two eggs in an unlined scrape not far from water. Breeding biology poorly known.



CONSERVATION STATUS

While still locally abundant, some breeding sites have been eliminated by damming, such as Lake Volta in Ghana. Also subject to human disturbance, but not under immediate threat.

SIGNIFICANCE TO HUMANS

None known. ◆

Australian pratincole

Stiltia isabella

SUBFAMILY

Glareolinae

TAXONOMY

Glareola isabella Vieillot, 1816, Australasia. Monotypic.

OTHER COMMON NAMES

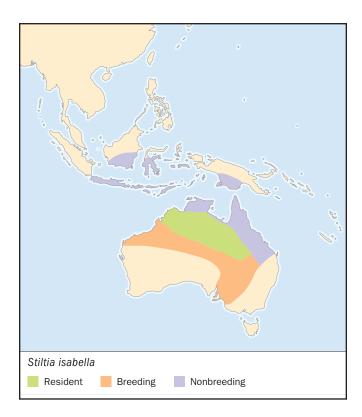
English: Australian courser, long-legged pratincole, isabelline pratincole; French: Glaréole isabelle; German: Stelzenbrach-schwalbe; Spanish: Canastera Patilarga.

PHYSICAL CHARACTERISTICS

7.5–8.7 in (19–22 cm); about 2.3 oz (about 65 g). Slender and elegant with long legs and exceptionally long, pointed wings. Mostly light brown, paler on neck, with dark brown upper belly and white lower belly. Looks like a long-winged courser with a pratincole's head. Bill bright red at base. Rump white.

DISTRIBUTION

Breeds over much of inland and northern Australia. Non-breeding birds migrate to extreme northern Australia, New Guinea, and eastern Indonesia.



HABITAT

Breeds in arid stony country or on short-grass plains, usually within a mile (1.6 km) or so of water; less often on shorelines of inland lakes and pans. Non-breeding birds occur on airfields, grassy plains, and fallow fields.

BEHAVIOR

Usually gregarious, but sometimes solitary. Highly migratory in flocks that fly high with sweet, penetrating calls. Flight very light and tern-like. Runs swiftly on ground. Usually silent at breeding sites.

FEEDING ECOLOGY AND DIET

Catches insect prey by running pursuit on ground or in flight. On ground uses a wing to stop prey from escaping. May also feed on non-flying arthropods and some seeds. Drinks often, especially in hot weather.

REPRODUCTIVE BIOLOGY

Nests solitarily or in small, loose groups on open shorelines and semi-desert plains, usually within a mile (1.6 km) of water. Two eggs are laid on bare soil, sometimes with a ring of small stones, droppings, or dry plant fragments around the site. Both parents incubate for about 20 days. Chicks are precocial, but are fed by parents for about a month. Between feedings, chicks hidden under shrubs or in shallow burrows. Young fly at about five weeks.

CONSERVATION STATUS

Common to abundant throughout range; not threatened.

SIGNIFICANCE TO HUMANS

May be hunted for food in Indonesia. •

Egyptian plover

Pluvianus aegyptius

SUBFAMILY

Cursoriinae

TAXONOMY

Pluvianus aegyptius Linnaeus, 1758, Egypt. Monotypic.

OTHER COMMON NAMES

English: Crocodile bird, Egyptian courser; French: Pluvian fluviatile; German: Krokodilwächter; Spanish: Pluvial.

PHYSICAL CHARACTERISTICS

7.5–8.3 in (19-21 cm); 2.6–3.2 oz (73–92 g). Small, plover-like, with gray back, buff underparts and boldly marked black and white head-and-neck pattern.

DISTRIBUTION

Tropical Africa from Senegal to Ethiopia, and south to Angola and Congo (Zaire).

HABITAT

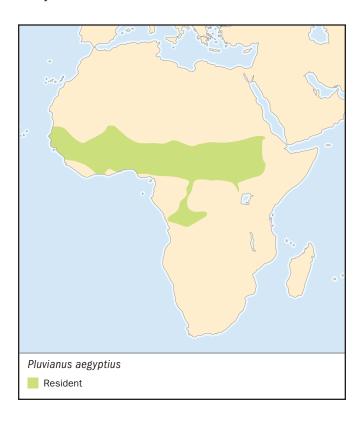
Major lowland rivers with sand and gravel bars.

BEHAVIOR

In pairs when breeding, but may form flocks of up to 60 birds when moving about according to changes in water level.

FEEDING ECOLOGY AND DIET

Feeds on invertebrates, mainly insects, caught by running after prey on ground or by a leap into the air; may also probe and scratch in damp sand for food.





REPRODUCTIVE BIOLOGY

Breeds mostly in dry season when river levels low. Lays two to three eggs in deep scrape in sand, incubating eggs in partly buried position for 28–31 days. Eggs may be wetted with soaked belly plumage in hot weather. Chicks leave nest as soon as hatched, but may be buried in sand by parents when disturbed; parents may wet sand over chicks in the heat of the day. Young fly when about five weeks old.

CONSERVATION STATUS

Common in suitable habitat, but some populations may be threatened by damming of rivers. No longer occurs in Egypt, where first described, so numbers may be dropping in parts of range.

SIGNIFICANCE TO HUMANS

None known. ◆

Burchell's courser

Cursorius rufus

SUBFAMILY

Cursoriinae

TAXONOMY

Cursorius rufus Gould, 1837, Potchefstroom, South Africa. Monotypic.

OTHER COMMON NAMES

French: Courvite de Burchell; German: Rostrennvogel; Spanish: Corredor Rufo.

PHYSICAL CHARACTERISTICS

7.8–8.7 in (20–22 cm); 2.7–3.4 oz (76–95 g). More or less uniform brown, paler and more rufous below, shading to dark

brown bar on upper belly; lower belly white; eye-stripe blackand-white; hind-crown blue-gray. Legs long and white. Bill moderately long and decurved.

DISTRIBUTION

Southern Africa from Angola and Namibia to inland South Africa and southern Botswana.

HABITAT

Desert, semi-desert, open, short grassland.

BEHAVIOR

Usually in pairs or small parties of up to 10 birds. Rather shy, running quickly away when disturbed. Takes flight when hard pressed.

FEEDING ECOLOGY AND DIET

Feeds mainly on insects caught by surface pecking or by digging with bill in soft soil or sand. Rarely takes seeds.

REPRODUCTIVE BIOLOGY

Breeds at almost any time of year, laying two blackish eggs on bare ground, often among antelope droppings. Incubation and fledging periods not known. Chicks highly precocial, but are fed by parents for a few weeks after hatching.

CONSERVATION STATUS

Formerly common over most of its range, Burchell's courser has undergone a significant decline in numbers. Reasons for this are not known, but the species is sensitive to disturbance and possibly to overgrazing of semi-desert habitat.

SIGNIFICANCE TO HUMANS

None known. ◆

Double-banded courser

Smutsornis africanus

SUBFAMILY

Cursoriinae

TAXONOMY

Cursorius africanus Temminck, 1807, (Namaqualand), South Africa. Eight well-defined subspecies described, some geographically isolated.

OTHER COMMON NAMES

English: Two-banded courser; French: Courvite á double collier; German: Doppelband-Rennvogel; Spanish: Corredor Escamoso Chico.

PHYSICAL CHARACTERISTICS

7.9–9.4 in (20–24 cm); 2.0–3.7 oz (56–104 g). Small and graceful with long white legs and a short bill; mostly buff with heavily scaled dorsal plumage and lightly streaked blackish on neck; two bold black bands encircle the mantle and upper breast.

DISTRIBUTION

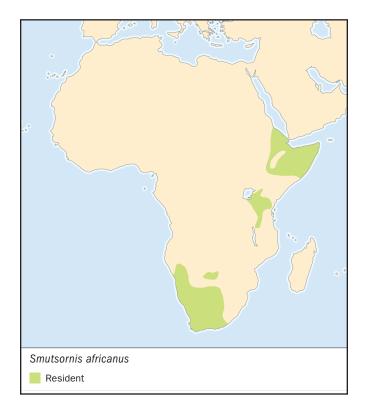
Discontinuously from South Africa to Somalia and Ethiopia.

HARITAT

Semi-desert with low shrubs, overgrazed grassland, and dry alkaline plains.

BEHAVIOR

A typical courser, but more wary and better camouflaged than most species. Runs very fast when disturbed and in pursuit of prey. May stand behind shrub for concealment. Largely nocturnal in summer, otherwise active by day as well. Mostly solitary or in pairs.



FEEDING ECOLOGY AND DIET

Catches insects by pursuing them on the ground, but does not dig.

REPRODUCTIVE BIOLOGY

Breeds throughout the year. Lays a single egg on bare ground, usually among antelope droppings or small stones. Both sexes incubate for 26–27 days. Chick leaves the nest site within 48 hours and is fed by the parents for several weeks. Young flies at about six weeks of age.

CONSERVATION STATUS

The double-banded courser is common throughout most of its range and is not in need of special conservation measures.

SIGNIFICANCE TO HUMANS

None known. ◆

Three-banded courser

Rhinoptilus cinctus

SUBFAMILY

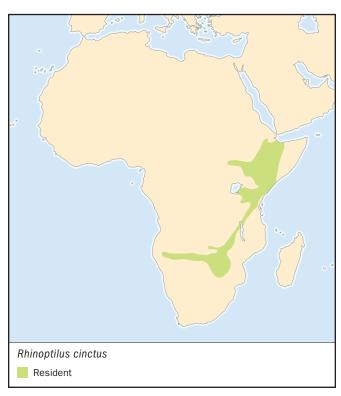
Cursoriinae

TAXONOMY

Hemerodromus cinctus Heuglin, 1863, near Gondokoro, White Nile. Three subspecies.

OTHER COMMON NAMES

English: Heuglin's courser, Seebohm's courser; French: Courvite á triple collier; German: Bindenrennvogel; Spanish: Corredor Escamoso Grande.



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PHYSICAL CHARACTERISTICS

9.8–11 in (25–28 cm); 4.2–5.3 oz (119–150 g). Two or three rather poorly defined subspecies are recognized.

DISTRIBUTION

Eastern Africa from extreme northern South Africa and Namibia to southern Sudan and Ethiopia.

HABITAT

Dry thorn scrub, bushy grassland, and sparse mopane woodland.

BEHAVIOR

Usually singly or in pairs, less often in groups of up to six birds. Largely nocturnal. When disturbed may freeze before running swiftly away, then taking flight for a short distance. Roosts by day in shade of bush or tree.

FEEDING ECOLOGY AND DIET

Catches insects on the ground. Little else known.

REPRODUCTIVE BIOLOGY

Nests mainly in dry season, making a deep scrape under a bush or tree. Clutch of two eggs partly buried in loose soil and incubated by both parents for about 25–27 days. Chicks are highly precocial, but the fledging period is unknown.

CONSERVATION STATUS

The species is quite common over most of its range and is not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

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Gordon Lindsay Maclean, PhD, DSc

Plovers and lapwings

(Charadriidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Charadriidae

Thumbnail description

Charadriids are small-to-medium, chunky shorebirds with rounded head, usually a "steep" forehead, short neck, and large eyes; typically black, brown, gray, and/or white; often with a bold pattern. Legs are short to medium and bill is typically shorter than the head

Size

5.5-16 in (14-40 cm); 1.25-10.5 oz (35-298 g)

Number of genera, species

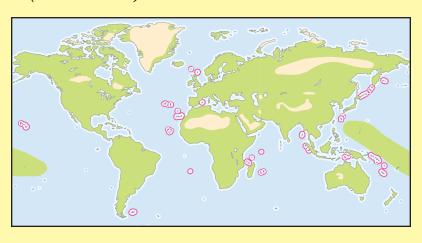
10 genera, 66 species

Habitat

Shorelines, wetlands, and open areas such as pastures, moors, and tundra

Conservation status

Critical, 1 species; Endangered, 2 species; Vulnerable, 5 species; Near Threatened, 6 species



Distribution

Worldwide except for Antarctica

Evolution and systematics

The family Charadriidae, including lapwings and plovers, is a fairly homogeneous group, although the number of genera has been extensively debated. Conservatively there are as few as six genera containing 56 species. Sibley and Monroe suggest as many as 11 genera containing 67 species, but in 1934, Peters divided the family into 34 genera with 61 species. In 2002, most authorities recognized 10 genera. Early efforts to understand the relationships within this family centered on skull characteristics, back color, and presence of a hind toe. These characteristics are no longer considered taxonomically significant. The two largest genera are *Vanellus* (lapwings) and *Charadrius* (ringed plovers and sandplovers).

Lapwings, with one exception, have a broad, black band near the tip of the tail; a terminal white band also is often present. The white-tailed lapwing (*Vanellus leucurus*) has a solid white tail and is sometimes placed, along with the sociable plover (*Vanellus gregarius*), in the genus *Chettusia*. Most lapwings, excepting *V. vanellus* and *V. miles*, also have a distinctive black-and-white wing pattern. Typically, primaries are black with a broad, white wing stripe extending diagonally across secondary coverts and secondaries. The blacksmith plover (*Vanellus armatus*) is sometimes placed in its own genus (*Antibyx*).

Charadrius plovers typically have a dark, complete or partial breast band and/or a white forehead with a dark line connecting the bill and eye. The shore plover (Thinornis novaeseelandiae) is sometimes included in Charadrius.

Sibley and Monroe place the red-kneed dotterel (*Charadrius cinctus*) in the monotypic genus *Erythrogonys*, and the black-fronted dotterel (*Charadrius melanops*) in the monotypic genus *Elseyornis*. They also place the shore plover in *Charadrius*.

Smaller genera are *Pluvialis* (including the black-bellied plover [P. squatarola] and three golden-plovers), Eudromias (Eurasian dotterel E. morinellus), Oreopholus (tawny-throated dotterel O. ruficollis), wrybill (Anarbynchus frontalis), the inland dotterel (Peltohyas australis), Mitchell's plover (Phegornis mitchellii), and the Magellanic plover (Pluvianellus socialis). The common name "dotterel" is also used for some Charadrius species. The wrybill shares many characteristics with members of *Charadrius*, however, because of an unusual bill that bends to the right at about a 12° angle, it is placed in its own genus. The inland dotterel was formerly included in the courser family, Glareolidae. The Magellanic plover has unusually short legs and a bill that is unusually sharp for a plover. Some scientists consider the Magellanic plover more closely related to turnstones than to plovers; some place it in its own family, Pluvianellidae.

Physical characteristics

Charadriids are chunky, small to medium-sized shorebirds with short to medium-length legs, and a bill that is usually shorter than the head. Rarely colorful, most are Family: Plovers and lapwings Vol. 9: Birds II



A lapwing (Vanellus vanellus) with chicks at its nest. (Photo by Roger Wilmshurst. Bruce Coleman Inc. Reproduced by permission.)

black-and-white with shades of gray and brown, though many are boldly patterned with either dark rings around the neck and strong facial markings or boldly marked black and white wings. Many lapwings have colorful wattles on the head and spurs on the wings. The spurs are used as weapons in territorial disputes and in nest defense. The hind toe is absent or greatly reduced in all species.

Distribution

The family is worldwide in distribution with the exception of Antarctica. The genus *Charadrius* is found throughout the world with a Holarctic center. Lapwings (*Vanellus*) are found throughout much of the world but are absent from North America. The center of lapwing distribution is apparently Africa. Five separate dispersals from Africa to Eurasia and two to South America probably account for the current distribution of *Vanellus*.

Several Charadriids limited to the southern tips of southern continents may be the relic descendants of a now extinct Antarctic species or of migratory Northern Hemisphere species that established breeding populations on their wintering ranges.

North American representatives are American golden-plover (*Pluvialis dominica*), Pacific golden-plover (*P. fulva*), black-bellied plover (*P. squatarola*), mountain plover (*Charadrius montanus*), semipalmated plover (*C. semipalmatus*), long-billed plover (*C. placidus*), Wilson's plover (*C. wilsonia*), piping plover (*C. melodus*), killdeer (*C. vociferus*), and snowy plover (*C. alexandrinus*).

Habitat

Charadriids are primarily birds of open areas and are found along shorelines of salt and/or freshwater bodies and flooded areas or on moors or tundra. Open grasslands and farmlands are often favored. Many species take advantage of humanaltered habitats such as agricultural lands, sewage ponds, golf courses, airports, and even gravel roads and rooftops. Lapwings are primarily freshwater birds, but some are found on arid grasslands. The long-toed lapwing feeds and sometimes nests on floating vegetation. Golden-plovers are also primarily freshwater birds, while the black-bellied plover prefers coastal areas.

Migratory species may summer and winter in very different habitats and visit additional habitats along migration routes.

Behavior

Charadriidae includes migrant and resident species. Most are at least semi-gregarious during migration and on wintering grounds, where they form small-to-large communal foraging and roosting flocks. Mitchell's plover is unusual in that it is rarely seen in groups larger than six. While most are strong and graceful fliers, they are most often seen rapidly running. They are active both during the day and night. Most are quite vocal and their vocalizations have often given rise to local names. The familiar "killdee killdee" given to killdeer inspired both the accepted common name and the specific name *vociferus*.

Feeding ecology and diet

Most forage by rapidly running, then suddenly stopping, looking, and pecking at prey. Foot trembling or patting of the substrate, presumably to reveal potential prey, is seen in many species. The spur-winged lapwing (Vanellus spinosus) stands on one leg and moves the other back and forth to flush potential prey, including small lizards. The wrybill uses its unusual bill to extract mayfly larvae and fish eggs that cling to the underside of stones. The inland dotterel feeds in groups on plants during the day, but at night is more active, solitary, and feeds on invertebrates. The Magellanic plover feeds by pecking and often actively scratches and digs. It turns over stones in a manner similar to that of a turnstone. The red-kneed dotterel, the most aquatic member of the family, swims well and often feeds by wading, and submerges its head. It rarely feeds on dry ground. The white-tailed plover feeds mostly in shallow water and occasionally submerges its head while searching for food. Berries, especially crowberries, may be particularly important to plovers arriving in frozen tundra habitats where few insects are yet available. Gulls have been reported stealing food from both northern lapwings and golden-plovers.

Reproductive biology

Most charadriids lay their eggs in scrapes on the ground. The shore plover is unusual in nesting at the end of a tunnel in thick vegetation, under loose stones, or even in an abandoned petrel burrow. Shore plovers vigorously defend their

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nests, but feeding areas are communal. Other plovers also commonly feed away from the breeding territory in communal feeding areas.

Clutch size varies from 2–6, but is most often four. Clutches of six are rare. Incubation requires 18–38 days. Young are precocial and leave the nest shortly after hatching; they fledge at between 21 and 42 days of age. Adults, with one exception, do not feed the young. The Magellanic plover lays two eggs, but only one chick typically survives and is fed by the adults until after fledging. Reportedly some feeding is by regurgitation.

Some species prefer nesting on recently burned ground, a preference that provides some protection from future fires, but which also provides chicks with access to a flush of arthropods that take advantage of new plant growth following a fire.

Most are solitary nesters, but the sociable and white-tailed plovers commonly nest in semi-colonial groups. Sociable plover groups include up to two dozen pairs with nests about 150 ft (46 m) apart. Each pair defends its own small territory. White-tailed plover colonies may contain several hundred pairs, and nests may be only a few yards apart. The little-ringed plover (*C. dubius*) occasionally nests communally with inter-nest distances of as little as 26 ft (8 m). Killdeer often nest near other killdeer in areas with favorable habitat.

Many plovers are seasonally monogamous and some retain the same mates in subsequent breeding season. Snowy plovers in western North America are facultatively polyandrous and polygynous. The southern lapwing (*Vanellus chilensis*), while typically monogamous, will engage in cooperative breeding. It and the wrybill are the only members of the family in which two birds of the same sex have definitely been observed caring for a single clutch.

In most species parental responsibilities are shared, although the female may desert the male after laying a second clutch. The Eurasian dotterel female takes little interest in caring for her first clutch and may lay additional clutches for later mates. She rarely assists in caring for the young, but may rejoin the family group when the young are nearly grown. In the mountain plover the female often initiates a second clutch that she incubates, leaving the male to care for the first clutch. Mountain plovers produce a maximum of one brood per adult, although it may re-nest up to four times. Most plovers produce from one to three broods annually, but those nesting in warm climates have the potential to produce more. Parental care includes incubation, brooding, leading the chicks to feeding areas, and protecting them from predators by giving warning calls, performing distraction displays, and, less commonly, attacking potential predators. Distraction displays, including injury feigning and false brooding, are particularly well-developed in this family.

Some plovers, including white-fronted (*C. marginatus*) and Kittlitz's (*C. pecuarius*), typically nest in sand and cover the nest with sand when unattended. The white-fronted sand-plover brings water to the nest in its belly feathers. Other plovers such as the killdeer wet their belly feathers to help cool the eggs on extremely hot days. Adults in hot climates often spend much of their time shading eggs as opposed to incubating.



Blacksmith plover (*Hoplopterus armatus*) at its nest with eggs. (Photo by Leonard Lee Rue III. Bruce Coleman Inc. Reproduced by permission.)

The nesting season may be long in species residing in warm climates. The chestnut-banded sandplover's (*C. pallidus*) nesting season may last nearly all year. The killdeer in Puerto Rico breeds year-round.

Conservation status

Charadriidae includes one Critically Endangered species, two Endangered species, five that are Vulnerable, and an additional six that are Near Threatened. The only charadriid listed as Critically Endangered is the Javanese lapwing (*Vanel-lus macropterus*), which is probably extinct. It has not been seen since 1940. Reportedly always uncommon, it frequented steppe-like marshes and river deltas on the west side of the north coast and the east side of the south coast of Java.

The Endangered St. Helena plover (*C. sanctaehelenae*) is the only surviving endemic land bird on St. Helena. There are only about 325 individuals of this grassland species remaining. A decline in available habitat, a fluctuating invertebrate food supply, human disturbance, and predation of nests by cats and the common myna (*Acridotheres tristis*) contribute to its decline.

The Endangered shore plover is restricted to South East Island in the Chatham Islands. Only about 159 birds remain. Recovery efforts include a captive breeding program and translocation. One translocated pair raised two chicks on Motuora Island, but in general translocation has been unsuccessful due to failed dispersals to the mainland and predation by the owl morepork (*Ninox novaeseelandiae*). Loss of habitat, expansion of fur seal (*Arctocephalus forsteri*) colonies, storms, and predation by cats, brown rats (*Rattus norvegicus*), and brown skua (*Cartharacta lonnbergi*) contribute to endangerment. Current trends may require upgrading to Critically Endangered.

Family: Plovers and lapwings Vol. 9: Birds II



A piping plover (*Charadrius melodus*) catches a sand worm in Connecticut. (Photo by Paul J. Fusco. Photo Researchers, Inc. Reproduced by permission.)

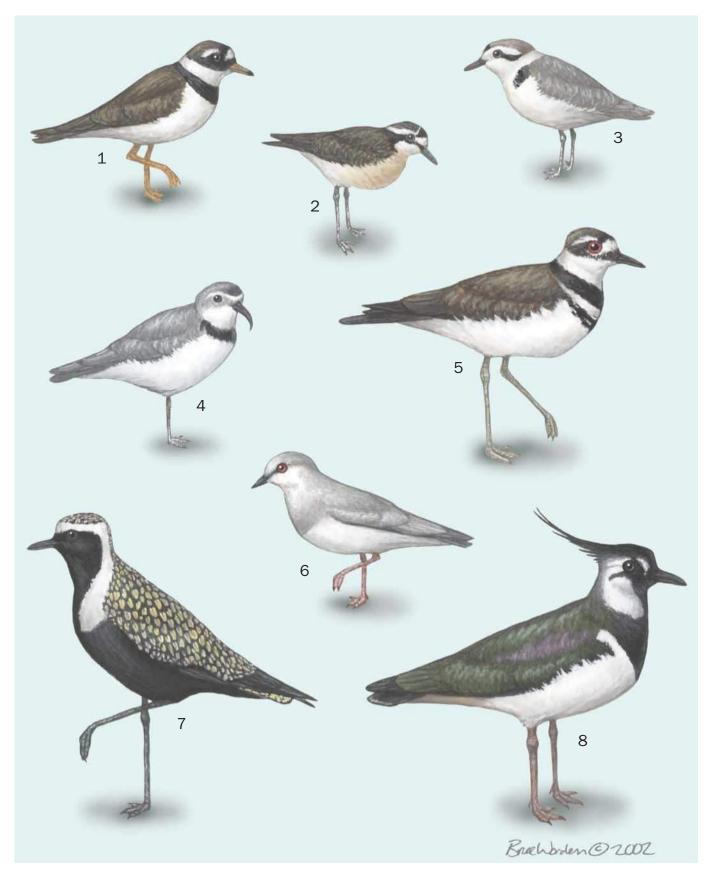
The New Zealand dotterel (*C. obscurus*), mountain plover (8,000–9,000 birds), piping plover (5,913), wrybill (3,000–5,000), and sociable lapwing (2,500–10,000) are listed as Vulnerable. The New Zealand dotterel has a limited distribution

in New Zealand. The northern population nests along the coastline, and the southern population nests on bare hilltops, bogs, and grasslands of Stewart Island. Extensive predator protection is potentially allowing populations to stabilize, although population trends are unclear. The Stewart Island population increased from a low of 62 in 1991–92 to 150 in 1999. The entire population is estimated at around 1,600 birds. The Mountain plover nests in short-grass prairie, dry scrub, and fallow fields and is often associated with prairie dogs (Cynomys sp.). Falling population numbers are primarily attributable to hunting and decline in habitat. Piping plover populations are estimated at 5,913 and are improving apparently due to conservation efforts. Drought, inappropriate water management, dredging, human development, efforts to stabilize beaches, and beach disturbance are listed as primary causes of population decline.

The Magellenic plover, Madagascar plover (*C. thoracicus*), Malaysian plover (*C. peronii*), Javan plover (*C. javanicus*), hooded plover (*C. rubricollis*), and Mitchell's plover (*Phegornis mitchelli*) are Near Threatened.

Significance to humans

Black-bellied plovers and golden-plovers were game birds commonly sold in markets in North America in the late 1800s and probably continue to be eaten in some cultures. Conservation of species, such as the snowy and piping plovers that nest on scantily vegetated beaches, is often in conflict with human use of beaches for leisure activities.



1. Ringed plover (Charadrius hiaticula); 2. Kittlitz's sand plover (Charadrius pecuarius); 3. Snowy plover (Charadrius alexandrinus); 4. Wrybill (Anarhynchus frontalis); 5. Killdeer (Charadrius vociferus); 6. Magellanic plover (Pluvianellus socialis); 7. American golden plover (Pluvialis dominica); 8. Northern lapwing (Vanellus vanellus). (Illustration by Bruce Worden)

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Species accounts

American golden-plover

Pluvialis dominica

SUBFAMILY

Charadriinae

TAXONOMY

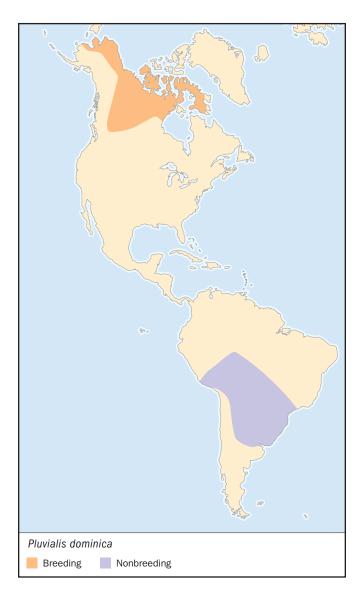
Pluvialis dominica P. L. S. Müller, 1776. Monotypic.

OTHER COMMON NAMES

English: American lesser golden-plover; French: Pluvier doré d' Amérique, Pluvier bronzé; German: Sibirischer, Goldenregenpfeifer; Spanish: Chorlito Dorado Americano.

PHYSICAL CHARACTERISTICS

9.5–11 in (24–28 cm); weight quite variable, ranging from about 3.5 to 7 oz (99–198 g), with post-migration weights



much lower. During breeding season, upperparts are black; yellowish edgings on the feathers of the upperparts give the birds a golden-spangled appearance. The forehead and sides of the neck are white. Face and underparts are black. In winter it is speckled brown above with pale underparts.

DISTRIBUTION

Across Canada and Alaska in tundra habitats; possibly on Chukoctskiy Peninsula, Wrangel Island, and Herald Island in Russia. Winter in grasslands of South America south to northern Argentina and Uruguay. May winter in Central America and along the Atlantic and Gulf coasts of North America, with most records from Florida. It is difficult to distinguish records of migratory stragglers from winter residents. Rarely individuals remain on the wintering grounds throughout the year.

Often found outside its normal range with reported occurrences along western African coast, the Netherlands, Ireland, Okinawa, New Guinea, and New Zealand.

HARITAT

Most common in the Arctic and sub-Arctic tundra and favors rocky slopes with scattered low vegetation for breeding. A variegated surface of rocks, gravel, lichen, and vegetation is preferred. Moves young to wetter areas with more shrubs and grasses for cover. During migration, found in a variety of open habitats, including inland and coastal areas. Winter primarily on grasslands of South America and less commonly on the coastal wetlands. Agricultural lands are not used.

BEHAVIOR

Apparently migrate in small flocks, although large spring buildups are known from northwest Indiana and northeast Illinois with reports of more than 25,000 birds. Rapid fliers capable of long-distance flights. Flight speed may exceed 112 mph (180 kph). Some individuals establish small winter territories. Nonterritorial individuals maintain individual spacing through lowlevel aggression. Wintering birds typically form communal roosts. Occasionally gather in large flocks at freshwater wetlands on wintering grounds to drink and bathe. Solitary nesters, but often forage in communal groups away from the breeding territory.

FEEDING ECOLOGY AND DIET

Feeds on a variety of terrestrial and aquatic invertebrates. Also some berries, seeds, and vegetation. Runs, stops, and pecks as is typical of foraging in plovers. Also pecks small invertebrates off of leaf surfaces.

REPRODUCTIVE BIOLOGY

Most breed in the first year. Males, but not females, exhibit strong fidelity to breeding territories, which are large and defended by aerial displays and vocalizations. Formation of new pair bond is more common than retention of a mate from the previous season. Nests are shallow scrapes sparsely lined with lichens and/or dry grasses, pebbles, and leaves. Four eggs are laid. Both sexes incubate eggs and care for young. Males usually incubate during the day and females at night. Distraction displays, including false brooding, are given. Adults may attack some avian and mammalian predators, including foxes. May renest, but raise only a single brood. Incubation is about 26 days. Hatching is fairly synchronous (usually one day) and earlier hatched young forage near nest while attentive adult incubates.

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CONSERVATION STATUS

In 2002, populations appear stable, but populations declined drastically due to extensive hunting during the nineteenth and early twentieth centuries. For example, 48,000 were shot in a single day in Louisiana in 1821, and birds could be purchased for 25 cents a dozen in Maine in the 1850s. Populations rebounded with enactment of protective laws. Currently serious threats are probably loss of habitat in wintering areas due to agricultural and human encroachment. Pesticide exposure may also be a problem.

SIGNIFICANCE TO HUMANS

Hunted in Guyana, Suriname, French Guiana, and Barbados. •

Ringed plover

Charadrius hiaticula

SUBFAMILY

Charadriinae

TAXONOMY

Charadrius hiaticula Linnaeus, 1758. Two subspecies.

OTHER COMMON NAMES

English: Common ringed plover; French: Grand Gravelot; German: Sandregenpfeifer; Spanish: Chorlito de Collar, Chorlitejo Grande.

PHYSICAL CHARACTERISTICS

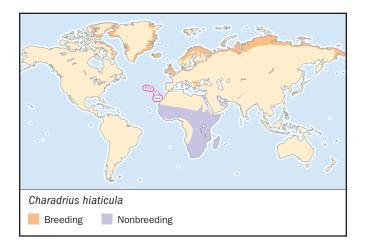
7–8 in (18–20 cm). Males in breeding season: 2–2.54 oz (57–72 g); females 1.98–2.65 oz (56–75 g). Upperparts, including crown, are sandy brown. Neck has a black ring with a white ring above it. White underparts, forehead, and superciliary line. Dark frontal bar and line running under the eye from the bill. In breeding male, bill is orange with black tip. Legs orange.

DISTRIBUTION

Breeds from northeastern Canada east to northeastern Siberia and winters in Africa, southern Europe, the Persian Gulf, and India.

HABITAT

Coastal during the breeding season, selecting nesting sites on beaches, near coastal tundra ponds, or on muddy plains. Rarely nests along rivers and occasionally found away from water. Fa-



vors nest sites near high tide mark on sandy or shingled beaches. On migration and during winter found along seashores and coastal marshes where vegetation is low or occasionally in dry open areas. May be found on coral reefs exposed at low tide.

BEHAVIOR

Outside of the breeding season most often seen in small flocks of up to 50 birds, but occasionally solitary and may also be seen in large flocks of up to 1,500 birds. Aggressive to neighbors on wintering grounds.

FEEDING ECOLOGY AND DIET

As is typical of plovers, it forages by running, stopping, lunging, and then running on. Foot patting or trembling is common. Forages during the day and at night. Eats a variety of invertebrates.

REPRODUCTIVE BIOLOGY

Strongly territorial during breeding season. Nesting densities are typically low with fewer than one pair per hectare, but contiguous nesting territories of about 98 ft (30 m) in diameter occur. Birds may mate with the same partner in consecutive breeding seasons. Some birds arrive on breeding territory already paired. Both sexes incubate eggs and care for chicks. A clutch of four eggs is laid in a hollow in the sand. The nest is often lined with small pebbles. Incubation requires about 25 days, and birds fledge at about 23 days. Both sexes engage in injury feigning displays. Commonly double brooded, especially in southern populations. Nest sometimes reused, but new sites as much as 1,640 ft (500 m) from the first may be chosen.

CONSERVATION STATUS

Populations are healthy and some populations in England and Scotland are expanding their ranges inland.

SIGNIFICANCE TO HUMANS

None known. ◆

Killdeer

Charadrius vociferus

SUBFAMILY

Charadriinae

TAXONOMY

Charadrius vociferus Linnaeus, 1758. Three subspecies.

OTHER COMMON NAMES

French: Pluvir kildir; German: Keilschwanz-Regenpfeifer; Spanish: Playero Sanero, Chorlito Tildio.

PHYSICAL CHARACTERISTICS

8–11 in (20–28 cm); 3.3 oz (95 g). Medium-sized and monomorphic, with two black bands across the breast and a dark line extending between the eyes. Underparts are white and upperparts are gray-brown with rufous edging on some feathers. Rump and uppertail-coverts are bright rufous. Wings and tail are long.

DISTRIBUTION

Ranges across all of North America with the exception of most of Alaska and northern Canada. It extends southward throughout Central America, Columbia, and Venezuela, and along the west coast of South America to Peru and Chile. Also found on Family: Plovers and lapwings Vol. 9: Birds II



Bermuda, throughout the Bahamas, Greater and Lesser Antilles, Cayman Islands, and Virgin Islands. There are accidental records from many places, including Hawaii, Russia, Greenland, Britain, Spain, and France. Breeding occurs across the North American range and south into Central America as well as the West Indies. Also reported breeding in Peru, northwest Chile, and southwest Ecuador. Resident over most of southern and coastal United States as far north as southern Alaska, West Indies, and areas of Central and South America.

HABITAT

Favors open areas, including sandbars, mudflats, closely mowed or grazed pastures and fields, graveled roads and parking areas, and even paved parking lots. It uses similar habitats during migration, but most likely to be seen in wet areas.

BEHAVIOR

While they are graceful, rapid flyers, most commonly observed on the ground. Movement involves running a short distance, stopping, bobbing the head, and running again. Their loud calls of "killdee killdee" give the species its common name. They often serve as a sentinel species for mixed shorebird flocks and are frequently found in small to medium flocks in the winter, although individuals appear to protect a small personal space. Both migratory and resident populations are present. Resident pairs may maintain a breeding territory all winter. Migrant flocks that stopover on these territories are largely ignored, but territories are defended from other residents. Killdeer spend considerable time displaying in small groups, especially during fall and late winter to early spring.

FEEDING ECOLOGY AND DIET

Feeds along water edges, on shorelines, closely mowed pastures, and mudflats. Often forages by running short distances, stopping, peering, and pecking. Birds commonly pat the ground with one foot as they are foraging. Feeds on a variety of adult and larval invertebrates. Small vertebrates, including frogs and minnows, are sometimes eaten, as well as seeds and other plant materials.

REPRODUCTIVE BIOLOGY

Seasonally monogamous in the United States. Non-migratory individuals commonly mate for life. Migrants have been observed with the same mate on breeding territories in consecutive years. Parental responsibilities are shared by both sexes. Lays four eggs in a scrape on the ground, preferring closely mowed pasture and graveled areas. Flat, gravel-covered rooftops are popular nesting sites. Both sexes participate in scrape formation. The bird crouches in the selected area and digs with the feet, pushing dirt to the rear and using the breast to form the scrape. Pair members take turns scraping. The displaced bird moves away from the scrape, tossing loose materials over the shoulder as it moves away. These loose materials eventually form a simple lining for the scrape. Incubation requires about 25 days, and hatching is usually fairly synchronous. Nests are rarely left unattended, especially when temperatures are high. Belly soaking (wetting of the breast feathers at a nearby pond or stream) is commonly used to cool eggs on extremely hot days. Precocial young are led to a feeding area soon after hatching. Fledging requires approximately 25-30 days, and fledged chicks may remain with the parents after fledging. Performs well-developed distraction displays and engages in false brooding when eggs or chicks are threatened.

CONSERVATION STATUS

Populations appear stable over much of their range, although they may be declining in eastern North America. Human activities have increased available habitat for killdeer. Newly created habitats include gravel roadsides, parking lots, rooftops, golf courses, airports, and pastures. Unfortunately, many of these habitats act as ecological sinks when chicks are unable to get off rooftops, cars destroy eggs, or birds are killed through the ingestion of pesticides used to control their prey.

SIGNIFICANCE TO HUMANS

None known. ◆

Kittlitz's plover

Charadrius pecuarius

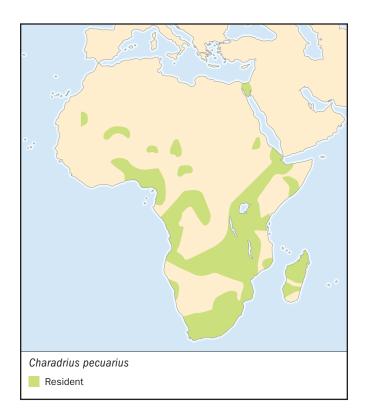
SUBFAMILY

Charadriinae

TAXONOMY

Charadrius pecuarius Temminck, 1823; Cape of Good Hope. Monotypic.

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OTHER COMMON NAMES

English: Kittlitz's sandplover; French: Pluvier patre, Pluvier de Kittlitz; German: Hirtenregenpfeifer; Spanish: Chorlitejo Pecuario.

PHYSICAL CHARACTERISTICS

5.25–6.5 in (13–16 cm); 0.67–1.7 oz (19–48 g). Characterized by a white forehead delineated by a black frontal bar and black line from bill to eye, which continues around the back and side of the neck. Crown brown with sandy edges on the feathers. Except for frontal bar, crown does not meet black markings, leaving a white ring around sides and back of crown. Upper dark brown with sandy feather edgings. Flight feathers blackish. Bill black, legs black to greenish gray. Sexes similar but black frontal bar less extensive and lighter in females. In juveniles the head color is buff and brown instead of black and white.

DISTRIBUTION

Africa and Madagascar.

HABITAT

Flat, exposed areas, including sand banks, mud banks, and dry veld. Frequently found far from water, rarely on sandy or rocky seashores.

BEHAVIOR

Usually in pairs, but in winter found in small flocks (usually around 20 birds), but one flock of 270 reported. Often flocks with wintering Calidris species. Concentration of birds during non-breeding season are partially a result of receding water levels. They are gregarious even in the breeding season. May roost in mixed flocks or separately. Usually resident, but some populations undergo poorly understood seasonal movements.

FEEDING ECOLOGY AND DIET

Often feeds in groups of two to five birds. As is typical of plovers, it runs, stops, pecks, then runs on. It often pats its foot on foraging surface. Commonly feeds on moonlit nights.

REPRODUCTIVE BIOLOGY

Somewhat gregarious in breeding season, sometimes nesting in semi-colonial groups (nests as close as 26 ft [8 m] but usually at least 59 ft [18 m] apart). Nest sites include sandy areas, sandy patches in open grassland, dry mud, and even droppings of cattle or horses. During copulation the male reportedly grabs the female's neck with his bill and falls onto his back, pulling the female with him so she ends up on top with her legs in the air. Two eggs are laid, and both sexes incubate and care for the young. When leaving the nest unattended in the middle of the day, or when disturbed, incubating bird quickly kicks sand over the eggs or newly hatched chicks. May stand over eggs and/or use belly soaking to cool eggs. Reportedly moves eggs up to 12 in (30 cm) in response to nest flooding. Incubation requires about 25 days, and chicks fledge at about 30 days, although brooding 42-day-old captive chicks have been observed. Both adults give injury-feigning distraction displays and false brooding when nest or young are threatened. One pair initiated a second nest while caring for previous brood.

CONSERVATION STATUS

Common over much of the open habitat of Africa. Flooding is major cause of egg and chick loss, but predation and motor vehicles are also concerns.

SIGNIFICANCE TO HUMANS

None known.

Snowy plover

Charadrius alexandrinus

SUBFAMILY

Charadriinae

TAXONOMY

Charadrius alexandrinus Linnaeus, 1758. At least six subspecies are recognized.

OTHER COMMON NAMES

English: Kentish plover, sandplover; French: Gravelot à Collier interrompu; German: Seeregenpfeifer; Spanish: Chorlitejo Patinegro.

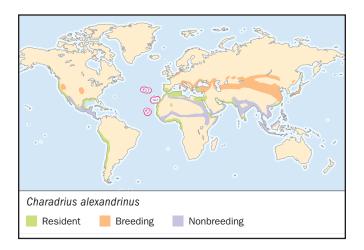
PHYSICAL CHARACTERISTICS

6–6.75 in (15–17 cm); 1–2 oz (28–57 g). Upperparts pale brown, especially pale in North American population. Breast band restricted to the lateral edges of the breast; white ring around the neck. Crown may be rufous. In breeding males a distinct, dark frontal bar marks the end of a white forehead and a dark line extends from bill to ear. Bill is black, and legs and feet are dark gray to black.

DISTRIBUTION

Breeds along the western U.S. coast from Washington to lower California and intermittently along the Gulf Coast from Marco Island, Florida, to the north coast of the Yucatan Peninsula. Breeds inland in south central Oregon, Salton Sea and eastern California, western and central Nebraska, northwestern Utah, and southern Arizona. Also breeds in the West Indies and on islands off the coast of Venezuela. Winters in

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the Gulf drainage south to Yucatan and northern South America and in the Pacific drainage from central California to western Mexico. A resident population (*C. a. occidentalis*) is found on the coast of Peru and Chile. *C. a. alexandrinus* breeds in Eurasia from southern Sweden to the northern Sahara to western India and the steppes of central Asia through western China. Winters from the Mediterranean Basin south to tropical Africa, Angola, and Sri Lanka. *C. a. seebobmi* is resident in Sri Lanka. *C. a. dealbatus* breeds in eastern China and Japan and winters from Japan to Taiwan and the Philippines and from southeastern China to Indochina and the Greater Sundas.

HABITAT

Prefers open coastal areas, including sand and shingle beaches, estuaries, lagoons, and mudflats as well as inland along saline lakes. May also be found along rivers and on sparsely vegetated steppes. In North America it favors beaches and both coastal and inland salt flats. Inland it is found along braided river channels. Nests primarily on sandy coastal beaches, dunes, spoil islands, and salt flats or inland near brackish or saline wetlands. Several hundred birds nest and winter at agricultural wastewater ponds in the San Joaquin Valley and at the Salton Sea formed in southern California as a result of accidental flooding in the early 1900s. Mostly coastal outside the breeding season. Rare in freshwater habitats.

BEHAVIOR

Species includes both resident and migrant populations. Most birds in flocks of up to 300 during winter, although some defend winter territories. Small groups of birds may take off in coordinated flights when disturbed. Both chicks and adults can swim, and adults may lead chicks across ponds and rivers.

While territories are important sites for nesting and feeding, some birds frequently forage communally at undefended feeding areas. Feeding areas as much as 3.7 mi (6 km) from the nest have been documented.

FEEDING ECOLOGY AND DIET

Runs, stops, looks, and pecks as is common in plovers, but also probes at the bases of plants and runs into dense masses of flies with bill open and snapping. May also charge after solitary insects. Occasionally pats substrate with foot. Mostly gathers food from sand surface both above and below mean high tide mark. Inland, often forages in 0.39–0.79 in (1–2 cm) deep water or on wet surfaces.

REPRODUCTIVE BIOLOGY

Frequently retain their mate for more than one year, and one pair remained mated for at least six years, apparently as a result of territorial fidelity. Rarely male may mate with two females and alternate incubation at the two resulting nests. Birds often show nest site fidelity. Nest is often located near an item such as piece of driftwood or small clump of vegetation that distinguishes an otherwise uniform landscape. Nests are formed by scraping and lined by both sexes randomly picking up bits of debris and tossing it over their shoulders and into the nest. Lining eventually includes such items as pebbles, fish bones, and arthropod skeletons. During copulation male grasps the female's neck and falls backward, pulling her with him. Clutch size is usually three, but varies from 2–6.

Both sexes incubate, but at least in some localities the female incubates more during the day and the male at night. Incubation requires from 23–32 days. Young are precocial and leave nest soon after hatching.

In western North America females desert broods soon after hatching, mate with a different male, and initiate another nest. This allows for the production of multiple broods. Males also take a new mate and re-nest, in some cases as early as 10 days before the current brood fledges. Birds may move several hundred kilometers to re-nest. Females may mate with original mate to produce a third brood. In some localities only one brood is produced. Parental care includes leading chicks to food, watching and warning of danger, and giving injury-feigning distractions.

Breeding territories may be small. In some localities average distance between nests was 120 ft (36 m). Breeding typically occurs during the first year.

CONSERVATION STATUS

North American Pacific and Gulf Coast populations are shrinking, with current populations estimated at 21,000 individuals in the United States. The Pacific Coast population is listed as Threatened by the U.S. Fish and Wildlife Service. Habitat loss and destruction is an important factor contributing to population decline. Chief problems are increased recreational use of beaches, regular raking to keep beaches attractive to humans, and use of beach grass (*Ammophila arenaria*) to stabilize beaches. Inland habitat has been lost as a result of human-mediated changes such as dam construction and growth of vegetation. Less important factors include pesticides, entanglement in monofilament line, being run over and stepped on, and shooting and trapping.

SIGNIFICANCE TO HUMANS

None known. ◆

Wrvbill

Anarhynchus frontalis

SUBFAMILY

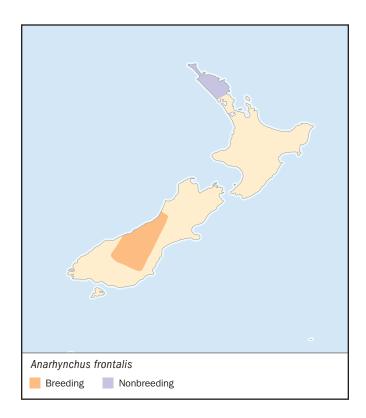
Charadriinae

TAXONOMY

Anarhynchus frontalis Quoy and Gaimard, 1830, New Zealand. Monotypic.

OTHER COMMON NAMES

English: Wry-billed plover, crook-bill plover; French: Pluvieranarhyngue; German: Schiefschnabelregenpfeifer; Spanish: Chorlitejo Piquituerto. Vol. 9: Birds II Family: Plovers and lapwings



PHYSICAL CHARACTERISTICS

7.75–8 in (19.7–20 cm); weight: males 2.1 oz (59.5 g), females 2.0 oz (56.7 g). Unique in having a bill that bends to the right at about a 12° angle. White forehead extends backwards. Dark gray band extends from bill, continues under eye, gradually lightening toward crown. Crown is nearly black where it meets white forehead. Rest of upperparts are uniform bluish gray, including wing coverts that are edged in white. Flight feathers are brown with outermost flight feathers gray with white edges. A broad, black band covers upper breast. Bill is black and legs are dark gray. Female similar, but breast band paler and narrower and crown is light where it meets white forehead. Breast band absent in juveniles and winter plumage.

DISTRIBUTION

Canterbury and Otago, South Island, New Zealand. Winters mainly on the Firth of Thames at Manukau Harbor, and on the Kaipara River, North Island, New Zealand.

HABITAT

Nest on large expanses of stones near rivers. During nonbreeding season most often found on silty mudflats near high tide mark on sheltered coasts and estuaries.

BEHAVIOR

Large pre-migratory flocks at the Firth of Thames perform elaborate mass aerial displays.

FEEDING ECOLOGY AND DIET

Probes in mud, but also sweeps the bill sideways, capturing tiny crustaceans from water surface. Also pecks and probes between stones and sweeps tiny invertebrates from under stones in riffle areas. Feeds on spiders, insects, crustaceans, small mollusks, small fish, and eggs. Larval mayflies and caddisflies are commonly eaten.

REPRODUCTIVE BIOLOGY

Have strong fidelity to breeding territories and even nest sites. Birds often pair with same mate in consecutive years, perhaps because of nest site tenacity. Breeding does not occur until second or third year. Typically nest on higher banks and parts of islands in wide areas of shingle with fairly large stones. Male forms scrape, lined by pebbles flicked into the scrape or regurgitated from the crop. Clutch size is two. Parental duties are shared. One male shared incubation of a four-egg clutch with two females. Incubation requires about 31 days, and young fledge at about 29 days. Typically nest again after first clutch fledges.

CONSERVATION STATUS

Classified as Vulnerable; population of 3,000–5,000 birds appears to be declining. Breeding habitat is deteriorating due to increasing recreational use of rivers and to invasion of weeds, apparently as a result of hydroelectric plants upriver. Predation by stoat (*Mustela erminea*), cats, and kelp gulls (*Larus dominicanus*) is probably significant.

SIGNIFICANCE TO HUMANS

Shot for sport until protected in 1940. ◆

Magellanic plover

Pluvianellus socialis

SUBFAMILY

Pluvianellinae

TAXONOMY

Pluvianellus socialis G. R. Gray, 1846. Sometimes placed in its own family, Pluvianellidae. Monotypic.

OTHER COMMON NAMES

French: Pluvier Magellan; German: Magelanregenpfeifer; Spanish: Chorlito de Magallanes.

PHYSICAL CHARACTERISTICS

7.75 in (20 cm); weight: males 2.8–3.6 oz (79–102 g), females 2.5–3.1 oz (71–88 g). Upperparts, head, and neck are ashy gray grading to a brownish gray on the upper chest and white on the cheeks, throat, and forehead. Dark area between eye and bill. Underparts are white. In flight a broad, white wing stripe is evident. Bill is black with a small pink spot near base. Turnstone-like in appearance. Iris is black. Legs are short and both legs and feet are coral pink. Females are slightly darker and heavier. In juveniles dorsal surface has golden tint, eye is white with lavender tinge, and legs and feet are orangeish. First winter birds have yellow mark at base of bill. Hind toe is well-developed unlike other plovers.

DISTRIBUTION

Breeds in extreme southern Chile and Argentina, including Tierra del Fuego. Winters northward to Valdez peninsula, south-central Argentina, and occasionally as far north as Buenos Aires province.

HABITAT

Breeds along shores of shallow fresh water or brackish lakes and lagoons—most of which are glacial—in the steppe-like regions of Tierra del Fuego and southern Patagonia. Winters mostly along the coast in sheltered bays, lagoons, and river mouths.



BEHAVIOR

Pair members act as a unit in territorial defense. Most spend the winter in sheltered bays and river mouths.

FEEDING ECOLOGY AND DIET

Feeds by pecking at the water surface and scratching the ground with strong claws. They sometimes dig deeply into the sand, which is uncharacteristic of shorebirds. They also flip shells and bits of debris in the manner of a turnstone. Larvae of chironomid flies are the primary winter food, but a variety of tiny arthropods are eaten during the breeding season.

REPRODUCTIVE BIOLOGY

Some populations nest up to 3,900 ft (1,200 m). Separate breeding and feeding territories are maintained. Breeding territories tend to be linear (984–1,640 ft [300–500 m]). Nest scrape lined with small pebbles and usually only a few feet from water. Clutch size is usually two. Four-egg clutches occur, probably the result of two females laying in the same nest. Both sexes incubate eggs and care for young. Injury feigning distraction displays are unknown. Hatching is asynchronous and second-hatched nestling often starves. Relative to other plovers, young are weak and remain in nest vicinity for several weeks. Unlike other plovers, parents feed young—often by regurgitation. Fledging occurs around 28–30 days, but adults may feed young until at least 40 days old.

CONSERVATION STATUS

Near Threatened. Factors contributing to small population size include hostile environment and the effect of grazing animals and introduced herbivores on natural grasslands.

SIGNIFICANCE TO HUMANS

None known. ◆

Northern lapwing

Vanellus vanellus

SUBFAMILY

Vanellinae

TAXONOMY

Vanellus vanellus Linnaeus, 1758, Sweden. Monotypic.

OTHER COMMON NAMES

English: Eurasian plover, green plover, pewit; French: Vanneau huppé; German: Kiebitz; Spanish: Avefría Europea.

PHYSICAL CHARACTERISTICS

11.5–13 in (29–33 cm). Spring weights: males 6–9 oz (170–255 g), females 7.7–9.9 oz (218–280 g). Adult summer and fall weights average 8.2 oz (232 g). Elongated black crest, thick blackish neck band, and glossy green back are diagnostic. Face is black with a dark line extending under the eye. Tail is white and has a broad sub-terminal black band. Tail coverts are cinnamon rufous. Underparts are white, grading to a light cinnamon on the undertail coverts.

DISTRIBUTION

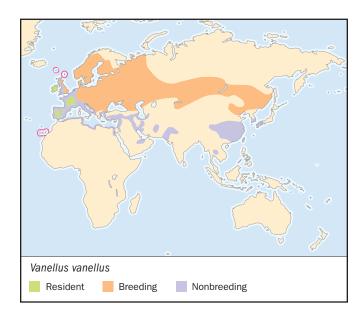
Breeds in Europe and Asia from the British Isles (occasionally to Iceland) to south Ussuriland and south to northwest Morocco, eastward to north Greece, Iran, and Mongolia. Winter range extends southward to the Mediterranean Basin, northwestern India, and eastern China. Breeding has also been reported from Japan.

HABITAT

Habitat requirements are broad, and the species can be found nesting from boreal to steppe and even desert habitats. Like other charadriids prefers broad open areas, including grasslands, fields, moors, bogs, and heathlands.

BEHAVIOR

Migrating flocks are usually small, but huge flocks are also recorded. Winter flocks often contain 100 or more birds, and flocks of over 5,000 have been reported. During winter some individuals feeding in flocks vigorously defend small feeding



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territories. They also spend time on communal areas where bathing, resting, and preening occur.

FEEDING ECOLOGY AND DIET

Foraging behavior is typical charadriid behavior of running, stopping, and pecking. They feed extensively on earthworms, but diet also includes a variety of invertebrates. Reliance on earthworms decreases during unusually dry weather. During unusually cold weather they may eat cattle dung. They are often the victims of kleptoparasitism by gulls—especially blackheaded gulls (*Larus ridibundus*).

REPRODUCTIVE BIOLOGY

Mature in the first year, lapwings often do not nest until their second or even third year. Solitary nesting is common, but breeding densities are sometimes high (nine pairs in less than a hectare). Fidelity to territory is high, with 70% of lapwings returning to birthplaces in the spring. Male performs elaborate territorial and courtship displays over breeding territory. Flights include a non-vocal humming sound and a three-motif

song. At times, the primaries emit loud buzzing noises. Seasonal monogamy is the rule but a weak pair bond and weak territories increase the probability of polygynous mating. Male may fly directly onto the female's back for copulation. A single brood is produced. Four is usual clutch size, occasionally three. Incubation requires about 24–34 days. Parental duties are shared, but one parent—usually the female—deserts before the brood fledges. Fledging occurs in 30–42 days. There are reports of males with two to three females, and simultaneous bigamous matings by males seem to occur often.

CONSERVATION STATUS

Not threatened. European breeding area has expanded especially northward.

SIGNIFICANCE TO HUMANS

Eggs were commonly collected for food. There are reports from Holland of a single collector taking over 2,000 eggs in a single season. It remained legal to collect the eggs in Britain until at least the 1970s. ◆

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Bette 7. S. Jackson, PhD

Sandpipers

(Scolopacidae)

Class Aves

Order Charadriiformes
Suborder Charadrii
Family Scolopacidae

Thumbnail description

Small to medium-sized waders with short to long legs; bill short to long, may be straight, decurved, or slightly recurved.

Size

4.7-26 in (12-66 cm);.03-3.0 lb (14.5-1,360 g)

Number of genera, species

23 genera; 86 species

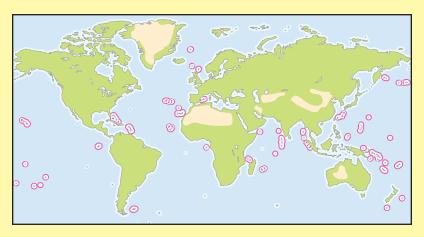
Habitat

Coastal and inland wetlands; breed in tundra, marshland, grassland, steppe, scrub, and forest

Conservation status

Extinct: 2 species; Critical: 2 species; Endangered: 2 species; Vulnerable: 6 species;

Near Threatened: 10 species



Distribution

Worldwide, except Antarctic

Evolution and systematics

The fossil record suggests that the family Scolopacidae arose about 40 million years ago in the early Tertiary, during explosive evolution after a wave of extinctions at the end of the Cretaceous. Some fossil material, possibly representing the genera Limosa (godwits) and Tringa (shanks), is available from the late Eocene, the period when this radiation probably occurred. Although there is great diversity within the Scolopacidae, morphological and biochemical evidence suggest all groups currently included in the family have a common ancestor. Recent osteological studies suggest this ancestor may also have given rise to the jacanas (Jacanidae) and the painted snipes (Rostratulidae), while DNA-DNA hybridization studies suggest these two groups, with the seedsnipes (Thinocoridae) are the most closely related outgroups of a monophyletic scolopacid family. The relationship of the Scolopacidae with plovers (Charadriidae) is disputed, and most recent authors suggest that the two are not sister groups as formerly assumed.

Although phalaropes (*Phalaropus* and *Steganopus*) have often been separated into their own family, molecular genetic techniques confirm they belong within Scolopacidae, as do other morphologically and behaviorally diverse taxa such as woodcocks (*Scolopax*) and turnstones (*Arenaria*). All three groups are given subfamily status (Phalaropodinae, Scolopacinae, and Arenariinae respectively) within Scolopacidae, which also has three other subfamilies: the Gallinagininae (snipes), Tringinae (shanks and allies), and Calidrinae (sandpipers). The Tringinae are usually subdivided into three tribes, the Numeniini (godwits and curlews), Tringini (shanks), and

Prosoboniini (Polynesian sandpipers). Four subfamilies, the Scolopacinae, Arenariinae, Calidrinae, and Phalaropodinae, are probably monophyletic.

Within the family, 86 species (64 monotypic) are currently recognized in 23 genera (12 monotypic). Most species breed in Arctic or boreal environments, but when the family first appeared the climate was warmer. About 1.5 million years ago, at the end of the Pliocene, the earth's climate became similar to that of today and since then, during the Pleistocene, alternating ice ages and interglacial periods have had great impacts on the geographical distribution of scolopacid waders and extent of their habitats. Such climatic changes may have played a major role in evolution of species and subspecies. Recent DNA studies suggest that extant subspecies of the dunlin (Calidris alpina) originate from climatic events that caused repeated fragmentation of populations towards the late Pleistocene, from about 200,000 years ago. On the other hand, the five subspecies of the red knot (Calidris canutus) appear to have arisen only about 10,000 years ago and may all be derived from a small population that survived during retreat of northern ice-caps.

Physical characteristics

Scolopacid waders vary in length from about 5–26 in (12–66 cm) and in many species the bill makes up a large proportion of total length. Great variation in bill morphology reflects great diversity of food resources exploited and a wide range of habitats used. The bill is often long and decurved, this feature being especially prominent in the curlews

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A ruddy turnstone (*Arenaria interpres*) eats a mussel at Barnegat Light State Park, New Jersey. (Photo by Paul J. Fusco. Photo Researchers, Inc. Reproduced by permission.)

(Numenius), while godwits and the Terek sandpiper (Xenus cinereus) have an upcurved bill. Turnstones have a short, relatively strong, wedge-shaped bill, while the spoon-billed sandpiper (Eurynorbynchus pygmaeus) has a spatulate bill tip. In most species the bill tip contains many tactile receptors for locating buried prey, while the tip of the upper mandible is flexible, allowing it to be opened and closed while probing, to grasp prey. Compared with plovers, most species have relatively narrow skull and small eyes, correlated with use of more tactile foraging methods. In woodcock and snipe, the eyes are placed high on the side of the head, to give 360° vision that aids predator detection.

Body shape varies from slender to stocky; the tail is short and the neck and legs are often fairly long. Feet usually have three long front toes and a short hind toe, and in some species are partially webbed. Most species can run rapidly and, although they can swim, many species habitually wade in shallow water. In most species, wings are long and pointed, well-adapted to long-distance migration.

Sexes are usually indistinguishable in plumage features. Females are often slightly larger and longer-billed, especially in the Tringinae, but males are larger in some Calidrinae. Nonbreeding plumages are typically dull and cryptic, upperparts being brown, gray, or blackish with pale streaks or spots, and the underparts pale with variable dark markings. Breeding plumage is often much brighter, with extensive rufous or black areas. Breeding-plumage male godwits are more brightly colored than females, but the ruff (Philomachus pugnax) takes sexual dimorphism to the extreme in the family: the male is almost 25% larger than the female and develops a ruff and head tufts of erectile feathers during the breeding season. In contrast, female phalaropes, which court males and defend territories, are more brightly colored than males. Many species have white on the tail, rump, or lower back, and often a white bar on the upperwings. The bill, legs, and feet are sometimes brightly colored and in some species may change color with age or season, becoming brightest prior to breeding.

Three eco-morphological groups are distinguishable: the snipes, sandpipers, and phalaropes. The snipes and woodcocks have very long bill and very cryptic plumage. Phalaropes are small, plumpish but elegant birds with straight, narrow bill and short legs. The remaining genera are lumped into the sandpiper group: wading birds with short to long legs and short to very long, narrow bill.

Downy hatchlings of scolopacid waders are cryptically colored and patterned, and have well-developed legs. Most have a small bill that gives little indication of length and shape of the adult bill.

Distribution

The family occurs virtually worldwide, with the exception of the Antarctic. Most species inhabit the Northern Hemisphere during the breeding season, occurring in boreal, subarctic, and Arctic regions, and only a few breed in temperate or tropical zones. Northern-breeding species are highly migratory and many winter widely in the tropics and the Southern Hemisphere, from South America and Africa through southern Asia to Australasia.

Some scolopacid waders breed farther north than members of any other bird family. The sanderling (*Calidris alba*) nests north to Franz Joseph Land, the Zemlya Islands, and the northernmost tip of Greenland, areas not reached by the northernmost-breeding *Pluvialis* and *Charadrius* plover species.

All polytypic genera are represented in both Eurasia and North America, generally having different species in each region, but a few species have a circumpolar breeding distribution. *Numenius* has four North American and three Eurasian breeding species, and one circumpolar species, the whimbrel (*Numenius phaeopus*). *Calidris* has seven representatives in Eurasia, four in North America, and seven that breed in both regions. The snipe genus *Gallinago* has one northern-breeding species, the common snipe (*Gallinago gallinago*), that breeds across virtually the entire Holarctic region.

Migrations are usually approximately north-south, so that Nearctic breeding species and subspecies typically winter in the Americas and Palearctic breeding taxa in Europe, Africa, Asia, and Australasia. Although many migrant species have very extensive wintering areas, some have very restricted breeding ranges. The western sandpiper (*Calidris mauri*) that winters coastally in the United States and south through Central America to Peru breeds only around the Bering Strait, while the sharp-tailed sandpiper (*Calidris acuminata*) that winters throughout Australasia and Melanesia east to Tonga breeds only in a restricted area of north-central and northeast Siberia.

Only 11 species breed in the tropics. All are primarily resident, and most have restricted ranges. They include three woodcock species, the rufous woodcock (*Scolopax saturata*) of Sumatra, Java, and New Guinea, the Sulawesi woodcock (*Scolopax celebensis*), and the Moluccan woodcock (*Scolopax rochussenii*). Seven other species are snipes: the widely distributed African snipe (*Gallinago nigripennis*), the Madagascar snipe

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Western sandpipers (*Calidris mauri*) at Grays Harbor, Washington during spring migration. (Photo by F. Stuart Westmorland. Photo Researchers, Inc. Reproduced by permission.)

(Gallinago macrodactyla), and five South American species, including the noble snipe (Gallinago nobilis) that is restricted to the northern Andes from Venezuela to Ecuador, and the imperial snipe (Gallinago imperialis) that has a patchy distribution in Peru. The remaining species, the Tuamotu sandpiper (Prosobonia cancellata), occurs only in French Polynesia.

Habitat

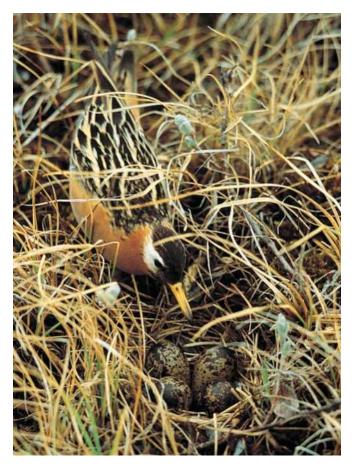
Although scolopacid waders occupy a wide range of habitat types in the nonbreeding season, breeding habitats are less diverse and almost all species nest in inland habitats, predominantly in freshwater wetland systems, the only species sometimes breeding at coastal salt marshes being the common redshank (*Tringa totanus*), Nordmann's greenshank (*Tringa guttifer*), and the willet (*Catoptrophorus semipalmatus*).

Species such as the jack snipe (Lymnocryptes minimus) and Gallinago snipes breed in marshes, swamps, floodplains, bogs, and moist grasslands, although some also use more wooded habitats. The wood snipe (Gallinago nemoricola) of central Asia breeds mainly in woodland and scrub. The dowitchers (Limnodromus) and most godwits also breed in marsh, bog, or wet grassy habitats, but the bar-tailed godwit (Limosa lapponica) nests in tundra and woodland. Curlews exploit many

breeding habitat types, including taiga, woodland, tundra, moorland, bogs, wet grassland, farmland, prairies, and lakeshores. Most shanks, and the two tattler (*Heteroscelus*) species, breed in wet wooded and forested areas such as muskeg and taiga. Most *Calidris* sandpipers breed north of the taiga in the low to middle Arctic tundra zone, while species such as red knot, purple sandpiper (*Calidris maritima*), and sanderling breed still farther north, in tundra that may be gravelly, stony, or rocky.

Woodcocks inhabit forests and other wooded habitats. The two migratory species, the American woodcock (*Scolopax minor*) and the Eurasian woodcock (*Scolopax rusticola*) often breed in deciduous woodland. Both occupy similar habitat in wintering areas, but most other migrant scolopacid species occupy different habitats, and take different food, in breeding and wintering areas. Many species winter at tropical, non-tidal wetlands, including river deltas, floodplains, lakeshores, pans, lagoons, and marshes. Species commonly using such habitats include the curlew sandpiper (*Calidris ferruginea*), little stint (*Calidris minuta*), wood sandpiper (*Tringa glareola*), marsh sandpiper (*Tringa stagnatilis*), spotted redshank (*Tringa erythropus*), bar-tailed godwit, and the snipes. In Africa, ruff and black-tailed godwit (*Limosa limosa*) rely extensively on manmade habitats such as rice fields. Buff-breasted sandpipers

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A gray phalarope (*Phalaropus fulicaria*) at its nest on Wrangel Island Nature Reserve, Russia, in the Arctic Ocean. (Photo by L. Veisman. Bruce Coleman Inc. Reproduced by permission.)

(Tryngites subruficollis) winter on pampas and grasslands in South America.

Coastal intertidal sand and mud attract different species, such as curlews, common redshank, terek sandpiper, willet, turnstones, and many *Calidris* sandpipers. Species such as the greenshank (*Tringa nebularia*) and other large *Tringa* species are equally at home in freshwater and marine wetlands. The two phalaropes are pelagic in winter.

The common sandpiper (Actitis hypoleucos) and the spotted sandpiper (Actitis macularia) show little seasonal variation in habitat preferences, both inhabiting margins of waterbodies such as rivers, ponds, and lakes all the year. A few species, notably the rock sandpiper (Calidris ptilocnemis), the purple sandpiper, and surfbird (Aphriza virgata), winter on rocky shores that offer high densities of marine invertebrate prey.

Behavior

Many species are territorial during the breeding season, but others, such as the Asian dowitcher (*Limnodromus semi-palmatus*), the common redshank, and some godwits and curlews are colonial or semi-colonial. Outside the breeding season most species feed and roost mainly in flocks. Only

those that forage visually tend to scatter widely. All species are strong fliers and tightly packed flocks often perform spectacular and complex aerial movements with great precision.

Outside the breeding season, activity patterns often relate to tides, birds feeding by day or night at low tides and roosting at high tides. On the northernmost breeding grounds, where daylight is continuous, activity levels are high and little rest is taken during the six to eight weeks when breeding takes place.

Reasons for this diversity of mating systems may be related to the short breeding season and ability of a single parent to incubate eggs and raise young unaided in situations where food is abundant and predators are few.

Song is an important component of display flights in the family. Snipes, however, accompany display flights by a variety of bleating or winnowing sounds produced by modified tail feathers during high-speed descents. The least vocal species are the phalaropes, which have no elaborate flight display or song, and species such as the ruff, which display in leks on the ground. Most species also have loud alarm calls given when an intruder approaches the breeding territory, while characteristic short alarm calls are uttered to warn of danger and to instigate and coordinate flocking.

Most species that breed at moderate to high latitudes in the Northern Hemisphere undertake extensive southward migrations after breeding. Generally, more northern breeding populations undertake the longest migrations and the temperate breeders the shortest migrations. Many species migrate along well-defined north-south "flyways." Migrants fly in flocks, usually of one species, and may fly at altitudes of over 16,000 ft (5,000 m). These birds can navigate with great precision and, by accumulating very large fat deposits, can make sustained flights of several thousand miles.

Feeding ecology and diet

Scolopacid waders eat predominantly invertebrates, including lumbricid, polychaete, and oligochaete worms; mollusks; crustaceans; arachnids; insects; small fish; and amphibians. On northern breeding grounds most migratory species appear to eat predominantly insects and arachnids, which are abundant. On migration and on wintering grounds, very different animal prey may be taken and some species become dietary specialists. Few species take predominantly plant material, although ruffs and black-tailed godwits periodically eat only rice. When newly returned to the breeding grounds, many species may find animal food scarce and may temporarily supplement their diet with seeds and shoots, while great knots (*Calidris tenuirostris*) feed predominantly on berries throughout the breeding season. Berries may also have been the staple food of the Eskimo curlew (*Numenius borealis*) when breeding.

Four principal feeding techniques may be distinguished in the family. Pecking with occasional probing is characteristic of short-billed species of shorelines and relatively dry-land habitats, such as the common sandpiper. Another technique, probing soft substrates, is practiced by snipe, woodcock, and most other species in the family. The third method, running Vol. 9: Birds II Family: Sandpipers

with the bill submerged to chase fish, is used by shank species such as the greenshank and the greater yellowlegs (*Tringa melanoleuca*). In the nonbreeding season large *Tringa* species operate in flocks to drive schools of small fish into shallow water.

The fourth technique, rapidly pecking tiny prey from the water, is practiced by species with a short, relatively fine bill—phalaropes and some *Calidris* species. Phalaropes forage while swimming, when they take shrimps, copepods, and other planktonic animals from the water. They often spin around rapidly, probably to bring deeper prey closer to the surface. Small sandpipers such as the little stint and the western sandpiper often feed by stitching—making rapid vertical pecks into the substrate.

Several species have specialized feeding habits on the non-breeding grounds. Turnstones turn over stones, shells, and seaweed to locate hidden prey. Mollusks dominate the diet of the surfbird, which hammers or tugs at its prey with its strong, short bill. Other species, such as the red knot, also take many mollusks. The spoon-billed sandpiper feeds like the much larger spoonbills (*Platalea*, family Threskiornithidae), sweeping its spatulate bill from side to side in the water to catch small prey. The Terek sandpiper makes short sprints to catch small burrowing crabs when they surface to feed or court. Several curlew species take larger burrowing crabs.

Some species hold winter feeding territories and scolopacid waders have been the subjects of classic studies on feeding dispersion and territoriality in relation to prey availability. Results suggest that defense of resources is not tenable at very low or very high food densities, but occurs at intermediate prey densities and may enhance short-term food availability, prevent long-term depletion, and reduce the disturbance of prey.

Reproductive biology

Mating systems in the family are remarkably varied, although most species are monogamous. Polygyny, in which males pair with more than one female, is characteristic of species that display in leks and also occurs in the Eurasian woodcock, the white-rumped sandpiper (*Calidris fuscicollis*), and the sharp-tailed sandpiper. Polyandrous species (female mates with more than one male) include the spotted sandpiper (which also shows sex-role reversal) and possibly the spotted redshank and the upland sandpiper (*Bartramia longicauda*). Phalaropes are usually monogamous, though polyandry is recorded in all three species. They also show sex-role reversal: females defend territories and court males that undertake incubation duties and raise the chicks alone.

Many species pair rapidly after arrival on the breeding grounds and begin nesting within a few days. Attraction of mates is often achieved by persistent flight singing, followed by ground displays associated with nest-site selection. Some species, such as Temminck's stint (*Calidris temminckii*) sing from perches. The ruff, buff-breasted sandpiper and great snipe (*Gallinago media*) have ground leks at which males display to visiting females and mating occurs.

The nest of most scolopacid waders is a shallow scrape or depression on open ground or in herbage, usually sparsely lined with soft vegetation. A few species make more substantial nests. Baird's sandpiper (*Calidris bairdii*) builds a cup nest in herbage and Nordmann's greenshanks build substantial twig and lichen nests in trees. Green sandpipers (*Tringa ochropus*) and solitary sandpipers (*Tringa solitaria*) use old tree nests of other birds.

The most common clutch size is four eggs, but two to three eggs are laid by dowitchers and by woodcocks and snipes of temperate and tropical latitudes. Scolopacid eggs are pyriform, with a cryptic pattern of brown to black markings on a paler ground. Incubation begins when the clutch is complete and takes about three weeks. Chicks hatch almost simultaneously, are precocial and can walk and feed when a few hours old. They leave the nest within a day of hatching and are brooded and guarded by one or both parents. Only woodcocks and snipes feed their chicks. Parental distraction displays include repetitive display flights, running away like rodents with feathers fluffed like fur and making mammal-like squeaks, and injury-feigning.

Parental duties are shared roughly equally by both sexes in many species, although the female tends to leave chicks earlier. In some species, the female leaves before brood-rearing, or even incubation, is complete. Males of polygynous species undertake no parental care, while in successively polyandrous species, the male raises the first brood while the female may lay and raise another clutch.

When chicks are old enough not to need brooding, the broods of different parents and even different species may form crèches, allowing some adults to desert young early. The remaining attendants desert the young at fledging or immediately afterwards, and most adults migrate south before the young.

In most species, fewer than half the fledglings survive the first year. Although some species breed when one year old, first-year birds of many species remain on wintering grounds and return to breed only when two or three years old. In many Northern Hemisphere breeding areas, breeding success is cyclical and thought to be linked to the population cycles of lemmings (Cricetidae), which in turn influence levels of predation on breeding birds. As a result, curlew sandpipers suffer increased predation of eggs and young by arctic foxes (*Alopex lagopus*) in years of decreased populations of lemmings, the foxes' normal prey.

Conservation status

Twenty species are of conservation concern, including 10 that are considered Near Threatened. Two species have become extinct since 1600, both from French Polynesia: the white-winged sandpiper (*Prosobonia leucoptera*) from Tahiti, and Ellis's sandpiper (*Prosobonia ellisi*) from Moorea. Both probably occurred along highland streams and were exterminated during the eighteenth century, probably by introduced rats. The only surviving member of the genus, the Tuamotu sandpiper, is endangered, having a very small range and population.

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Of the two Critically Endangered species, the Eskimo curlew may be extinct as there have been no sightings since the mid-1980s. This small curlew, which bred in Canada and wintered in South America, was hunted close to extinction in the late nineteenth century. Its fate was sealed by the almost complete loss to agriculture of the prairie habitat on which it relied during spring passage. The slender-billed curlew (*Numenius tenuirostris*), which breeds in Siberia and winters in northwest Africa, has declined dramatically in numbers, the key factor probably being hunting in the nineteenth century, possibly aggravated by habitat loss.

The endangered Nordmann's greenshank breeds in the Russian Far East and winters coastally in south Asia. It is threatened by habitat loss throughout its range, and also by hunting and disturbance. Of the six vulnerable species, the spoon-billed sandpiper is threatened by habitat loss. The bristle-thighed curlew (Numenius tabitiensis) that breeds in western Alaska and winters on oceanic islands in the Pacific (including the Hawaiian islands) suffers heavy losses to introduced predators while flightless during its autumn molt on the wintering grounds. The wood snipe, which breeds in the Himalayas, suffers habitat loss and hunting on its southern Asian wintering grounds. The Chatham snipe (Coenocorypha pusilla) is confined to four small islands off New Zealand and is vulnerable to local extinction by introduced species. Two Asian woodcocks, the Amami woodcock (Scolopax mira), of the Nansei Shoto islands in southern Japan, and the Moluccan woodcock, which is known from only three localities, are threatened by loss of forest habitats.

All ten Near Threatened species, including one woodcock, four snipe, two curlews, the Asian dowitcher, and the buff-breasted sandpiper, are threatened by habitat loss and by hunting. Habitat loss and disturbance are potential threats to many wader species, especially in tropical regions and at temperate staging areas close to large human populations. In northern breeding areas habitat loss may not have been so significant, but has still adversely affected some species. Pressures on habitats are likely to increase, while hunting is still a significant factor and rapid climate change may have significant impacts on habitats and migratory flight routes.

Significance to humans

The common snipe has been closely associated with folklore in Europe and America, and its arrival in spring has been related to events of significance. For example, in Newfoundland it is associated with the arrival of lobsters inshore, while in the United States it is associated with appearance of some commercial fish species. In many parts of Europe the snipe is associated with rain, while some Eskimos of Alaska believe that killing a snipe would bring bad weather.

In Australia, where the return of waders coincides with the first rains of the wet season and is thus associated with good health, one Aborigine tribe carries out "sandpiper dances" as part of its initiation ceremonies. Other species may be associated with sexual appetite, and in the Russian Far East, the lekking behavior of ruffs has impressed the local people of the Chukchi Peninsula so much that they celebrate it with an imitative dance.

The principal significance of scolopacid waders to humans has always been for food and sport. In Europe in the Middle Ages, ruffs were captured on southward passage and were fattened for consumption during winter. Red knots were also highly regarded as a food item. Snipe and woodcock have long been a major quarry of hunters worldwide, and are shot annually in large numbers in Europe and North America. An estimated 1.5 million common snipe are killed by hunters annually in Europe and half a million in North America, while annually up to 3.7 million Eurasian woodcock are shot in Europe and about 2 million American woodcock in North America.

In North America, European immigrants slaughtered an immense number of scolopacid waders in the nineteenth century—godwits, dowitchers, knots, and many other species, even small sandpipers. They were not only trapped and shot, but also blinded by lights at night so that they could be captured by hand. The precipitous decline of the once abundant Eskimo curlew can be attributed to such market hunting, and by the beginning of the twentieth century, this species had become a rarity.

Waders are rarely considered nuisance species, but in some Sahel countries, ruffs and black-tailed godwits are often considered pests because they eat rice. Many species are potentially beneficial by virtue of the insect pests they eat. Upland sandpipers, which breed on North American plains, serve farmers in this way. This role was so unappreciated that in the nineteenth century they were poisoned in the belief that they ate grain.



1. Ruff (*Philomachus pugnax*); 2. Tuamotu sandpiper (*Prosobonia cancellata*); 3. African snipe (*Gallinago nigripennis*); 4. Female Wilson's phalarope (*Steganopus tricolor*); 5. Female ruddy turnstone (*Arenaria interpres*); 6. Long-billed curlew (*Numenius americanus*); 7. Spotted redshank (*Tringa erythropus*); 8. Great knot (*Calidris tenuirostris*); 9. Eurasian woodcock (*Scolopax rusticola*); 10. Spoon-billed sandpiper (*Eurynorthynchus pygmeus*). (Illustration by Gillian Harris)

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Species accounts

Eurasian woodcock

Scolopax rusticola

SUBFAMILY

Scolopacinae

TAXONOMY

Scolopax rusticola Linnaeus, 1758, Sweden. Monotypic.

OTHER COMMON NAMES

French: Bécasse des bois; German: Waldschnepfe; Spanish: Chocha Perdiz.

PHYSICAL CHARACTERISTICS

13–13.8 in (33–35 cm); 0.29–0.92 lb (144–420 g). Mainly rufous brown to reddish above, buffy below. Broad wings. Sexes similar.

DISTRIBUTION

Eastern Atlantic islands, British Isles, north and central Europe, and central Asia to Sakhalin and Japan. Winters from Europe and North Africa to Southeast Asia.

HABITAT

Moist forest or woodland with clearings and dense undergrowth.

BEHAVIOR

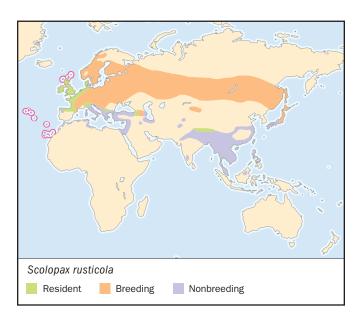
Solitary. Male has crepuscular "roding" display flight, with quiet grunting and sharp pietz notes.

FEEDING ECOLOGY AND DIET

Crepuscular or nocturnal feeder, probing moist soil for worms and insects; also takes food from surface.

REPRODUCTIVE BIOLOGY

Breeds March–July. Polygynous; female cares for eggs and young. Nests in a shallow depression under shrubs; produces two to six eggs with incubation in 21–24 days; fledges at 15–20 days.



CONSERVATION STATUS

Not threatened, although some European populations decreasing; habitat loss is a threat to breeding and wintering birds.

SIGNIFICANCE TO HUMANS

Up to 3.7 million birds killed by hunters per year in Europe. ◆

African snipe

Gallinago nigripennis

SUBFAMILY

Gallinagininae

TAXONOM

Gallinago nigripennis Bonaparte, 1839, Cape of Good Hope. Three subspecies.

OTHER COMMON NAMES

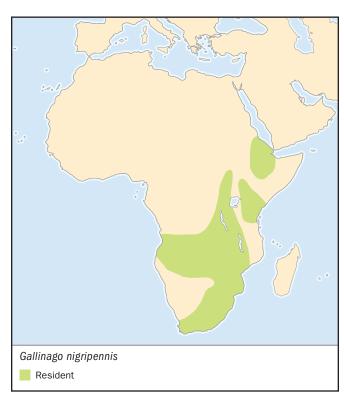
English: Ethiopian snipe; French: Bécassine Africaine; German: Afrikanische bekassine; Spanish: Agachadiza Africana.

PHYSICAL CHARACTERISTICS

9.8–11.4 in (25–29 cm); 0.2–0.36 lb (90–164 g). Darker upperparts contrast with white belly. Female similar to male but bill slightly longer.

DISTRIBUTION

G. n. aequatorialis: Ethiopia, Eritrea, Uganda, Kenya and east DRC, south to east Zimbabwe and north Mozambique; G. n. angolensis: Angola, Namibia, Botswana, Zambia and west Zimbabwe; G. n. aequatorialis: south Mozambique and South Africa.



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HABITAT

Wetlands with short emergent vegetation, tussocks, and exposed soft mud.

BEHAVIOR

Flushes with zigzag flight and harsh call. Male has display flight with "drumming" produced by vibrating outer tail feathers. In East Africa, nests at high altitudes and moves lower after breeding.

FEEDING ECOLOGY AND DIET

Mainly crepuscular or nocturnal forager, probing for worms and insect larvae.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds mainly during or after rains. Nests in a pad of grass hidden in tussock on moist to flooded ground. Clutch consists of two to three eggs.

CONSERVATION STATUS

Locally common to abundant. Vulnerable to habitat loss through wetland destruction.

SIGNIFICANCE TO HUMANS

None known. ◆

Long-billed curlew

Numenius americanus

SUBFAMILY

Tringinae

TAXONOMY

Numenius americanus Bechstein, 1812, New York. Two subspecies.

OTHER COMMON NAMES

French: Courlis à long bec; German: Rostbrachvogel; Spanish: Zarapito Americano.

PHYSICAL CHARACTERISTICS

19.7–25.6 in (50–65 cm); male 0.98–1.74 lb (445–792 g), female 1.25–2.09 lb (570–951 g). A large curlew with a droplet-shaped billtip. Speckled black and cinnamon-buff upperparts; cinnamon underparts. Female averages larger, with a longer bill.

DISTRIBUTION

N. a. parvus: south British Columbia east to Manitoba and south to California and South Dakota, wintering from California and Louisiana to Mexico; N. a. americanus: Nevada east to South Dakota and south to Texas, wintering from California and Texas to Mexico, Honduras, Costa Rica, and Guatemala.

HABITAT

Breeds on prairies; nonbreeders occur at marshes, estuaries, and farmland.

BEHAVIOR

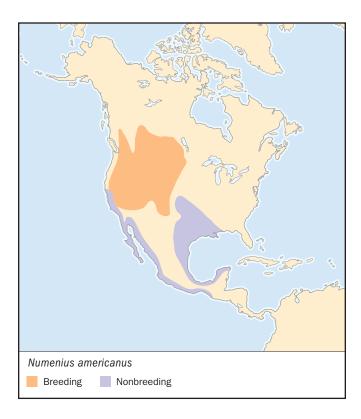
Territorial when breeding.

FEEDING ECOLOGY AND DIET

Eats insects, in nonbreeding season also crustaceans, mollusks, worms, toads, and berries.

REPRODUCTIVE BIOLOGY

Monogamous. Lays April–May. Nests in short grass; clutch contains three to five eggs; incubation is 27–28 days; fledges at 41–45 days.



CONSERVATION STATUS

Breeding range has contracted westwards due to loss of prairies to agriculture. Population of *N. a. parvus* was 6,400 in 1992, apparently declining; species' overall numbers may be stable.

SIGNIFICANCE TO HUMANS

Previously heavily hunted, now fully protected. •

Spotted redshank

Tringa erythropus

SUBFAMILY

Tringinae

TAXONOMY

Scolopax erythropus Pallas, 1764, the Netherlands. Monotypic.

OTHER COMMON NAMES

English: Dusky redshank; French: Chevalier arlequin; German: Dunkler wasserläufer; Spanish: Archibebe Oscuro.

PHYSICAL CHARACTERISTICS

11.4–12.6 in (29–32 cm); 0.21–0.51 lb (97–230 g). Black both above and below, with white dots on upperparts. In flight, a white wedge on the back and white underwings are visible. Female is slightly larger and paler overall.

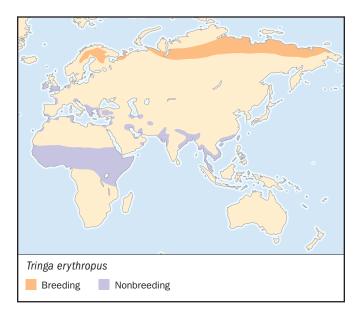
DISTRIBUTION

Scandinavia and northwest Russia across northern Siberia to Chukotskiy Peninsula. Winters from Europe to equatorial Africa, east through Persian Gulf to Southeast Asia and Taiwan.

HABITAT

Breeds in lightly wooded tundra and heathland; nonbreeders prefer lakeshores, lagoons, and muddy coasts.

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BEHAVIOR

Nonbreeders form flocks, often feeding in dense packs in deep water.

FEEDING ECOLOGY AND DIET

Eats insects, small crustaceans, mollusks, worms, fish, and amphibians. Pecks at prey, sweeps water with bill; sometimes feeds while swimming.

REPRODUCTIVE BIOLOGY

Monogamous; sometimes polyandrous. Lays eggs May–June; nests in tussocks or moss. Clutch contains three to five eggs. Female usually leaves before eggs hatch.

CONSERVATION STATUS

Wintering numbers in Europe stable in 1970s. Population in Europe and West Africa 75,000–150,000 (1994); 45,000–75,000 winter East Africa and Asia.

SIGNIFICANCE TO HUMANS

None known. ◆

Tuamotu sandpiper

Prosobonia cancellata

SUBFAMILY

Tringinae

TAXONOMY

Tringa cancellata Gmelin, 1789, Kiritimati, Christmas Island. Monotypic.

OTHER COMMON NAMES

French: Chevalier des touamotou; German: Südseeläufer; Spanish: Andarríos de Tuamotu.

PHYSICAL CHARACTERISTICS

5.9–6.7 in (15–17 cm); 0.07–0.1 lb (32–44 g). Small, brown sandpiper with a very short, thin bill. Extensive buff spots and feather edges on upperparts; underparts lighter with brown spots and bars on breast, flanks, and undertail.

DISTRIBUTION

Tuamotu Archipelago (French Polynesia).



HABITAT

Beaches, shores, and scrub on tiny atolls, preferring open areas along shorelines.

BEHAVIOR

Sedentary, but may visit islands where it does not nest.

FEEDING ECOLOGY AND DIET

Eats mainly insects; also plant material. Forages among coral rubble and leaf-litter.

REPRODUCTIVE BIOLOGY

Breeding known in May and August. Nest of fragments of shell, coral and plants, placed on pebbly shoreline. One nest had two eggs.

CONSERVATION STATUS

Endangered because of its small range and population (in 2000 estimated at 250–999 birds on up to 14 islands). It is declining through disturbance, habitat loss, and the introduction of predators to its islands. Former range spanned 2,300 mi (3,700 km) of the central Pacific.

SIGNIFICANCE TO HUMANS

None known. ◆

Ruddy turnstone

Arenaria interpres

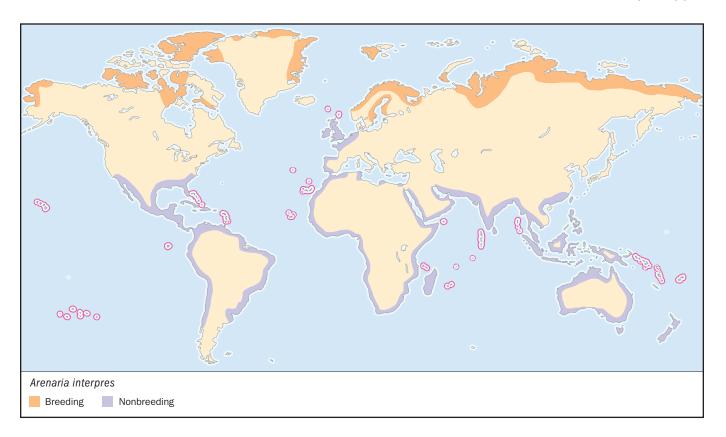
SUBFAMILY

Arenariinae

TAXONOMY

Tringa interpres Linnaeus, 1758, Gotland, Sweden. Two subspecies.





OTHER COMMON NAMES

French: Tournepierre à collier; German: Steinwälzer; Spanish: Vuelvepiedras Común.

PHYSICAL CHARACTERISTICS

8.3–10.2 in (21–26 cm); 0.18–0.42 lb (84–190 g). Black and white head, neck, throat, and chest; rufous-chestnut upperparts with black-brown patches; white underparts. Female has more streaking on crown, a brownish nape, duller upperparts, and pale flecks on the breast patch.

DISTRIBUTION

A. i. interpres: northeast Canadian Arctic, Greenland, north Eurasia and northwest Alaska, wintering western Europe, Africa, South Asia, Australasia, South Pacific islands, and Pacific coast of North America; A. i. morinella: northeast Alaska and Arctic Canada; winters from South Carolina and Gulf of Mexico to Chile and north Argentina.

HABITAT

Breeds on stony coastal plains, marshy slopes and flats, and tundra; winters on rocky and stony coasts, sandy beaches with seaweed, and exposed reefs.

BEHAVIOR

Relatively tame; often in flocks.

FEEDING ECOLOGY AND DIET

Gleans insects, crustaceans, mollusks, worms, echinoderms, fish, and carrion; sometimes birds' eggs. Flips over stones, shells, and seaweed with bill, catching prey thus exposed; pushes large objects with breast; scavenges frequently.

REPRODUCTIVE BIOLOGY

Monogamous and solitary. Lays May–July. Nests are open or concealed in hummocky vegetation; clutch contains two to four eggs; incubation 22–24 days; fledges at 19–21 days.

CONSERVATION STATUS

No significant decreases in numbers reported.

SIGNIFICANCE TO HUMANS

None known. ◆

Great knot

Calidris tenuirostris

SUBFAMILY

Calidrinae

TAXONOMY

Totanus tenuirostris Horsfield, 1821, Java. Monotypic.

OTHER COMMON NAMES

French: Bécasseau de l'anadyr; German: Großer knutt; Spanish: Correlimos Grande.

PHYSICAL CHARACTERISTICS

10.2–11 in (26–28 cm); 0.25–0.55 lb (115–248 g). Largest member of its genus; cryptic coloration in shades of black and white with chestnut scapulars. Female averages larger and has less chestnut in scapulars.

DISTRIBUTION

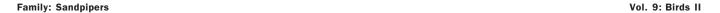
Northeast Siberia; winters in Southeast Asia and Australia, also Arabia, India, Pakistan and Bangladesh.

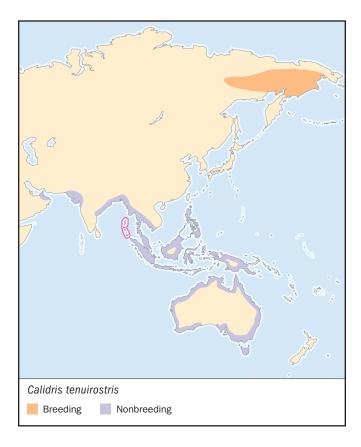
HABITAT

Breeds on montane tundra, in gravelly areas with short vegetation or scattered small trees; nonbreeders occupy coastal mudflats and sandflats, estuaries, lagoons and beaches.

BEHAVIOR

Territorial when breeding.





FEEDING ECOLOGY AND DIET

Breeding birds eat mainly berries but feed chicks on insects. In nonbreeding season eats mainly bivalve mollusks, also gastropods, crustaceans, annelids, and sea cucumbers. Forages mainly by probing; feeds in large flocks.

REPRODUCTIVE BIOLOGY

Monogamous. Lays eggs May–June. Clutch contains four eggs; incubation is 21 days, by both parents; female leaves after chicks hatch; fledges at 20–25 days.

CONSERVATION STATUS

About 270,000 winter in Australia, where apparently declining. Hunting and habitat loss at stopover zones in China may be a major threat.

SIGNIFICANCE TO HUMANS

None known. ◆

Spoon-billed sandpiper

Eurynorhynchus pygmeus

SUBFAMILY

Calidrinae

TAXONOMY

Platalea pygmea Linnaeus, 1758, Surinam. Monotypic.

OTHER COMMON NAMES

French: Bécasseau spatule; German: Löffelstrandläufer; Spanish: Correlimos Cuchareta.



PHYSICAL CHARACTERISTICS

5.5–6.3 in (14–16 cm); male averages 1 oz (29 g), one female 1.2 oz (34 g). Distinctive spatulate bill. Red-brown head, neck, and breast with dark brown streaks; blackish upperparts with buff and rufous fringes; white belly. Female slightly larger.

DISTRIBUTION

Chukotskiy Peninsula to north Kamchatka; winters from India to Indochina, south China and Singapore.

HABITAT

Coastal sand ridges, lakes, and marshes. Winters on muddy coasts and mudflats.

BEHAVIOR

Territorial. Male's display flight includes hovering, circling and diving, and uttering a buzzing trill.

FEEDING ECOLOGY AND DIET

Insects, crustaceans, worms, mollusks, and seeds. Feeds in shallow water or wet mud, sweeping the spatulate bill from side to side.

REPRODUCTIVE BIOLOGY

Monogamous. Nests June–July in moss, sedges, and creeping osiers. Clutch contains four eggs; incubation occurs in 18–20 days, by both parents; female leaves when chicks are four to six days old.

CONSERVATION STATUS

Vulnerable, with a small, declining population (2,500–10,000 in 2000) because of habitat loss throughout range, compounded by disturbance and some hunting.

SIGNIFICANCE TO HUMANS

None known. ◆

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Ruff

Philomachus pugnax

SUBFAMILY

Calidrinae

TAXONOMY

Tringa Pugnax Linnaeus, 1758, Sweden. Monotypic.

OTHER COMMON NAMES

English: Reeve (female); French: Combattant varié; German: Kampfläufer; Spanish: Combatiente.

PHYSICAL CHARACTERISTICS

Male 10.2–12.6 in (26–32 cm), 0.29–0.56 lb (130–254 g); female 7.9–9.8 in (20–25 cm), 0.15–0.37 lb (70–170 g). Males have head tufts and ruffs of variable color (buff, chestnut, dark purple, black, white), often barred or spotted. Females lack this specialized plumage and are considerably smaller than males.

DISTRIBUTION

Europe through Siberia to Chukotskiy Peninsula and Sea of Okhotsh; winters in Africa, also Mediterranean, Middle East, and Indian subcontinent.

HABITAT

Lowland marshes, deltas, and damp grasslands in tundra; winters at grassland, plough, rice fields, inland freshwater habitats, and coastal pools.

BEHAVIOR

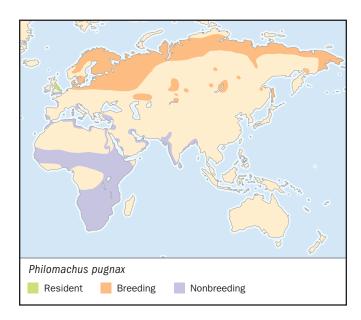
Mates at traditional leks, where males gather to display and fight and females visit.

FEEDING ECOLOGY AND DIET

Eats insects, crustaceans, mollusks, worms, small aquatic vertebrates, rice, seeds, and plants. Sometimes feeds while wading or swimming.

REPRODUCTIVE BIOLOGY

Nests May–August. Incubation and brood rearing done by female. Clutch contains three to four eggs with an incubation of 20–23 days; fledges at 25–28 days.



CONSERVATION STATUS

Population possibly over 2 million. Declining in West Africa; breeding range has contracted in west due to wetland drainage, but has increased in east Russia.

SIGNIFICANCE TO HUMANS

None known.

Wilson's phalarope

Steganopus tricolor

SUBFAMILY

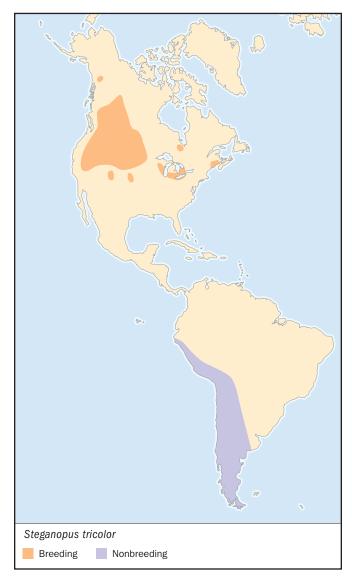
Phalaropodinae

TAXONOMY

Steganopus tricolor Vieillot, 1819, Paraguay. Monotypic.

OTHER COMMON NAMES

French: Phalarope de Wilson; German: Wilsonwassertreter; Spanish: Falaropo Tricolor.



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PHYSICAL CHARACTERISTICS

8.7–9.5 in (22–24 cm); male 0.07–0.24 lb (30–110 g), female 0.11–0.28 lb (52–128 g). Sexual dimorphism. Female has grayish white cap and nape; black band from bill through eye to side of breast; orange foreneck and upper breast; blue-gray mantle and wing-coverts; reddish chestnut edging on mantle and scapulars. Male has generally darker and duller upperparts.

DISTRIBUTION

Alberta and California east to Great Lakes. Winters from North Peru to Uruguay and Tierra del Fuego.

HABITAT

Marshy wetlands on prairies; winters at ponds in pampas, mudflats, and high-altitude saline lakes.

BEHAVIOR

Often very tame.

FEEDING ECOLOGY AND DIET

Takes mostly aquatic insects and crustaceans. Feeds while swimming, spins less than other phalaropes; usually pecks from water or mud, also upends, probes, and scythes through water with bill.

REPRODUCTIVE BIOLOGY

Usually monogamous; sometimes polyandrous. Male incubates eggs and cares for young. Lays eggs May–June. Nest scrape in fairly tall, dense vegetation near water. Clutch contains four eggs with an incubation of 18–27 days. Hatching success 12–50%, sometimes 0%.

CONSERVATION STATUS

Population estimated at 1 million in 1994 and considered stable in 2000.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

- Del Hoyo, J., A. Elliott, and J. Sargatal, eds. *Handbook of the Birds of the World.* Vol. 3. Barcelona: Lynx Edicions, 1996.
- Higgins, P. J., and S. J. J. F. Davies, eds. Handbook of Australian, New Zealand and Antarctic Birds. Vol. 3. Melbourne: Oxford University Press, 1996.
- Matthiessen, P. *The Wind Birds. Shorebirds of North America*. Shelburne, Vermont: Chapters Publishing Ltd., 1994.
- Rosair, D., and D. Cottridge. *Hamlyn Photographic Guide To The Waders Of The World*. London: Hamlyn, 1995.
- Stattersfield, A. J., and D. R. Capper, eds. Threatened Birds Of The World: The Official Source For Birds on the IUCN Red List. Cambridge: BirdLife International, 2000.

Periodicals

- Boland, J. M. "An Overview Of The Seasonal Distribution Of The North American Shorebirds." Wader Study Group Bulletin. 62 (1991): 39–43.
- Jonsson, P. E., and T. Alerstam. "The Adaptive Significance Of Parental Role Division And Sexual Size Dimorphism In Breeding Shorebirds." Biological Journal of the Linnean Society 41 (1991): 301–314.
- Underhill, L. G., R. P. Prys-Jones, E. E. Syroechkovski, et al. "Breeding of Waders (Charadrii) and Brent Geese (*Branta bernicla bernicla*) at Pronchishcheva Lake, Northeastern Taimyr, Russia, in a Peak and a Decreasing Lemming Year." *Ibis* 135 (1993): 277–292.

Organizations

- African-Eurasian Migratory Waterbird Agreement (AEWA). UN Premises in Bonn, Martin Luther-King Str, Bonn, D-53175 Germany. E-mail: aewa@unep.de Web site: http://www.wcmc.org.uk/AEWA/
- International Waterbird Census. Web site: http://www.wetlands.org/
- Wader Specialist Group, Mr. David Stroud. Monkstone House House, City Road, Peterborough, PE1 1JY United Kingdom. Phone: +44 1733 866/810. Fax: +44 1733 555/ 448. E-mail: stroudd@jncc.gov.uk
- Wader Study Group, The National Centre for Ornithology. The Nunnery, Thetford, Norfolk JP24 2PU United Kingdom.
- Western Hemisphere Shorebird Reserve Network (WHSRN).
 Manomet Center for Conservation Science, P O Box 1770,
 Manomet, MA 02345 USA. Phone: (508) 224-6521. Fax:
 (508) 224-9220. E-mail: info@manomet.org Web site:
 http://www.manomet.org/WHSRN/index.html/
- Woodcock and Snipe Specialist Group. Director, European Wildlife Research Institute, Bonndorf, Glashuette D-79848 Germany. Phone: 949 7653 1891. Fax: 949 7653 9269. E-mail: wildlife@ewi.t-online.de
- Working group on International Wader and Waterfowl Research (WIWO). Stichting WIWO, c/o P O Box 925, Zeist, 3700 AX The Netherlands. Web site: http://www.wiwo-international.org/

Barry Taylor, PhD

Seedsnipes (Thinocoridae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Thinocoridae

Thumbnail description

Medium-sized, short-legged, cryptically colored birds with stubby bills, recalling grouse or sandgrouse

Size

6-12 in (16-30 cm); 0.1-0.8 lb (50-400 g)

Number of genera, species

2 genera; 4 species

Habitat

Desert, semi-desert, steppe grassland, and alpine cushion plant communities. From sea level to 18,000 ft (5,500 m)

Conservation status

Not threatened



Distribution

South America in Patagonia, Andes, and Pacific Peru and northern Chile

Evolution and systematics

Seedsnipes have traditionally been considered charadriiform birds, and biochemical evidence supports this relationship and places seedsnipes in the scolopacid assembly. Their
closest relative is the plains-wanderer (*Pedionomus torquatus*),
an Australian species that at one time was placed near the
hemipodes (Gruiformes), and is included there in this work.
However, plains-wanderers have a skeleton with a broad, twonotched sternum and a broad pelvis that is remarkably similar to that of a *Thinocorus* seedsnipe. Biochemical evidence also
supports the relationship between plains-wanderers and seedsnipes. Seedsnipes probably had a long independent evolution
and possess several derived characters such as a superficially
passerine-like skull. Seedsnipes differ from most other shorebirds in having a crop, gizzard, and long intestinal caeca that
evidently are adaptations to their vegetarian diet.

Physical characteristics

Seedsnipes have stubby bills and short legs. The two larger species (*Attagis*) superficially resemble grouse, and the two smaller species (*Thinocorus*) resemble sandgrouse. A membrane with narrow slits for openings, which may serve to pro-

tect against dust storms, covers the nostrils of seedsnipes. The body feathers, which are plentiful and downy at their bases, provide evidence of the extremely cold environments seedsnipes can tolerate. As seen in pigeons and some other families of birds, the feathers fall off easily, probably to confuse predators. The wings are fairly narrow, long, and pointed, with 10 primaries (outer flight feathers) and 15 secondaries (inner flight feathers). The scapulars (tracts of feathers at sides of shoulders) are long and nearly reach the tip of the wing. The tail has 12 rectrices (tail feathers) and is relatively short and rounded to slightly wedge-shaped. The feet have three long front toes and a small but distinct hind toe. Unlike most sandgrouse, the tarsi and toes are unfeathered. There are two downy plumages, the second appearing just before the emergence of contour feathers. At least in the small seedsnipes, the immature plumage may soon be replaced (perhaps only partially) by a second immature plumage. The molt of the primaries is sometimes irregular.

Distribution

Seedsnipes are entirely restricted to the Neotropical region, where they inhabit the Andes and the adjacent Patagonia and

Family: Seedsnipes Vol. 9: Birds II



Rufous bellied seedsnipe (Attagis gayi) and chick in wetlands of the high Andes in Argentina. (Photo by Fletcher & Baylis. Photo Researchers, Inc. Reproduced by permission.)

Peruvian coast. Rufous-bellied seedsnipes (Attagis gayi) occur at very high elevations in the Andes of Ecuador and from central Peru to Tierra del Fuego-in the north they are found only above 13,000 ft (4,000 m), but in the south they are found down to 3,300 ft (1,000 m). White-bellied seedsnipes (Attagis malouinus) only inhabit a small area on the southern end of South America, where they nest below rufous-bellied seedsnipes in the Andes and descend to the adjacent Patagonian steppe in winter. Least seedsnipes (T. rumicivorus) are widely distributed in southern Argentina and Chile; in winter some migrate as far north as the plains of northeastern Argentina and Atacama, Chile. Populations of least seedsnipes also inhabit the Andean altiplano of northwestern Argentina, Bolivia, and adjacent Chile (perhaps also in southeasternmost Peru), and the coastal deserts of northernmost Chile and most of Peru. Gray-breasted seedsnipes (T. orbignyianus) are found in the Andes from northern Peru to Tierra del Fuego and on adjacent mesetas of Patagonia. They generally occur above least seedsnipes in the southern end of the continent but descend in winter, when they have reportedly been seen as far from the Andes as Córdoba.

Habitat

Seedsnipes are found in cold and windswept habitats rarely visited by humans. Rufous-bellied seedsnipes frequent rocky slopes, scree, short grass, bogs, and cushion plant communities near the snowline. White-bellied seedsnipes breed on stony slopes and bleak, windswept, alpine moorland, especially in places with crowberry heaths (*Empetrum*) and *Azorella*

cushions. In winter white-bellied seedsnipes descend to stony, dry riverbeds and wide shores of partly dried-up lakes. On the Peruvian coast least seedsnipes are often seen flying through desert devoid of vegetation on their way between small patches of low vegetation formed by the sea fog. On the altiplano and on the Patagonian steppe, they occur in sandy areas with scattered bunch grass and low herbaceous vegetation. Gray-breasted seedsnipes are typical of puna grassland and prefer areas with scattered stones and cushion plants as well as short grass bordering bogs.

Behavior

Seedsnipes spend most of their time walking slowly and quietly on the ground while feeding. Like sandgrouse, seedsnipes have the habit of turning their cryptically colored backs toward the observer, which makes them extremely difficult to detect. They will often allow close approach before they walk away or take off while emitting loud calls. The small species fly with a snipe-like, zigzag pattern. During the breeding season seedsnipes are found in pairs or groups of 5–6 birds, but in winter they usually occur in flocks, sometimes as large as 80 or more birds.

Feeding ecology and diet

Seedsnipes are entirely vegetarian. They bite off buds and tips of leaves with a downward jerk of the head and swallow them whole. Seedsnipes usually bend down to feed, but occasionally they will reach up to take a bud from an herb. Succulents form an important part of the diet, and apparently



A gray-breasted seednipe (*Thinocorus orbignyianus*) chick is protected in the shade of a rock. (Photo by G. Lasley/VIREO. Reproduced by permission.)

Vol. 9: Birds II Family: Seedsnipes

seedsnipes do not drink. Seeds are not an important food item, except perhaps for least seedsnipes.

Reproductive biology

During breeding, seedsnipes appear to be territorial and are often found in pairs. The nest is a simple depression on the ground, loosely lined with lichens, mosses, or other plant material. The four, or sometimes three, snipe-like eggs are covered with nest lining or soil whenever the nest is left unattended. When surprised while incubating, seedsnipes feign injury in the manner of other shorebirds. The incubation period of least seedsnipes is about 26 days. No precise data exist for the other species. Soon after hatching the young are led away from the nest by both parents and are able to find food on their own. They are brooded by the female when they are small, and the male participates in guarding the chicks. After about seven weeks the young are able to fly. There is some indication, at least for the small Thinocorus species, that they become sexually mature so rapidly that they can breed in the same season they were hatched. This would enable them to take advantage of climatically favorable years, especially in the Peruvian desert where the El Niño phenomenon provides abundant food sources once every four to ten years.

Conservation status

None of the four species of seedsnipe appear to be threatened. No population surveys have been carried out, but numbers of the large Attagis species were probably always moderate and have only locally been affected by pollution and hunting in the vicinity of mines. In Ecuador, rufous-bellied seedsnipes are confined to the highest peaks for much of the year, and researchers estimate that no more than 200 or 300 pairs reside in the country, most within national parks. In Peru and Chile they also are protected in several national parks and reserves. A substantial part of the range of white-bellied seedsnipes also lies within protected areas. The Thinocorus species are common to locally abundant and have probably benefited from the grazing of the Patagonian steppe and the burning of high Andean woodland. Least seedsnipes are one of the most common birds on the Patagonian plains, and large numbers of the altiplano population have been reported from northern Chile and in winter from Bolivia. The coastal Peruvian desert population is fairly small but may increase considerably in climatically favorable years. Gray-breasted seedsnipes are common in the Andean Puna and their numbers have probably increased because of the burning of high altitude woodlands.

Significance to humans

Seedsnipes are found in habitats so inhospitable to man that they have had little significance to humans. Their loud calls have given rise to onomatopoetic local names, but the common or even abundant *Thinocorus* species are not sought after as game.



1. Least seedsnipe (*Thinocorus rumicivorus*); 2. Gray-breasted seedsnipe (*Thinocorus orbignyianus*); 3. Rufous-bellied seedsnipe (*Attagis gayi*); 4. White-bellied seedsnipe (*Attagis malouinus*). (Illustration by Jacqueline Mahannah)

Vol. 9: Birds II Family: Seedsnipes

Species accounts

Rufous-bellied seedsnipe

Attagis gayi

TAXONOMY

Attagis gayi I. Geoffroy Saint-Hilaire and Lesson, 1831, Santiago, Chile. Three subspecies recognized.

OTHER COMMON NAMES

English: Gay's seedsnipe; French: Attagis de Gay; German: Rotbauch-Höhenläufer; Spanish: Agachona Grande, Agachona Ventrirrufa.

PHYSICAL CHARACTERISTICS

10–11 in (27–30 cm); 10.6–14.1 oz (300–400 g). Upperparts, wing lining, and breast with cryptic pattern of blackish, buff, and whitish. Dorsal feathers mostly black in *A. g. latreilli* and densely vermiculated in the southern forms. Belly is rufous (in *A. g. latreilli*) or pinkish cinnamon; it is palest in *A. g. gayi*. Vent densely barred in *A. g. latreilli* and plain or faintly barred in the southern forms. In flight, it shows no wingbar. Juvenile like adult but with more finely vermiculated upperparts.

DISTRIBUTION

A. g. gayi: the Andes from Tierra del Fuego to northern Chile and Argentina, above 3,300 ft (1,000 m) in the south, above 6,600 ft (2,000 m) further north; A. g. simonsi: above 13,000 ft (4,000 m) in the Andes from northern Argentina and Chile through Bolivia to central Peru; A. g. latreilli: above 14,000 ft (4,300 m) in the Andes of Ecuador.



HABITAT

Rocky slopes with scattered cushion plants near the snowline, scree with scattered low herbs, alpine bogs.

BEHAVIOR

In pairs or small groups, rarely larger flocks. Emits loud cackling vocalizations in flight.

FEEDING ECOLOGY AND DIET

Quietly browses on buds and leaf tips of herbs and cushion plants.

REPRODUCTIVE BIOLOGY

Monogamous. Nest is a crude scrape with little or no lining. Four eggs, covered with earth when not incubated.

CONSERVATION STATUS

Habitat rarely visited by humans. Range includes several national parks and reserves. Numbers locally decimated by hunting in the vicinity of mines.

SIGNIFICANCE TO HUMANS

None known except for hunting very locally. ◆

White-bellied seedsnipe

Attagis malouinus

TAXONOMY

Tetrao malouinus Boddaert, 1783, Islas Malvinas. Monotypic.

OTHER COMMON NAMES

French: Attagis de Magellan; German: Weissbauch-Höhenläufer; Spanish: Agachona Patagona.

PHYSICAL CHARACTERISTICS

10–11 in (26.5–29 cm). Head speckled and upperparts and breast cryptically patterned with blackish, rufous, and buff. Rump densely barred blackish and pale buff. Chin, belly, and narrow tip of tail white. In flight shows conspicuous white band on underwing.

DISTRIBUTION

Breeds at 2,100–6,600 ft (650–2,000 m) in southernmost Chile and Argentina. Descends to adjacent lowlands in winter. Apparently straggles to Islas Malvinas.

HABITAT

Scree and moorland, especially with crowberries (*Empetrum*) and *Azorella* cushions. In winter on stony, dry riverbeds and wide shores of partly dry lakes.

BEHAVIOR

In pairs or family groups, in winter in large flocks. Emits loud calls in flight.

FEEDING ECOLOGY AND DIET

Reportedly feeds on crowberries and other plant material.

REPRODUCTIVE BIOLOGY

Four eggs, little else known.







CONSERVATION STATUS

Habitat almost never visited by humans, parts of range protected.

SIGNIFICANCE TO HUMANS

None known. ◆

Gray-breasted seedsnipe

Thinocorus orbignyianus

TAXONOMY

Thinocorus orbignyianus I. Geoffroy Saint-Hilaire and Lesson, 1831, Santiago, Chile. Two subspecies recognized (*T. o. or-bignyianus* and *T. o. ingae*) that differ only in size.

OTHER COMMON NAMES

English: D'Orbigny's seedsnipe; French: Thinocore d'Orbigny; German: Graubrust-Höhenläufer; Spanish: Agachona Mediana.

PHYSICAL CHARACTERISTICS

9 in (23 cm), *T. o. ingae* averaging smallest: 3.9–4.9 oz (110–140 g). Female slightly smaller than male. Upperparts with cryptic pattern of whitish, buff, and dusky; light borders narrowest in juveniles. Throat and belly white, demarcated with blackish towards face and breast, which are gray in male, streaked dusky and buff in female and juvenile. Tail prominently white tipped, rounded to slightly wedge shaped. In flight it shows a faint white wingbar above and a broad white wingbar below that contrast with the dark wing linings.

DISTRIBUTION

T. o. orbignyianus: Tierra del Fuego north along the Andes to central Argentina/Chile; T. o. ingae: Andes from northern Argentina/Chile to northern Peru.

HABITAT

Dry puna with scattered bunchgrass, cushion plants, low herbs, and short grass bordering highland bogs.

BEHAVIOR

In pairs or family groups. Territorial males countersing from hummocks or rocks, or they perform elaborate display flight at twilight or night in which they fly in wide circles and descend with stiff, lowered wings and raised tail. When flushed, flies with snipe-like zigzag flight.

FEEDING ECOLOGY AND DIET

Browses quietly, bites off buds and leaf tips of young grass, herbs, and succulents.

REPRODUCTIVE BIOLOGY

Possibly lays several broods in a season. Nest is a simple scrape loosely lined with plant debris. Four eggs. Length of incubation period unknown. Both parents guard the young.

CONSERVATION STATUS

Common and widespread, benefits from clearance of high altitude woodland.

SIGNIFICANCE TO HUMANS

None known. ◆

Vol. 9: Birds II Family: Seedsnipes

Least seedsnipe

Thinocorus rumicivorus

TAXONOMY

Thinocorus rumicivorus Eschscholtz, 1829, Concepción Bay, Chile. Three subspecies recognized (*T. r. cuneidauda*, *T. r. bolivianus*, and *T. r. rumicivorus*) that differ in size, hue, and details of vermiculations on the upperparts. A fourth, *T. r. pallidus*, from the Santa Elena peninsula in southwestern Ecuador is often listed, but it appears to be inseparable from *T. r. cuneicauda*.

OTHER COMMON NAMES

English: Chilean seedsnipe, Patagonian seedsnipe, Pygmy seedsnipe; French: Thinocore de Patagonie; German: Zwerghöhenläufer; Spanish: Agachona Chica.

PHYSICAL CHARACTERISTICS

6–7 in (16–17 cm), *T. r. bolivianus* 8 in (19–20 cm); 1.8–2.1 oz (50–60 g). Much like gray-breasted seedsnipe. Upperparts with cryptic pattern of whitish, buff, and dusky; light borders narrowest in juvenile. Throat and belly white, demarcated with blackish (more broadly so than in gray-breasted seedsnipe) towards face and breast, which are gray in male and streaked dusky and buff in female. Male with blackish borders of throat and breast connected by blackish line down center of breast. Tail prominently white-tipped and distinctly wedge-shaped. In flight shows a faint white wingbar above and a broad white wingbar below, contrasting with the dark wing linings. Juveniles much like females, but white throat not distinctly demarcated and breast diffusely spotted rather than streaked.

DISTRIBUTION

T. r. cuneicauda: coastal desert of Peru and extreme northern Chile, and, at least formerly, southwestern Ecuador; T. r. bolivianus: altiplano of northwestern Argentina, Bolivia, and northern Chile; T. r. rumicivorus: lowlands to 3,900 ft (1,200 m) in Patagonia and southern Chile where partly migratory, wintering north as far as the plains of northeastern Argentina and Uruguay, the mountains of Córdoba (to above 6,600 ft [2,000 m]) and Atacama, Chile.

HABITAT

Sandy areas with scattered bunch grass, low herbs, and succulents. In Patagonia, often on wide gravelly shores and areas with tiny annual herbs around partly dry claypan lakes. In Bolivia, in highland semidesert. In Peru, in sparse fog vegetation of coastal desert. Often on cultivated land.

BEHAVIOR

In pairs or family groups, in winter in larger flocks. Territorial males countersing from tops of bushes or fence posts. Display flight much like that of gray-breasted seedsnipe. When flushed, flies with snipe-like zigzag flight.

FEEDING ECOLOGY AND DIET

Like gray-breasted seedsnipe, browses on tips or buds of young grass, succulents, and small herbs, which are swallowed whole.



REPRODUCTIVE BIOLOGY

Probably multibrooded. Young apparently sexually mature when four months old and possibly breed the same season they were hatched. Nest is a simple scrape loosely lined with plant debris. Four eggs, covered with earth or nest-lining material when not incubated. Length of incubation period about 26 days. Both parents guard the young, which fly when seven weeks old.

CONSERVATION STATUS

Apparently favored by sheep grazing in Patagonia and irrigation in the Peruvian desert. Common to locally abundant in Patagonia. Ten specimens were collected on the Santa Elena peninsula in southwestern Ecuador in 1898. Although taken in January and February (the presumed breeding season), all were in fresh plumage and may have been mere stragglers from Peru. Subsequently there are but two possible sightings from Ecuador. If those ten specimens did breed in Ecuador, the reason for their disappearance remains unknown because plenty of seemingly suitable habitat persists.

SIGNIFICANCE TO HUMANS

None known. ◆

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Family: Seedsnipes Vol. 9: Birds II

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Niels K. Krabbe, PhD

Sheathbills

(Chionidae)

Class Aves

Order Charadriiformes

Suborder Charadrii

Family Chionidae

Thumbnail description

Medium-sized, chunky birds with dove-like or fowl-like body form, uniform white plumage, short legs, facial caruncles or warts, and compressed bill with characteristic horny sheath

Size

13.4–16.1 in (34–41 cm); 1.0–1.72 lb (450–760 g); wingspan 29.1–31.5 in (74–80 cm)

Number of genera, species

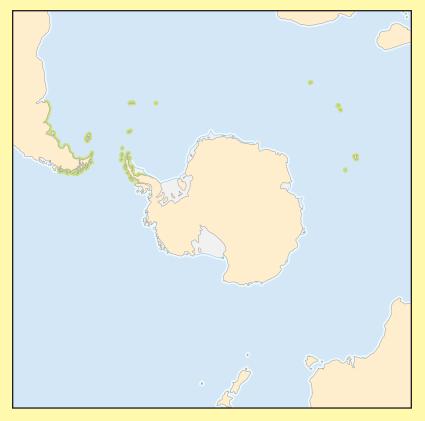
1 genus; 2 species

Habitat

Coastal plains, rocky and sandy intertidal zones, occasionally ice floes

Conservation status

Not threatened



Distribution

Antarctic Peninsula, subantarctic islands, mainland and adjacent islands of southern South America

Evolution and systematics

Sheathbills are a distinct and peculiar group of birds in terms of their morphology, behavior, and distribution. There is general agreement that sheathbills are members of the order Charadriiformes, a diverse group containing auks (Alcidae), gulls (Laridae), and waders or shorebirds (Charadrii). However, the evolutionary relationships among sheathbills and other charadriiform families remains unresolved and is a continued source of contention among taxonomists. Results from morphological, behavioral, and biochemical approaches are varied and remain ambiguous. The DNA-DNA hybridization studies of Sibley and Ahlquist, published in the 1990s, offered a potential breakthrough and classified sheathbills as a sister-group to the plover-like birds (Charadriidae) and thickknees (Burhinidae). However, these studies have received sufficient criticism that their validity is questioned. It is probable that genetic comparisons involving mitochondrial and nuclear DNA will ultimately resolve the issue.

Sheathbills occur in areas where fossil bird evidence is scarce and it is difficult to determine a precise estimate for their origin. They likely radiated in the Miocene epoch or later (over 30 million years ago) from an ancestor that colo-

nized Antarctica from more temperate regions. The close association of sheathbills with seabird and seal colonies has undoubtedly been a major force in their evolution.

Sheathbills consist of a single genus with two recognized species, black-faced sheathbills (*Chionis minor*) and pale-faced sheathbills (*C. alba*). Their ranges do not overlap and they are further differentiated based on migratory behavior and physical characteristics. Within black-faced sheathbills there are four recognized subspecies based on geographical distribution on isolated archipelagos and islands.

Physical characteristics

Sheathbills are easily recognized by their stocky appearance, uniform white plumage, and characteristic sheathed bill. The bill is conical and the horny sheath, from which the species derives its name, covers a proximal segment of the upper bill. Adding to their distinct appearance is a bare portion of the face that is partially covered with wart-like caruncles. In pale-faced sheathbills, the sheath is greenish and the caruncles are pink, whereas all facial features are black in black-faced sheathbills. Sheathbills are well adapted for life in a

Family: Sheathbills Vol. 9: Birds II



A sheathbill feeds on an egg taken from a Macaroni penguin (*Eudyptes chrysolophus*) on South Georgia Island, Falkland Islands. (Photo by Robert W. Hernandez. Photo Researchers, Inc. Reproduced by permission.)

harsh South Pole environment and possess short, stout legs, an insulating coat of dense gray down, and a thick layer of subcutaneous fat. Indicative of their terrestrial habits, sheath-bills are one of few Antarctic and subantarctic birds lacking webbed feet.

Sexes are similar in appearance but dimorphic in size; males are generally 15% heavier than females and have larger bills and sheaths. Adult birds can be differentiated from younger individuals based on bill sheath size and extent of facial caruncles. Older birds also develop carpal spurs that are used in aggressive encounters and tend to have deeper and harsher voices.

Distribution

Sheathbills occur at sites along the Antarctic Peninsula, at various archipelagos and isolated islands of the sub-antarctic, and as far north as the southern regions of South America. In part, distribution of these birds is restricted to sites with penguin and other seabird colonies, which sheathbills depend on as a source of food for much of the annual cycle.

The two sheathbill species do not overlap in range. Palefaced sheathbills are partially migratory and are found along the Antarctic peninsula, subantarctic islands of the Atlantic Ocean, and certain regions of southern South America. The four subspecies of black-faced sheathbills are sedentary birds with an allopatric distribution (mutually exclusive geographic areas) among archipelagos and isolated subantarctic islands of the Indian Ocean.

Habitat

Sheathbills are predominantly terrestrial birds that inhabit areas of coastal plains and adjacent intertidal zones. For much of the year sheathbills occur in seabird colonies and focus activities in these areas. An exception is some black-faced sheathbills of the Kerguelen Islands, where birds without access to seabird colonies spend more time in intertidal zones. Outside the breeding season, sheathbills frequent rocky and sandy intertidal zones, wet meadows and bogs as far as 0.6 mi (1 km) inland, and even ice floes.

Behavior

Sheathbill activities throughout the annual cycle vary depending on the occurrence of seabirds and seals to exploit. For example, some black-faced sheathbills at Marion Island breed in colonies of migratory crested penguins (*Eudyptes*). These sheathbills are forced to shift territories during the nonbreeding season to intertidal areas or colonies of king penguins (*Aptenodytes patavonicus*). In contrast, most pale-faced sheathbills are migratory and leave breeding grounds with other seabirds.

Feeding ecology and diet

Sheathbills are omnivores. Their diet includes a wide range of animal and plant materials. Their opportunistic foraging Vol. 9: Birds II Family: Sheathbills

strategies are likely a response to the harsh and variable environments that they inhabit. Colonies of seabirds, particularly penguins, are the most prominent food source for sheathbills. At these colonies sheathbills are predators and scavengers that feed on eggs, chicks, and even excrement. Sheathbills also kleptoparasitize seabirds returning to colonies to provision chicks. They harass or jostle birds as adults regurgitate a bolus to their begging chicks and then scavenge food spilled during the transfer. Research indicates that this is an important food source for breeding sheathbills, but it has little overall impact on seabirds.

During spring, sheathbills also scavenge dead pups, placentas, and seal milk. In cases where seabirds and seals are absent, sheathbills consume large amounts of seaweed and various invertebrates. For nonmigratory populations, the intertidal zone is an important foraging area during winter.

Reproductive biology

Sheathbills are monogamous birds that maintain long-term pair bonds. In most cases, pairs defend nesting and feeding territories in seabird colonies. Territorial defense involves displays, vocalizations, chasing, and occasional physical battles.

Sheathbills first breed at three to five years of age and annual reproduction is usually synchronized with breeding activities of associated seabird colonies. This strategy provides for maximum food availability during the energetically costly breeding period. As a result, nesting dates of sheathbills are somewhat variable, with a clutch of one to three eggs laid in late November or December. Eggs are pear-shaped and white

with flecks of gray or brown. Nest sites are located in small caves and cracks in rocky areas. In some cases, birds occupy abandoned burrows excavated by other species. Locations of nest sites provide shelter from winds and precipitation and cover from predatory skuas (Stercorariidae). Crude nests are constructed from feathers, pebbles, bones, shells, lichens, grasses, and seaweed.

Chicks hatch asynchronously after an incubation period of 28–32 days and are semi-precocial and nidiculous, partially covered with brown down. Both adults participate in parental care duties as young remain at of near nests for one to three weeks and then fledge approximately 50–60 days following hatching. Studies have found that survival rate is higher for the first chick hatched in a nest and overall nest success ranges from 1.1 to 1.9 fledglings per nest. Starvation is the primary cause of mortality in young sheathbills.

Conservation status

Neither sheathbill species is listed as threatened or endangered. External threats to population persistence are limited due to the remote and harsh areas occupied. Introduced nonnative vertebrates, such as feral cats and mice, prey on chicks and eggs and deplete invertebrate food sources.

Significance to humans

Sheathbills have little contact with humans. At research bases they will feed on discarded food scraps and human excrement, and abandoned stations are sometimes used as artificial nesting sites.

Family: Sheathbills Vol. 9: Birds II

Species accounts

Black-faced sheathbill

Chionis minor

TAXONOMY

Chionis minor Hartlaub, 1841, Kerguelen Islands. Four subspecies.

OTHER COMMON NAMES

English: Lesser sheathbill, paddy; French: Petit chionis; German: Schwartzgesicht-Scheidenschnabel; Spanish: Picovaina de las Kerguelin.

PHYSICAL CHARACTERISTICS

15.0–16.1 in (38–41 cm); 1.2–2.0 lb (450–760g); wingspan 29.1–31.1 in (74–79 cm). All facial features black. Subspecies exhibit slight morphological differences. At higher latitudes birds are larger in size and have smaller appendages.

DISTRIBUTION

Four subspecies with allopatric distribution among sub-



Chionis minor



antarctic island groups in Indian Ocean. *C.m. marionensis*: Marion and Prince Edward Islands; *C.m. crozettensis*: Crozet Island; *C.m. minor*: Kerguelen Island; *C.m. nasicornis*: Heard and McDonald islands.

HABITAT

Penguin and other seabird colonies, seal haul-outs, rocky and sandy intertidal zones, and nearshore meadows and bogs.

BEHAVIOR

Black-faced sheathbills are nonmigratory and pairs or single birds maintain territories throughout year. Territories generally in penguin colonies, particularly those of king penguins.

FEEDING ECOLOGY AND DIET

Omnivorous. Kleptoparasitize seabirds and feed on eggs, chicks, and excrement. At seal haul-outs scavenge dead pups and steal milk. Also forage on terrestrial and marine invertebrates and algae.

REPRODUCTIVE BIOLOGY

Monogamous. Two to three eggs laid from December to January. Incubation lasts 27–33 days. Chicks are semi-precocial and nidiculous, fledging 55–60 days after hatching. Breeding occurs in association with seabird colonies, with the exception of some birds of Kerguelen Islands. These birds tend to produce smaller clutches and fledge fewer young annually.

Breeding occurs in association with seabird colonies, with the exception of some birds of Kerguelen Islands. These birds tend to produce smaller clutches and fledge fewer young annually.

CONSERVATION STATUS

Not threatened. Population estimates for *C.m. marionensis*: 980 pairs; *C.m. crozettensis*: 2,000–3,000 pairs; *C.m. minor*: 3,000–5,000 pairs; *C.m. nasicornis*: 100–1,000 pairs.

SIGNIFICANCE TO HUMANS

Little interaction with humans. At research stations eat discarded food waste and excrement. ◆

Pale-faced sheathbill

Chionis alha

TAXONOMY

Vaginalis alba Gmelin, 1979, New Zealand. Monotypic.

OTHER COMMON NAMES

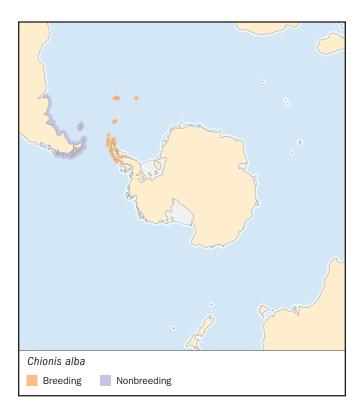
English: Greater sheathbill, snowy sheathbill, wattled sheathbill; French: Chionis blanc; German: Weißgesicht-Scheidenschnabel; Spanish: Picovaina de Malvinas.

PHYSICAL CHARACTERISTICS

13.4–16.1 in (34–41 cm); 1.2–1.7 lb (460–780 g); wingspan 29.5–31.5 in (75–80 cm). Similar to other sheathbills except that the bill sheath is greenish and caruncles are pink.

DISTRIBUTION

Breeder and year-round resident on Antarctic Peninsula and subantarctic islands of the Atlantic Ocean including South Shetland Islands, South Orkney Islands, and South Georgia Vol. 9: Birds II Family: Sheathbills



Island. Occurrence not confirmed on South Sandwich Islands but likely. Migrants observed wintering in southern regions of South America but little information exists on their exact origin.

HABITAT

Rocky and sandy coastal plains and intertidal zones; sites with seabird colonies and seal haul-outs.

BEHAVIOR

Pairs territorial during breeding season; occur in groups on wintering grounds; most birds migratory.

FEEDING ECOLOGY AND DIET

Omnivorous. Kleptoparasitize seabirds and eat eggs, chicks,

tidal zone.

biological



Chionis alba

and excrement. Also feed on algae and invertebrates of inter-

REPRODUCTIVE BIOLOGY

Monogamous with long-term pair bonds. One to three eggs laid from late November to December. Incubation period 28–32 days. Chicks are semi-precocial and nidiculous. Fledging occurs 50–60 days following hatching.

CONSERVATION STATUS

Not threatened. Population estimated at 10,000 pairs.

SIGNIFICANCE TO HUMANS

Interaction with humans limited to research stations where pale-faced sheathbills exploit discarded food and excrement. •

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Books

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Peter Martin Sanzenbacher, MS

Gulls and terns

(Laridae)

Class Aves

Order Charadriiformes

Suborder Lari Family Laridae

Thumbnail description

Gulls, skuas, and jaegers are heavy-bodied, long-winged birds with an intermediate length neck and tarsi, webbed feet, and heavy, slightly hooked bills; skimmers are slimmer with a longer, laterally compressed bill, short legs, and a forked tail; terns are smaller and slimmer than gulls; skuas have more strongly hooked bills than gulls; gulls and terns are sometimes listed as a single family, Laridae

Size

Gulls: 10–32 in (25–81 cm), 0.2–4.4 lb (100–2,000 g); terns: 8–22 in (20–56 cm), 0.1–1.7 lb (46–782 g); skimmers: 14–18 in (36–46 cm), 0.2–0.8 lb (111–374 g); skuas and jaegers: 17–24 in (43–61 cm), 0.5–4.6 lb (230–2,100 g)

Number of genera, species

Gulls: 7 genera, 51 species; terns: 10 genera, 44 species; skimmers: 1 genus, 3 species; skuas and jaegers: 2 genera, 7 species (genera treatment varies; some authors consider only 5 genera for terns)

Habitat

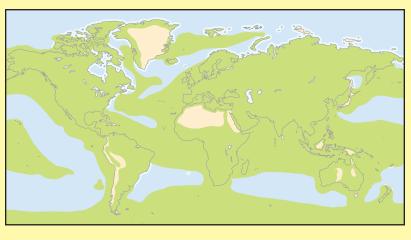
High Arctic and sub-Antarctic islands; temperate and tropical seacoasts to interior marshes and deserts; inland rivers

Conservation status

Critically Endangered: 1 species; Endangered: 1

species; Vulnerable: 6 species; Near

threatened: 9 species



Distribution

Gulls and terns have a worldwide distribution; skimmers are temperate to tropical; skuas and jaegers are temperate to polar

Evolution and systematics

Many authorities treat the skimmers (Rynchopidae) and the skuas and jaegers (Stercorariidae) as separate families, and some (including the authors of this text) separate the terns (Sternidae) as well. Here, the treatment of these groups is organized as a construction of subfamilies within the family Laridae.

In general, gulls can be divided into the large-white headed and the small dark-hooded tribes. On behavioral grounds, Moynihan treated all gulls in the genus *Larus*, but most taxonomists separate the unique gulls into their own genera, including the swallow-tailed gull (*Creagrus furcatus*) of the Galápagos, and several arctic species, among them Ross's gull (*Rhodostethia rosea*), ivory gull (*Pagophila eburnea*), kittiwakes (*Rissa*), and Sabine's gull (*Xema sabini*). Less often, two South Temperate species—the dolphin gull (*Leucophaeus scoresbii*) and the pacific gull (*Gabianus pacificus*)—are separated as well.

The main groups of terns include the crested terns (Hydroprogne, Thalasseus), black-capped terns (Sterna, Gelochelidon), marsh terns (Chlidonias), noddies (Anous, Procelsterna, Gygis), and Inca terns (Larosterna inca). The capped terns include small- and medium-sized birds in the genus Sterna. Sterna (as used here) is a relatively homogenous assemblage. The distinctive, large-bodied, crested terns (Thalasseus) are often placed in Sterna along with some unique capped terns such as the gull-billed (Gelochelidon nilotica), Caspian (Hydroprogne caspia), and large-billed (Phaetusa simplex) terns. Noddies are uniformly either all dark (black, brown, blue, and gray noddies) or all white (white tern). The Inca tern is all dark with dramatic yellow nape wattles.

The three species of skimmers, with their uniquely flattened bill, are closely related to each other and form a superspecies. Family: Gulls and terns Vol. 9: Birds II



Black tern (*Chlidonias niger*) nesting with young chick, Canada. (Photo by John Mitchell. Photo Researchers, Inc. Reproduced by permission.)

Gulls and terns are more closely related than either group is to skimmers, although some taxonomists believe that skimmers are closely related to noddies. Because of their unique bill and foraging method (skimming along the surface of creeks and channels), all species of skimmers are placed in one genus (*Rynchops*).

Skuas are believed to have derived from gulls, their closest relatives, about 10 million years ago. The three small skuas—pomarine skua (*Stercorarius pomarinus*), Arctic skua (*S. parasiticus*), and long-tailed skua (*S. longicaudus*)—called jaegers in the United States, have similar morphologies, suggesting that they split from the genus *Catharacta* early on. The three *Stercorarius* species breed in the Northern Hemisphere, while the large *Catharacta* skuas breed in the Southern and the Northern hemispheres at high latitudes. The large great skua (*C. skua*) is presumed to have invaded the Northern Hemisphere from the Southern secondarily.

Physical characteristics

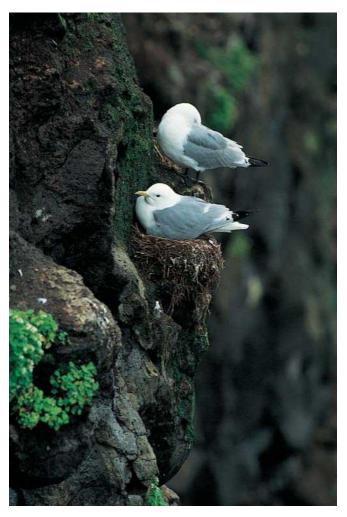
Gulls and terns are white and black, with shades in between. They are generally white below and light gray to black on top. Their white belly is believed to aid in plunge-diving for fish; it serves as camouflage against the pale sky, reducing conspicuousness to their underwater prey. Young birds are generally spotted, blotched, or streaked, affording camouflage on the various substrates they occupy, particularly during the pre-fledging period. Cryptic coloration is essential for the ground-nesting species that occur in large colonies. In all species of gulls and terns, males and females are indistinguishable on the basis of plumage. There is very little sexual size dimorphism.

Gulls are generally white bodied, with a darker mantle varying from pale silvery-gray to black (except for the all-white ivory gull). Several of the smaller species have a pale pink or cream-colored bloom on the breast early in the breeding season; this fades with time. Gulls have either a dark hood or mask or an all-white head during the breeding season.

Smaller gulls are generally either dark masked or dark headed. Generally, larger gulls are white headed, although the great black-headed gull is an exception. In almost all species the wingtips are black, the melanin pigment offering resistance to wear. Although several arctic species have white wing tips, most gulls have a complex pattern of white "windows" on the black outer primaries.

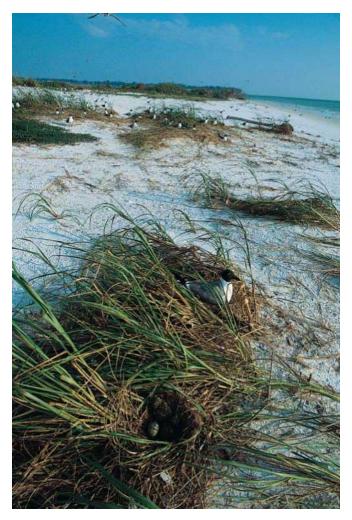
Gulls are heavy-bodied, long-winged birds with an intermediate length neck and tarsi, webbed feet, and heavy, slightly hooked bills. Gulls range in weight from 0.2–4.4 lb (100–2,000 g). All species have 12 rectrices (tail feathers), and the tail is rounded in all but a few species. Most gulls molt their flight feathers twice a year and their body feathers once a year. Adult plumage fills in at two to five years.

Most species of terns forage by plunge-diving for fish, and accordingly their bodies are streamlined. Terns have narrower, more elongated bodies than gulls and proportionately longer, more slender, and pointier wings. Their bills are generally slender and sharply pointed. Most terns are white below and gray above, with a black crown in nuptial plumage,



Black-legged kittiwakes (*Rissa tridactyla*) nesting on St. George Island, Alaska. (Photo by Rod Planck. Photo Researchers, Inc. Reproduced by permission.)

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A laughing gull (*Larus atricilla*) nesting in Pinellas National Wildlife Refuge, Florida. (Photo by Wendell Metzen. Bruce Coleman Inc. Reproduced by permission.)

although a few species are all dark or all white. Like some smaller gulls, the roseate tern has a delicate pink bloom on its breast that is very pronounced early in the season and is persistent until lost by wear. Terns exhibit no sexual differences in plumage patterns. Weight is 0.1–1.7 lb (46–782 g). Species reach adult plumage in two to six years.

Skimmers are heavy bodied with very long narrow wings and large laterally compressed or knife-like bills for skimming the water. The lower mandible is longer than the upper. Skimmers are the size of the large terns and are generally black above and pure white below, although there is a pale cream-colored tinge, particularly on the flanks, early in the nesting season. Females are about a third smaller in size and weight than males. Species range from 0.2–0.8 lb (111–374 g). The Indian skimmer (*Rynchops albicollis*) has a broad white collar, and the other two species (black skimmer, *Rynchops niger*, and African skimmer, *Rynchops flavirostris*) gain such a collar in their post-breeding molt. The bill is bright reddish-orange with a yellow tip in the African and Indian skimmers; it is red at the base with the distal half black in the black skimmer.

Young birds are a whitish-gray with darker gray splotches, making them blend in with their sand substrates.

Skuas and jaegers are similar in shape to gulls but have a heavier bill that is more strongly hooked. *Stercorarius* have both a light and a dark color phase, and the adult has two elongated central tail feathers. Females are larger than males, as is typical of terrestrial birds of prey. Juvenile skuas are generally darker than adults and have shorter, more rounded wings. Skua flight powers are more highly developed than those of gulls. This is necessary for their piracy behavior. The sharp, hooked bill and sharp claws of a skua help dismantle prey quickly.

Distribution

Gulls and terns are the most characteristic group of birds found along coastal regions in much of the world. Skimmers are restricted to coastal and riverine habitats in North and South America, Africa, and Asia. Skuas are temperate and polar. Although many species nest primarily along coastal regions on beaches or cliffs, others nest in marshes, on the tundra, or in inland lakes and rivers. The Indian skimmer breeds in southern Asia from Pakistan to Cambodia; the African skimmer breeds along rivers in Africa; the black skimmer breeds in North and South America. Gulls tend to concentrate near industrialized and heavily populated regions where there is abundant garbage, offal (fish or animal trimmings), or other sources of food. The ready availability of rubbish contributed to population explosions of several temperate species in the twentieth century. Three species of Stercorarius skuas and one Catharacta inhabit the Northern Hemisphere; three Catharacta species live in the Southern Hemisphere.

Habitat

There is wide variation in the habitat preferences of gulls, terns, skimmers, and skuas, although most feed and nest in association with water. While gulls nest and feed over a wider range of habitats, terns generally forage over water. This foraging constraint of terns somewhat limits their nesting distribution. Ground-nesting gulls and terns nest in places such as coastal or offshore islands that are inaccessible to predators. Those species that do not nest on islands nest on cliffs, in trees, or build floating nests over water, rendering them less susceptible to predators.

Colonies of nesting gulls can be found in coastal and estuarine habitats, as well as on large inland lakes. A few nest mainly on inland lakes or marshes, while two, the lava and swallow-tailed gulls (*Larus fuliginosus* and *Creagrus furcatus*, respectively) nest on remote oceanic islands, the Galápagos. Gulls nest in a wide variety of habitats, including sandy or rocky islets, beaches, marshes, river or lake sandbars, windswept sand dunes and cliffs, trees, and even buildings. Kittiwakes nest on cliff ledges or buildings, and Bonaparte's gulls (*Larus philadelphia*) normally nest in trees. Gray gulls (*Larus modestus*) uniquely breed in the barren, montane deserts of Chile, flying each day over the Andes to the Pacific Coast to obtain food for their young.

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During migration gulls fly to coastal and estuarine habitats, and in winter they generally remain along coasts or on large lakes. Outside the breeding season, gulls are found at virtually all latitudes where open water is available.

Terns also occur throughout the world and breed on all continents. They occupy a wide range of breeding habitats, including inland and coastal marshes; islands in oceans, rivers, lakes, and estuaries; sandy or rocky beaches; and on cliffs and in trees. Terns usually nest on the ground in remote or inaccessible places to avoid mammalian predators. When not breeding, most species migrate to coastal estuaries and the open ocean, although a few never leave their inland marshes and rivers.

Skimmers generally nest on sandy beaches along coasts, or on sandy riverine islands, although some black skimmers now nest on wrack (marine vegetation) in salt marshes.

The three species of *Stercorarius* breed mainly on the tundra in the Northern Hemisphere, while skuas inhabit a full range of marine habitats during the non-breeding season. The great, brown, and Chilean skuas (*Catharacta skua*, *C. lonnbergi*, and *C. chilensis*, respectively) nest on grass on islands, while the South Polar skua (*Catharacta maccormicki*) nests inland on snow-free mountain sites where there are breeding petrels and penguins that provide a source of eggs and chicks.

Behavior

Gulls, terns, skuas, and jaegers generally perform most of their foraging, breeding, and migrating during the day. The only gulls that are primarily nocturnal during the breeding season are the swallow-tailed gull of the Galápagos Islands and the gray gull that breeds in the deserts of northern Chile. Skimmers are the most nocturnal and have specialized eye structures to allow feeding and other activities at night.

Gulls and terns breed in either monospecific colonies or in monospecific groups within colonies that include other species. Some species such as Bonaparte's gull breed in very loose, small colonies with fewer than a dozen individuals scattered 0.6 mi (1 km) or more apart. Terns are more gregarious than gulls, and they generally breed, forage, and migrate in flocks that can range up to many thousands or even millions. Most gulls and terns in temperate zones breed at the same time of year, once a year, every year. Some tropical terns have shorter breeding seasons and can breed every eight months. In all species the territory is confined to the area immediately around the nest. Territory size generally increases with body size for gulls and decreases with body size for terns.

Gulls and terns of several species are very aggressive at mobbing potential predators, including human intruders. Although mobbing deters most avian predators, it is less effective against mammals. Species that nest on the ground frequently nest over water or on inaccessible islands to avoid mammalian predators.

Terns are often more active in early morning and late afternoon and sleep at midday. The daily activity patterns of coastal-nesting species of terns are often influenced by tidal cycles. At dawn terns leave their overnight roost or nest site



Herring gulls (*Larus argentatus*) fighting in New York. (Photo by Jeff Foott. Bruce Coleman Inc. Reproduced by permission.)

in search of food. These feeding flights may involve large flocks or prolonged streams of individuals and small groups. Following the breeding season terns leave the colony with their chicks and disperse for a few weeks. During this time the chicks practice plunge-diving but obtain most of their food from their parents. Following dispersal terns may gather in flocks of hundreds or thousands to migrate south; some northern species have some of the longest migration routes known.

Skimmers are unique in that they are largely nocturnal, although they do perform some activities during the day. Like gulls and terns, skimmers are highly social, either nesting in small to large conspecific colonies or within heterospecific colonies of gulls and terns. They generally forage solitarily or in small groups. Members of a pair usually face in opposite directions, increasing vigilance. When it is hot, adult and young skimmers often dig in the sand until they reach cooler temperatures.

Unlike gulls, terns, and skimmers, skuas and jaegers are not as highly social as nesting or foraging birds. Over the open ocean they frequently forage alone, although they will join foraging flocks over fish schools.

Feeding ecology and diet

Gulls have diverse foraging behavior and foraging habitats, and feed on a great variety of foods. They are important scavengers. Terns primarily plunge-dive or hover-dip for fish, and skimmers skim the surface of the water for fish; neither

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A great black-backed gull (*Larus marinus*) with a fish it pulled from the water. (Photo by Fritz Pölking. Bruce Coleman Inc. Reproduced by permission.)

scavenges. While gulls are generalist foragers, terns have a more restricted diet; many feed exclusively on fish, while others also forage on insects. Skuas are predators on other seabirds, scavengers around marine mammals, and feed also by piracy on terns, gulls, auks, and other marine birds. Terns are usually limited to feeding over water, while gulls feed on land, along the shore, and over water. Gulls, terns, and especially skuas engage in piracy. In many temperate places, terns and skimmers have been displaced by increasing gull populations that have extended their ranges into new geographical regions and new habitats.

Gulls forage in a variety of habitats, including the open ocean, the surf zone, intertidal mudflats, rivers and rivermouths, rocks and jetties, estuaries, bays, lakes, reservoirs and rivers, wet meadows and farm fields, sewage outfalls, refuse dumps, and even in the air. Many species feed along the shore on a variety of fish and invertebrates. Gulls are particularly characteristic of the intertidal zones. They also feed in a variety of human-influenced situations, including on landfills, behind farm equipment or boats, and by pan-handling from people at fast-food places or along the shore. They forage using a wide range of techniques, including walking on the ground, swimming in the water and dipping for food, and plunge-diving. They also drop hard-shelled animals from some height (33-66 ft [10-20 m]) to crack the shells and thus obtain food. In some species, individuals have specialized diets or foraging techniques when compared to their populations as a whole.

Terns generally dive for fish, either searching on their own or feeding over schools of predatory fish or marine mammals that force forage fish to the surface. Skimmers have a unique foraging method: they skim along the surface of the water, with the lower bill plowing below the water surface, for 82–328 ft (25–100 m) and then fly up, turn around, and often skim back in the other direction. Skimming is facilitated

by a laterally-compressed bill. Since theirs is a tactile method of foraging, skimmers are highly crepuscular and nocturnal. Foraging at night also reduces competition with other fisheating species that nest nearby. Skuas and jaegers use many different foraging behaviors, although they are legendary as pirates and predators on other seabirds. The larger *Catharacta* species prey on murres, larger gulls, and penguins. When food is scarce, they will feed on berries and carrion. They are opportunistic, and individual birds often specialize on a particular prey species.

Reproductive biology

Most gulls, terns, and skuas in temperate and polar zones breed at the same time of year, once a year, every year. While North American skimmers do likewise, skimmers that are dependent on the formation of sandbars and sandy islands in rivers must wait until such sandbars are exposed. Some tropical terns have shorter breeding seasons and can breed every eight months. All species are monogamous. Both members of the pair engage in territory defense, incubation of eggs, and care of the young. The eggs of most species are brown with dark splotches (skimmers have a whitish-ground color), and clutch size is two or three. Courtship feeding of the female by the male, selection of a nest site, and nest construction precede copulation. Incubation period is 20-30 days; brooding or pre-fledging phase is four to six weeks. Pairs that lose eggs or chicks may initiate a repeat nesting attempt. Following the breeding season, young gulls, skimmers, and skuas may remain with their parents for a few days or weeks. Young terns remain with their parents for weeks or months, perfecting the difficult task of plunge-diving. Some terns migrate with their parents and remain with them much of the winter.

Most gulls breed in colonies of a few to several hundred pair. Several other species, including grebes, ducks, cormorants, herons and egrets, gannets, alcids, shorebirds, and even penguins, nest within or adjacent to gull colonies. Although such species risk predation by nearby nesting gulls,



South polar skua (*Catharacta skua maccormicki*) bathing. (Photo by Joyce Photographics. Photo Researchers, Inc. Reproduced by permission.)

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Terns courtship feeding. (Illustration by Brian Cressman)

they are protected from other predators by the defending gulls. The nesting period usually lasts three to five months and occurs at the same time each year. An exception to the annual cycle is the swallow-tailed gull of the Galápagos, which breeds in all months of the year. For gulls in general, incubation averages 24–26 days. The first two chicks usually hatch within a few hours of one another, but the third chick may hatch a day or two later, giving it a distinct disadvantage when competing with siblings for food. The cryptic downy chicks are usually a pale gray or pale tan with dark splotches, and they blend in with their nest site. The chicks are brooded until they are a week to two weeks old and usually are guarded until they fledge. Unless disturbed by storms, floods, predators, or humans, gulls use their nests until the chicks can fly. The pre-fledging period in gulls ranges from four to seven weeks, depending on the size of the species. For some gulls parental care extends for a few weeks post-fledging.

In all species of gulls studied, pair-bonds are monogamous, with a high degree of mate fidelity from year to year. However, separation occurs when pairs are unable to work out incubation and brooding activities, when they are unsuccessful at raising offspring, or when one fails to return to the nest site. Paris that remain together lay earlier and raise more young than newly mated pairs. Some promiscuity occurs in gulls, with both sexes copulating with birds other than their mates.

Terns breed in traditional colony sites that may be used for several years or decades. Length of the breeding season varies (two months for arctic species, three to four months for temperate species, and three to five months for tropical species). Chicks remain with their parents for many weeks or months, slowly decreasing their dependence on their parents for food. Nesting colonies of terns range widely in size from a few widely dispersed pairs to dense colonies of a million or more. Intermediate-sized terns usually nest in colonies of tens

to hundreds of pairs, with a few colonies exceeding a thousand and some individuals nesting solitarily.

Most terns do not construct a nest but merely make a scrape in the sand, roll a few pebbles or shells around a scrape, or find a suitable cup-shaped place in the coral or rock for their eggs. Terns nesting in marshes construct a nest of vegetation on which eggs can float up if flooding occurs. White terns make no nest, but place their egg on a branch, ledge, or artificial object where it is can easily fall. Clutch size in terns varies from one to three eggs. In low food years, terns reduce the average clutch size, delay breeding, or forego breeding. Members of pairs share incubation duties and chick care, although females may incubate more often, and males may bring back more food.

Skuas and jaegers are monogamous and pair for life, are strongly territorial, and show high nest-site fidelity. Pomarine jaegers are an exception: their life cycle is partly dependent on lemming populations, and their cycle varies accordingly. Skua pairs meet on the territory and re-establish the pair bond each spring. Both sexes form the nest scrape following mutual displays and engage in incubation. Eggs are laid at two to three day intervals, and a clutch usually consists of two eggs. Hatching is asynchronous, allowing the larger and more aggressive chick to survive in poor-food years. Siblings are quite aggressive, leading to considerable wandering about the nest. Following any loss of the clutch, eggs are relaid, particularly early in the breeding season.

Conservation status

Because gulls, terns, and skimmers often breed in coastal regions, their breeding and foraging habitat is increasingly threatened as more and more people concentrate along coasts. Of the 98 species of gulls, terns, and skimmers, world popu-

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lation estimates range from a few hundred pairs (lava gulls, *Larus fuliginosus*) to several million pairs (herring gulls, *Larus argentatus*) and several tens of millions (sooty terns, *Sterna fuscata*). Chinese crested terns (*Thalasseus bernsteini*) are Critically Endangered. No skuas or jaegers are threatened or endangered, largely because of the low density of human populations at high latitudes.

Egging (collecting bird eggs for food), hunting, and exploitation for the millinery trade resulted in sharp declines of many species in the last two centuries. Human persecution has not ceased in all parts of the world. Current threats include habitat loss, habitat degradation, increased predation (often caused by cats and other animals introduced and maintained by humans), and overfishing by humans that reduces food supplies. Populations are also threatened by pollution, particularly oil spills that occur near nesting colonies or in favorite foraging grounds. Coastal populations are threatened by contaminants in runoff and from rivers. In the 1960s and 1970s egg shell thinning due to DDT was a problem, and in the 1980s in the Great Lakes of North America, organochlorines contributed to decreased hatching rates, lowered parental attendance, lower reproductive success, and congenital defects.

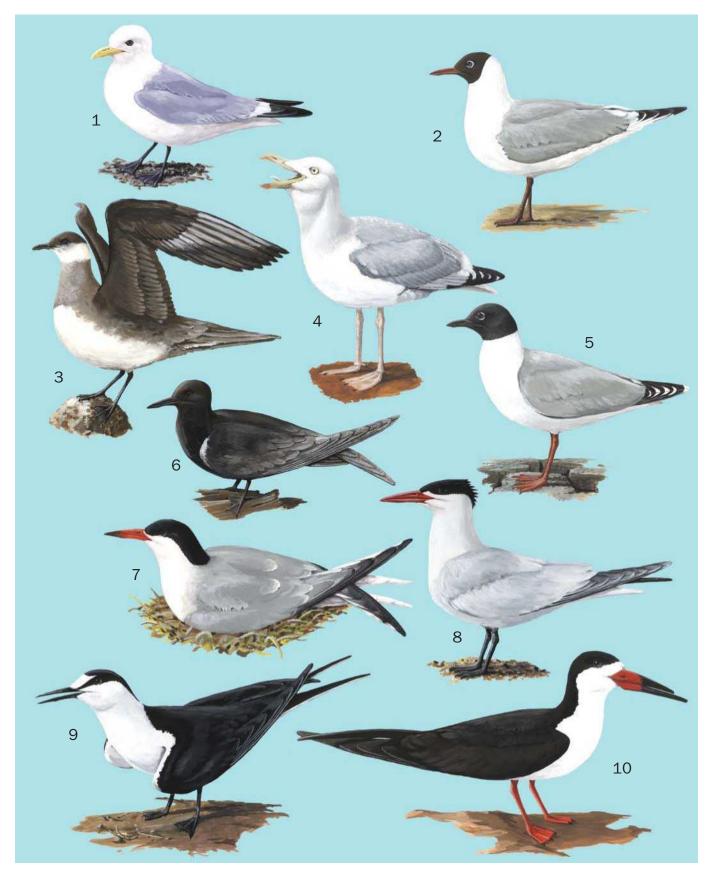
In many temperate regions, the large white-headed gulls expanded their numbers and ranges dramatically during the twentieth century, abetted by the availability of human refuse in uncontrolled garbage dumps. This new food source greatly increased the survival of juvenile gulls. The large gulls displaced smaller gulls and terns from their tra-

ditional nesting sites. They also preyed on the eggs and chicks of these species. New landfill practices and alternative refuse management has reduced this food source in many urban areas, and the populations of some gulls have begun to decline.

Conservation measures include protecting colonies from direct exploitation (hunting of adults, egging); creating suitable, secure nesting space; stabilizing ephemeral nesting habitats; constructing artificial nesting islands or platforms; removing predators (feral cats, large gulls, foxes); protecting from other predators; and reducing human disturbance at colony sites through sign-posting, fencing, or even wardening. More difficult but equally important is the protection of foraging sites and the prey base, which may involve fisheries management. For native human populations, measures must be instituted that allow sustained egging while protecting seabird reproduction.

Significance to humans

Feathers and whole bodies were used in the late 1800s for decorations on ladies' hats. In many parts of the world eggs are still collected for food, and the eggs of some species are considered an aphrodisiac. Meat may also be eaten by some peoples. Terns are used by fishers to guide them to flocks of predatory fish, and both gulls and terns were used by early mariners to indicate the presence of land. Because they mainly nest in tundra habitats, skuas and jaegers have been relatively unaffected by humans.



1. Black-legged kittiwake (*Rissa tridactyla*); 2. Common black-headed gull (*Larus ridibundus*); 3. Arctic skua (*Stercorarius parasiticus*); 4. Herring gull (*Larus argentatus*); 5. Saunder's gull (*Larus saundersi*); 6. Black tern (*Chlidonias niger*); 7. Common tern (*Sterna hirundo*); 8. Caspian tern (*Hydroprogne caspia*); 9. Sooty tern (*Sterna fuscata*); 10. Black skimmer (*Rynchops niger*). (Illustration by Brian Cressman)

Species accounts

Arctic skua

Stercorarius parasiticus

SUBFAMILY

Stercorariinae

TAXONOMY

Larus parasiticus Linnaeus, 1758, Sweden. Monotypic.

OTHER COMMON NAMES

English: Parasitic jaeger, parasitic skua, Arctic jaeger; French: Labbe parasite; German: Schmarotzerraubmöwe; Spanish: Pagalo Parisito.

PHYSICAL CHARACTERISTICS

16–18 in (41–46 cm), 0.7–1.3 lb (330–610 g); strikingly different morphs—a dark (uniform sooty brown) and light form (dark gray head, white neck and belly, dark back and wings). Some with cream underparts and hindneck, straw yellow ear coverts, sometimes a pale brown neckband.

DISTRIBUTION

Circumpolar within the band 57–80 degrees north, winters in Southern Hemisphere oceans close to coasts.

HABITAT

Breeds on tundra, moorlands, or grasslands; winters in oceans, often close to land.

BEHAVIOR

Diurnal; often associates with alcids, gulls, and terns, both while foraging and breeding.

FEEDING ECOLOGY AND DIET

Often nests close to other seabirds, where it obtains all its food from piracy or by preying on lemmings and the eggs and chicks of heterospecifics. In winter normally aggregates with other seabirds from whom it pirates.

REPRODUCTIVE BIOLOGY

Often solitary breeder or at the edge of colonies of other seabirds on tundra. Monogamous; lays one to two eggs; both sexes incubate the eggs and care for the young. Incubation period 26–27 days. Fledging period 26–30 days. Breeds at three or more years.

CONSERVATION STATUS

Not threatened; widespread but at low densities. Persecuted by humans in some regions.

SIGNIFICANCE TO HUMANS

Persecuted in some regions because of perceived damage to sheep and other livestock. •

Herring gull

Larus argentatus

SUBFAMILY

Larinae

TAXONOMY

Larus argentatus Pontoppidan, 1763, Denmark. Four subspecies are recognized.

OTHER COMMON NAMES

French: Goeland argente; German: Silbermöwe; Spanish: Gaviota Argéntea.

PHYSICAL CHARACTERISTICS

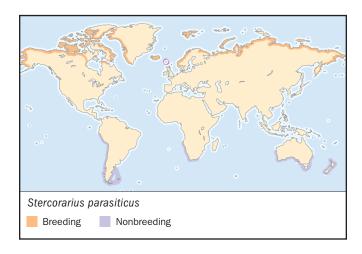
22–26 in (55–67 cm); 1.6–3.3 lb (720–1,500 g), depending upon location. Large gull with heavy body and powerful bill; white head, underparts, and tail; gray upperwings and mantle; yellow bill with red gonydeal spot during breeding; pink legs and feet. Juvenile basically gray-brown with pale spots and blackish primaries and tail. Full adult plumage takes about four years to fill in.

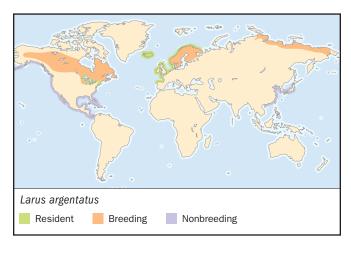
DISTRIBUTION

North America, Iceland, Faeroes, Britain to Germany and west to northeast Siberia and China.

HABITAT

Breeds along coasts and near inland lakes and reservoirs. Wide diversity of breeding habitats, including rocky cliffs and ledges,





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grassy islands, sandy beaches and islands gravel bars, salt marshes, and rarely in trees and on buildings. In non-breeding season, mainly coastal and near coasts. Also forages at garbage dumps.

BEHAVIOR

Diurnal, social, occurs mainly in flocks while foraging, and breeds in colonies (rarely solitarily), either with conspecifics or in mixed-species colonies. Mainly active in the early morning and late afternoon but can also forage at night.

FEEDING ECOLOGY AND DIET

Very variable in feeding methods, feeding habitats, and prey items. Omnivorous and highly opportunistic; diet includes fish, earthworms, crabs, other marine invertebrates, berries, carrion, and garbage.

REPRODUCTIVE BIOLOGY

Monogamous with long-term pair bonds, high nest-site fidelity. Generally lays three eggs April to early June. Nest is vegetation generally placed on the ground or a cup on bare rock. Both sexes guard territory, build the nest, incubate the eggs, and care for chicks. Incubation period 28–30 days. Brooding 40–45 days. Post-fledging care of up to 45 days. First breeding between three and seven years.

CONSERVATION STATUS

Not threatened. Increased markedly in mid-1900s due to exposed garbage dumps and offal from fishing, decreasing in some places with the closing of landfills. Declines in the Great Lakes due to pollutants.

SIGNIFICANCE TO HUMANS

Eggs eaten in some places; meat seldom eaten. Feathers collected in the late 1800s for the millinery trade. Serves a useful scavenger role. ◆

Common black-headed gull

Larus ridibundus

SUBFAMILY

Larinae

TAXONOMY

Larus ridibundus Linnaeus, 1776, England. Monotypic.

OTHER COMMON NAMES

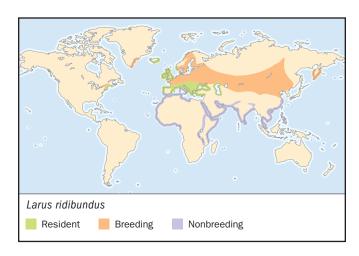
English: Black-headed gull; French: Mouette rieuse; German: Lachmöwe; Spanish: Gaviota Reidora.

PHYSICAL CHARACTERISTICS

14.5–17 in (37–43 cm); 0.4–0.7 lb (185–325 g). Small gull with a dark chocolate brown frontal hood, white eye crescents larger toward back of eye, and blood-red bill during breeding season. Gray mantle, black wings, and white neck, throat, and belly. Newly arriving birds at breeding colonies have pinkish bloom to breast that fades quickly. Nonbreeding adult has white head with dusky spot on ear coverts. Juvenile has rich buff to darker brown markings on upperparts and upperwing coverts.

DISTRIBUTION

Southern Greenland and Iceland through most of Europe to Central Asia and extreme southeast Russia and northeast China. Marginal, but possibly increasing in North America. Winters in West and East Africa, Malaysia, and Philippines.



HABITAT

Nests mainly in marshes and on sand dunes among grasses of Palearctic; always near water, chiefly inland and along coasts. Winters in marshes, rivers, and along coasts, but not pelagically (in the open sea).

BEHAVIOR

Diurnal, territorial, forages and nests in groups of conspecifics or with terns.

FEEDING ECOLOGY AND DIET

Relies mainly on aquatic and terrestrial insects, earthworms, and marine invertebrates, as well as fish. Also eats fruits and grains. Feeds by a variety of methods, including walking, swimming, seizing objects from water or land, foot paddling, or by plunge-diving for fish, often behind fishing boats.

REPRODUCTIVE BIOLOGY

Monogamous, high colony-site and nest-site fidelity, returns to site in late February to May. Most nest in small colonies of less than 100 pairs, some as large as 10,000 pairs. Usual clutch size of two to three eggs. Incubation period 22–26 days. Fledging period 32–35 days. Limited post-fledging care. Breeds when two to three years old.

CONSERVATION STATUS

Not threatened, although often displaced from traditional breeding colonies on sand habitats by herring gulls. Eggs still collected for food; some meat eaten.

SIGNIFICANCE TO HUMANS

Used extensively as a source of eggs in the past, when sections of colonies were "owned" by individuals who carefully managed them for sustained yield. Some colonies in England and elsewhere maintained for several centuries. ◆

Saunder's gull

Larus saundersi

SUBFAMILY

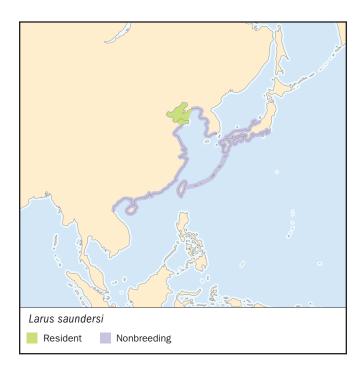
Larinae

TAXONOMY

Chroicocephalus saundersi Swinhoe, 1871, Fujian, China. Monotypic.

OTHER COMMON NAMES

English: Chinese black-headed gull; French: Mouette de Saunders; German: Saundermöwe; Spanish: Gaviota de Saunders.



PHYSICAL CHARACTERISTICS

11.4–12.6 in (29–32 cm), weight undocumented. Head and nape black, white eye crescents, neck white with pale gray upperparts, white flight feathers, tail white, underparts white, scarlet bill with dark subterminal band. Nonbreeding adult mainly white except for dark eye coverts (juvenile similar).

DISTRIBUTION

Coastal eastern China from Liaoning through Hebei and Shandong to Jiangsu. Spends the winter from South Korea to southern Japan and North Vietnam.

HABITAT

Breeds in coastal wetlands and winters along the coast or on freshwater near the coast; not pelagic.

BEHAVIOR

Diurnal; little known of its behavior.

FEEDING ECOLOGY AND DIET

Feeds mainly along coast on coastal mudflats and in coastal lagoons.

REPRODUCTIVE BIOLOGY

All known colonies are on coastal salt marshes. Normally lay three eggs, with clutches of five or six eggs suggesting femalefemale pairs.

CONSERVATION STATUS

Vulnerable; total population estimated below 5,000 and might be as low as 3,000. All seven known colonies are on lands slated for development for oil exploration, agriculture, or aquaculture.

SIGNIFICANCE TO HUMANS

This gull breeds in coastal salt marshes that are highly prized for agricultural development; therefore, their breeding is often disturbed. Villagers collect eggs for food. ◆

Black-legged kittiwake

Rissa tridactyla

SUBFAMILY

Larinae

TAXONOMY

Rissa tridactyla Linnaeus, 1758, Great Britain. Two subspecies are recognized.

OTHER COMMON NAMES

English: Kittiwake; French: Mouette tridactyle; German: Dreizehenmöwe; Spanish: Gaviota Tridactyle.

PHYSICAL CHARACTERISTICS

15–16 in (38–40 cm), 0.7–1.1 lb (305–512 g). Small white-headed gull with short legs, blue-gray mantle and upperwing coverts, outer wing slightly paler with sharply defined triangular all-black wingtip. Bill yellow and legs blackish. Nonbreeding adult has dusky gray crown band and nape, darker band across hindcrown, and dark mark around eye. Juvenile has black zigzag pattern across upperwings, black nuchal band, and black subterminal tail band.

DISTRIBUTION

R. t. tridactyla: North Atlantic from north-central Canada and northeastern United States through Greenland to western and northern Europe and on to the Taymyr Peninsula and Severnaya Zemlya; winters south to Sargasso Sea and western Africa. R. t. pollicaris: North Pacific from northeast Siberia, Kamchatka, Sea of Okhotsk and Kuril Islands through Bering Sea to Alaska; winters south to East China Sea and northwest Mexico.

HABITAT

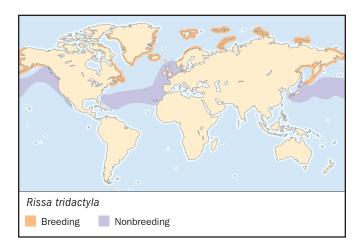
Breeds on coasts as far north as open water allows, nesting on high and steep cliffs with very narrow ledges, and on window ledges of buildings or on piers. Remains in arctic and temperate waters during winter; highly pelagic, often far from land along the continental shelf.

BEHAVIOR

Diurnal; known for its cliff-nesting habitat to avoid avian and mammalian predation.

FEEDING ECOLOGY AND DIET

Feeds mainly on marine invertebrates and fish by dipping, surface seizing, and plunge-diving. Recently exploiting garbage, foraging behind fishing vessels and at sewage outfalls. Also will



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scavenge and eat earthworms, small mammals, and even vegetation (grain, aquatic plants, potatoes).

REPRODUCTIVE BIOLOGY

May occupy colonies as early as January or February, often waiting for snow to melt from its northern nesting cliff ledges. Nests in mixed-species colonies, and monospecifically, of 10,000 kittiwakes or more. Courtship occurs on the ledges. Lays two eggs. Both sexes incubate the eggs and care for the young. Incubation 24–28 days. Fledging period 35–40 days. First breeds at four years of age.

CONSERVATION STATUS

Not globally threatened. Abundant and has generally increased and expanded into new breeding and foraging locations. Colonies can be threatened by overexploitation of eggs and by oil spills on foraging grounds. Slaughtered for the millinery trade in the late 1800s. Meat eaten by some peoples.

SIGNIFICANCE TO HUMANS

Kittiwakes are still egged in many of their northern colonies. In some places, sections of colonies are "owned" by individuals who egg them for sustained yield over many years. ◆

Caspian tern

Hydroprogne caspia

SUBFAMILY

Sterninae

TAXONOMY

Sterna caspia Pallas, 1770, Caspian Sea. Monotypic.

OTHER COMMON NAMES

French: Sterne caspienne; German: Raubseeschwalbe; Spanish: Pagaza Piquirroja.

PHYSICAL CHARACTERISTICS

19–22 in (48–56 cm), 1.3–1.7 lb (574–782 g). Largest tern with stout blood-red bill with some black at tip, slightly forked tail, black undersurface of primaries in flight. Generally black cap; white neck, throat, and belly; light gray mantle. Nonbreeding has forehead and crown whitish with dark spotting. Juvenile is gray above with brown bars, crown mainly white, tail and primaries dark gray.

DISTRIBUTION

North America, northeast Europe (Baltic), Africa, Madagascar, central and south Asia, Australia (coastal; sparse inland), New Zealand.

HABITAT

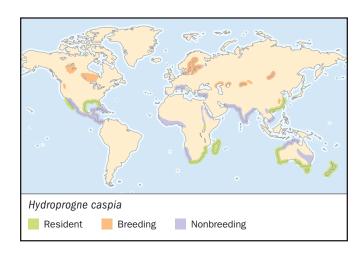
Breeds on sand, shell or rocky islands, occasionally on salt marshes. Winters along coasts and on large inland lakes and reservoirs.

BEHAVIOR

Mainly diurnal, territorial, with relatively small territories for terns.

FEEDING ECOLOGY AND DIET

Feeds mainly on small to medium-sized fish, including young salmon, sometimes the eggs and young of other birds or on carrion. Can take larger fish than most other terns. Forages on freshwater lakes, inland seas, and coastal estuaries. Feeds in small flocks but may feed solitarily and defend space.



REPRODUCTIVE BIOLOGY

Monogamous; both sexes incubate the eggs and care for the young; breeds April to June in Northern Hemisphere, September to December in Southern Hemisphere, and all year in Australia. Densely colonial in most places, may nest solitarily in Europe within colonies of other gulls and terns. Clutch is two to three eggs. Incubation period 26–28 days. Fledging period 35–45 days. Chicks form creches, and there is extended parental care beyond fledging. Most breed at three years of age.

CONSERVATION STATUS

Not threatened. Colonies vulnerable to human disturbance; may abandon. Many populations are vulnerable and have experienced declines. Listed as threatened in Canada, where some colonies are exposed to vandalism and deliberate persecution. Habitat loss due to succession threatens some colonies. Reliance on large fish exposes them to contaminants in regions such as the Great Lakes and elsewhere.

SIGNIFICANCE TO HUMANS

Feathers used for millinery trade in the late 1800s; extensive egging in some places. Viewed as a predator and pest by fish hatcheries, and harrassed or eliminated at breeding colonies in Washington State. ◆

Common tern

Sterna hirundo

SUBFAMILY

Sterninae

TAXONOMY

Sterna hirundo Linneaus, 1758, Sweden. Four subspecies usually are recognized.

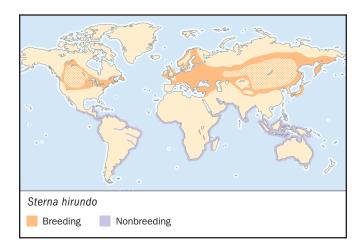
OTHER COMMON NAMES

French: Sterne pierregarin; German: Flußseeschwalbe: Spanish: Charrán Común.

PHYSICAL CHARACTERISTICS

12.6–15.4 in (32–39 cm), 0.2–0.3 lb (100–130 g). Typical small tern with black cap; white neck, throat, and belly; and gray back and upperwings. Breast sometimes suffused with pink at start of breeding cycle. Bill red with black tip in breeding season. Outer five primaries have dark outer webs. Nonbreeding

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adult has white forehead, crown black with white streaks. Juvenile is gray above barred with dark gray or brown. Black carpals distinctive in juvenal and non-breeding adult plumages.

DISTRIBUTION

Breeds in north temperate to subarctic zones in North America, Europe, and Asia, winters along coasts of Central and South America, both coasts of Africa, in coastal India and around coastal islands of Pacific (including around Australia).

HABITAT

Breeds in coastal and inland areas on sandy barrier beaches, in vegetated inter-dune areas, on rocky, sandy, or shell islands, on piers, and on seacliffs. Winters on coastal estuaries and up large rivers. Adapted to nesting on piers and other artificial sites and to feeding on jetties and piers.

BEHAVIOR

Diurnal; territorial during breeding season.

FEEDING ECOLOGY AND DIET

Feeds mainly on small fish obtained by plunge-diving. May also eat crustaceans, insects, and fish offal. Feeds in dense flocks in ocean, often with other terns and over predatory fish that force bait fish to the surface. Near colony, some common terns engage in piracy (both of conspecifics and other terns).

REPRODUCTIVE BIOLOGY

Lays mainly May through June. Usually colonial, although it may nest solitarily or in very small, loose colonies. Often nests with other terns or skimmers, frequently near vegetation for protection from weather or predators. Both sexes defend territory, incubate the eggs, and care for chicks. Lays three eggs. Incubation period 22–28 days. Fledging period 24–28 days, with extended parental care. Few breed at two years, most at three years.

CONSERVATION STATUS

Not threatened. Extensively impacted by millinery trade in late 1800s; often whole birds were used on hats. Some colonies still exposed to egging, and birds are eaten in some places. Coastal colonies vulnerable to development, and foraging birds exposed to contaminants and oil pollution. Also vulnerable to increases in predators associated with humans (dogs, cats, foxes, raccoons) and to tidal flooding.

SIGNIFICANCE TO HUMANS

Once heavily egged, and still egged by humans for food in many places. Often used by fishermen to indicate schools of predatory fish and to indicate presence of land. ◆

Sooty tern

Sterna fuscata

SUBFAMILY

Sterninae

TAXONOMY

Sterna fuscata Linnaeus, 1766, Santo Domingo. Eight subspecies are recognized.

OTHER COMMON NAMES

English: Wideawake tern; French: Sterne Fuligineuse; German: Rußseeschwalbe; Spanish: Charrán Sombrio.

PHYSICAL CHARACTERISTICS

14–18 in (36–45 cm), 0.3–0.5 lb (147–240 g). Small, distinctive black and white tern with long wings and tail. Black above, white below, white forehead with black line from bill to eye, deeply forked tail. Nonbreeding adult has variable white feather fringes above. Juvenile is blackish brown above, finely vermiculated and spotted with white, and gray-brown below.

DISTRIBUTION

Breeds on oceanic islands in subtropical to tropical regions, winters in oceans, rarely comes to land except to breed. Young spend many years at sea before reaching breeding age.

HABITAT

Breeds on oceanic and barrier islands on sand, coral, rock and artificial islands. Usually nests in open habitats, although it may nest near vegetation, particularly in the Caribbean. Winters in tropical and subtropical waters, pantropical, largely absent from cold waters.

BEHAVIOR

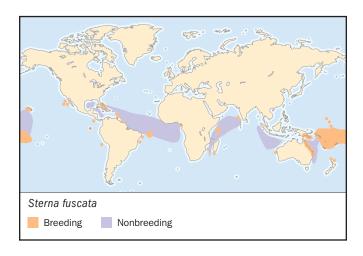
Remains at sea until breeding; does not land on water. Diurnal; territorial during the breeding season but has very small territories 20 in (50 cm) apart. Not very wary of humans and will often remain on nests with a person only 3–5 ft (0.9–1.5 m) away.

FEEDING ECOLOGY AND DIET

Feeds mainly on fish and squid; also eats crustaceans, insects, and infrequently offal. Feeds mainly by aerial dipping or contact dipping, but occasionally by plunge-diving.

REPRODUCTIVE BIOLOGY

Breeds in very large colonies, usually of 10,000 or more, often with other gulls and terns. Monogamous; both members of the pair defend nest, incubate the eggs, and care for the chicks.



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Breeds all year in some places but seasonal in others. Lays one egg (rarely two). Incubation period 26–33 days. Fledging period about 60 days (chicks grow slower than most *Sterna* chicks). Breeds at six to eight years; remains at sea from fledging until breeding.

CONSERVATION STATUS

Not threatened. One of the most abundant seabirds, with several colonies of over a million birds each. Exposed to predation, tick infestations, egging, and oil pollution, as well as low-flying jets.

SIGNIFICANCE TO HUMANS

Sooty terns are still egged in some parts of the world. ◆

Black tern

Chlidonias niger

SUBFAMILY

Sterninae

TAXONOMY

Sterna nigra Linnaeus, 1758, Sweden. Two subspecies are recognized.

OTHER COMMON NAMES

French: Guifette noire; German: Trauerseeschwalbe; Spanish: Fumarel Común.

PHYSICAL CHARACTERISTICS

9–11 in (23–28 cm), 0.1–0.2 lb (60–74 g). Small dark tern with head, neck, and breast black, becoming more slay gray on back and belly. Nonbreeding adult pale gray above, white below with dark patch on side of breast and white head. Juvenile resembles nonbreeding adult.

DISTRIBUTION

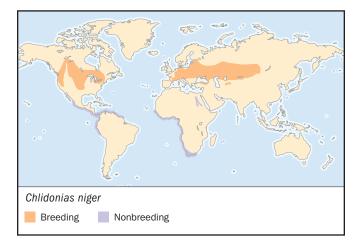
Inland temperate regions of North America, Europe, and eastern Asia.

HABITAT

Breeds on inland ponds, pools, lakes, peat bogs, and marshes; builds floating nest or nests on floating vegetation. Winters on wetlands and along coasts and estuaries.

BEHAVIOR

Diurnal; territorial.



FEEDING ECOLOGY AND DIET

Feeds on aquatic insects, small fish, snails, tadpoles, and frogs by aerial hawking, contact-dipping, and, rarely, plunge-diving.

REPRODUCTIVE BIOLOGY

Breeds May through June in North America and Europe in small colonies of 20 or fewer (rarely up to 100). Monogamous; both members of pair incubate the eggs and care for the young. Usually builds a floating nest. Lays two to three eggs. Incubation period 20–23 days. Fledging period about 25 days. Rarely mobs predators.

CONSERVATION STATUS

Not globally threatened. Many local populations vulnerable to declines due to wetland reclamation, storms, wave action, contaminants (pesticides), and lack of food due to introduced predatory fish (which eliminates the prey for the terns).

SIGNIFICANCE TO HUMANS

Often nest in small lakes or marshes slated for draining. •

Black skimmer

Rynchops niger

SUBFAMILY

Rynchopinae

TAXONOMY

Rynchops nigra Linnaeus, 1758, America. Species name changed from nigra to niger. Three subspecies usually are recognized.

OTHER COMMON NAMES

French: Bec en cisseaux noir; German: Amerikanischer Scherenschnabel; Spanish: Rayador Americano.



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PHYSICAL CHARACTERISTICS

16–18 in (41–46 cm); male is 0.7–0.8 lb (300–375 g), female is 0.5–0.7 lb (230–300 g). Females considerably smaller than males. Black cap, back of neck, back, wings, and tail; white forehead, front neck, and belly. Nonbreeding adult has white nuchal collar and somewhat browner upperparts. Juvenile resembles nonbreeding adult.

DISTRIBUTION

Coasts of United States, Mexico, and south into Mexico, and in inland rivers of central and northern South America. Winters along coasts of California south to Chile, and from Caribbean south to northeastern Argentina.

HABITAT

Breeds mainly along coasts (and inland rivers in South America) on sandy beaches, sandbars, shell banks, dredge spoil islands, and also on wrack on salt marsh islands. Winters in inland rivers, estuaries and marshes, and mudflats. along coasts.

BEHAVIOR

Notably nocturnal in breeding behavior and foraging. Mainly rests on colony site during day in breeding season. Territorial.

FEEDING ECOLOGY AND DIET

Has a unique foraging technique: forages by skimming the water with the lower mandible below the surface and the upper

mandible above water. Skims for 82–328 ft (25–100 m) before rising in the air to circle back and skim again. Feeds mainly on fish.

REPRODUCTIVE BIOLOGY

Monogamous, and both sexes engage in territorial defense, incubation of the eggs, and chick care. Breeds from mid-March to May in Northern Hemisphere. Usually nests within colonies of other terns and small gulls but sometimes nests in large conspecific colonies (Texas). Sometimes performs distraction display but normally relies on the aggressive behavior and mobbing of terns to protect its eggs and chicks. Lays two to seven eggs (usually three or four). Incubation period 21–26 days. Fledging period 28–30 days.

CONSERVATION STATUS

Not threatened. Breeding colonies often in conflict with recreationists and people living along sandy beaches. Eggs and young vulnerable to tidal flooding, human-enhanced predators (dogs, cats, foxes, raccoons), direct human disturbance, and egging. Riverine colonies in South America particularly vulnerable to flooding from heavy rains.

SIGNIFICANCE TO HUMANS

Although egging is rare in northern skimmers, much egging occurs in South America. ◆

Resources

Books

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Joanna Burger, PhD Michael Gochfeld, PhD, MD

Auks, puffins, and murres

(Alcidae)

Class Aves

Order Charadriiformes

Suborder Alcae Family Alcidae

Thumbnail description

Small to medium-sized marine diving birds with short, narrow wings, short tails, and a great variety of bill shapes and sizes

Size

6-18 in (12-45 cm): 0.17-2.4 lb (80 g-1.1 kg)

Number of genera, species

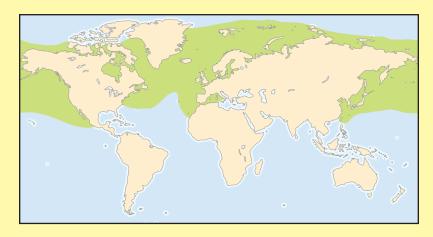
13 genera: 23 species

Habitat

Oceans, shorelines, and islands

Conservation status

Extinct: 1 species; Vulnerable: 4 species



Distribution

Circumpolar distribution in North Atlantic, North Pacific, and Arctic oceans

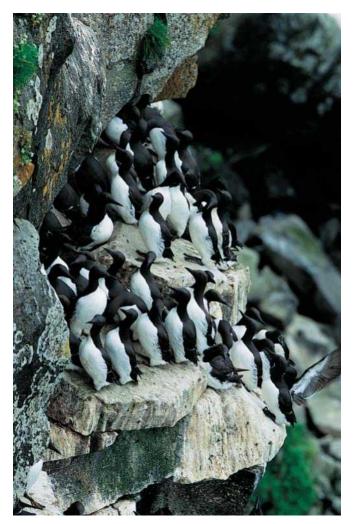
Evolution and systematics

The auks are quite different, both in appearance and behavior, from all other waders and gull-like birds. Although the alcids have been associated with several different families in the last century—penguins (Spheniscidae) and grebes (Podicipedidae) among them—current taxonomy leaves Alcidae in a separate suborder of the Charadriiformes. The predominance of species that breed in the North Pacific indicates that the family's ancestry may lie in that region, and some fossil evidence supports this premise. Existing geological information puts modern Alcidae in the North Pacific as early as six million years ago, but also suggests an unknown ancestry extending over 40 million years before that time. While the suborder is uniform enough to include all of the auks in one family, there are still some very interesting differences between species, both in physical characteristics and in life patterns. Not surprisingly, there are also some discrepancies among experts in alcid taxonomy. As of 2002, ornithologists recognize 13 genera and 22 living species, with some experts condensing the number of genera to as few at 10.

Although there are no formal subfamilies, the living auks can be divided into eight lineages. The dovekie or little auk (*Plautus alle*, also known as *Alle alle*) is the sole member of the first group. The second group numbers three species: the razorbill (*Alca torda*), the common murre (*Uria aalge*), and the thick-billed murre (*Uria lomvia*). Three species of guillemots (*Ceppbus*) form the third group, while the fourth and fifth are comprised of murrelets: *Brachyramphus* (two species) and *Synthliboramphus* (four species), respectively. The sixth group holds five species of auklet (genera *Ptychoramphus*, *Cyclor-rhynchus*, and *Aethia*) while the seventh holds a single species, the rhinoceros auklet (*Cerorhinca moncerata*). Comprising the final group are three species of puffin (*Fraturcula*). The great



A pigeon guillemot (*Cepphus columba*) with a fish it has caught. (Photo by Asa C. Thoresen/National Audubon Society. Photo Researchers, Inc. Reproduced by permission.)



Murres on guano-stained cliffs of St. Paul Island, Alaska. (Photo by Stephen J. Krasemann. Photo Researchers, Inc. Reproduced by permission.)

auk (*Pinguinus impennis*), a flightless North Atlantic seabird and the only extinct member of the Alcidae, disappeared in 1844.

Physical characteristics

The auks are well-developed for their role as marine birds; so well, in fact, that they use land only for breeding. Living species range 6–18 in (12–45 cm) in length and weigh 0.17–2.4 lb (0.4–1.1 kg). (The extinct great auk [*Pinguinus impennis*] reached over 11 lb [5 kg].) The wings are relatively narrow and short, and the tail is short. The foretoes are webbed, with no toe on the back of the foot. The plumage is generally black, white, and gray, although the *Brachyramphus* murrelets develop brown summer plumage.

Many peculiarities distinguishing this family involve adaptations to diving and underwater "flight." These include dense, firm plumage; short, narrow wings; displacement of the feet toward the back, and consequently, a rather upright posture when standing on land; great development of the sternum, the coracoids, and the furcula; strongly developed breast

muscles; large air sacs; a high blood hemoglobin content when compared to many land birds; and a high concentration of erythrocytes. While the alcids share many adaptations with their unrelated ecological counterparts in the Southern Hemisphere, the penguins (family Spheniscidae), the northern seabirds have almost all retained their flying abilities.

The larger species lose all their flight feathers at once in a molt shortly after the summer breeding season. The auks are then flightless for up to 45 days. Due to their small wings, most auks need a running, splashing start on the surface of the water to become airborne.

The bills of auks display a bewildering variety of forms and functions, unmatched by any other family and especially striking in such a small family. The razorbill was named because its long, sharp bill looks like an old–fashioned straight razor. The puffins have very deep bills that are laterally compressed. The dovekie has a very short, pointed bill that resembles that of a passerine. The guillemots have simple, straight bills. The parakeet auklet (*Aethia psittacula*) has the oddest-looking bill, with a lower half that turns up towards the tip—this feature apparently facilitates the capture of jellyfish.



This illustration from an 1850s book shows the great auk (*Pinguinus impennis*), which became extinct around 1844. (Photo by George Bernard/Science Photo Library. Photo Researchers, Inc. Reproduced by permission.)



Alcidae nesting sites. (Illustration by Patricia Ferrer)

Distribution

Exclusively in the Northern Hemisphere, throughout the Arctic, North Atlantic, and North Pacific.

Habitat

Alcids live almost exclusively on the surface of colder ocean waters, with breeding on shorelines, seaside cliffs, islands, and (in a few species) coastal forests.

Behavior

Their flight is fast and boisterous, although rather clumsy in appearance. The relatively small wings of most species require fast wingbeats, and most auks need some distance to become airborne. Auks are most often seen flying low over the surface of the ocean. Auks are superb swimmers and divers: studies using depth recorders attached to the birds have indicated that some species may reach depths of 600 ft (183 m). Under water, auks propel themselves with powerful beats of their half-open wings, while the legs are stretched back with the webbed feet functioning as a rudder.

Feeding ecology and diet

Auks draw their sustenance exclusively from the ocean. The larger species, such as murres, razorbills, guillemots, and puffins, prefer small fish that live in great numbers in the open ocean or on the ocean floor; they also feed, to a lesser degree, on small cephalopods, larger crustaceans, and other invertebrates. The smaller species, such as the dovekie, feed mainly on crustaceans, mollusks, chaetopods, and various other marine invertebrates. Many species fly well out over the ocean in search of food. Marbled murrelets (*Brachyramphus marmoratus*),



Tufted puffins (Lunda cirrhata) interact during their breeding season on St. Paul Island, Alaska. (Photo by Yva Momatuik & John Eastcott. Photo Researchers, Inc. Reproduced by permission.)

which nest further from the water than other auks, will commonly fly 50 mi (80 km) from their nesting areas to forage.

Auks do not skim food from the surface of the water, nor do they dive into the sea directly from the air. Instead, they rest on the surface, then poke their heads under and tip forward, thrusting their bodies down and driving themselves forward with their wings as they swim in search of prey. This technique is called "pursuit diving."

Reproductive biology

All auks are monogamous, although pairs do not always stay together for life. Most species also show a strong inclination to return annually to the same nesting site.

Eight species of alcids copulate only at sea, a somewhat mysterious breeding strategy. Theories include avoidance of predators, avoidance of interfering males of their own species, and the possibility that females use this situation to select the more fit males.

Both sexes share in incubation and rearing of the young. Most species lay only one egg, the weight of which is roughly one tenth to one fifth that of the female. The newly hatched chicks, which are able to see, are covered with a dense downy coat. In a strategy unique to the Alcidae, young birds of several species leave the nest two to three weeks after hatching and venture out to live on the sea with their male parent until they become independent. The plumage of the juveniles

resembles the winter plumage of the adults in color. Males and females have the same breeding plumage.

Conservation status

While the great auk is extinct, none of the extant species is considered Endangered. Several species, however, are classed as Vulnerable, with Xantus's murrelet (Synthliboramphus hypoleucus) and the marbled murrelet of particular concern. Xantus's murrelet, whose breeding grounds are restricted to the Baja peninsula and coastal islands off southern California, is threatened by introduced predators such as cats and rats as well as habitat degradation. The marbled murrelet population in the contiguous United States as of 1999 (perhaps 17,000 pairs) was estimated to be declining at about five percent per year due to habitat loss, and the U.S. Fish and Wildlife Service lists the species as Threatened. Human predation is no longer a critical threat to alcids, but oil spills and other ecological threats are cause for concern. Thousands of auks drown every year in fishing nets.

Significance to humans

The auks no longer support the kind of industry that flourished on the bodies of great auks, but significant hunting still takes place. Several species are hunted for subsistence in Greenland, Canada, and Alaska, and large hunts for two species are permitted in Newfoundland.



1. Common murre (*Uria aalge*); 2. Black guillemot (*Cepphus grylle*); 3. Great auk (*Pinguinus impennis*); 4. Marbled murrelet (*Brachyramphus marmoratus*); 5. Puffin (*Fratercula arctica*); 6. Thick-billed murre (*Uria lomvia*); 7. Razorbill (*Alca torda*); 8. Dovekie (*Plautus alle*). (Illustration by Patricia Ferrer)

Species accounts

Common murre

Uria aalge

TAXONOMY

Uria aalge Pontoppidan, 1763, Iceland. Five subspecies.

OTHER COMMON NAMES

English: Atlantic murre, common guillemot, thin-billed murre; French: Guillemot marmette; German: Trottellumme; Spanish: Arao Común.

PHYSICAL CHARACTERISTICS

15–17 in (38–43 cm); 33.5–37 oz (950–1,050 g). Black to brownish head and upperparts; white underparts. Black bill is long, slender, and pointed; mouth lining is yellow.

DISTRIBUTION

North American coast from New England northward to Labrador, central California to northern Alaska, and from Siberia as far south as Japan and Korea.

HABITAT

Rocky coastlines and adjoining seas.

BEHAVIOR

Pelagic. Rarely comes ashore except to breed. Common murres are fast fliers and sometimes travel in large flocks. Their most common vocalization has been described as purring.

FEEDING ECOLOGY AND DIET

Primarily fish; less commonly consumes a variety of marine invertebrates.

REPRODUCTIVE BIOLOGY

Breeds in large colonies, often with other species. Courtship and copulation take place on land. A single egg is laid on bare rock. The egg is marked with a distinct pattern so the parents can recognize it; a common murre will find and retrieve its own egg if the egg rolls away. Incubation takes 32–35 days. The chick is fledged at 20–22 days after hatching and follows the male parent out to sea to complete the period of parental care

CONSERVATION STATUS

Widespread and numerous. Concern in some areas due to hunting and habitat degradation.

SIGNIFICANCE TO HUMANS

The common murre is hunted legally in large numbers in Newfoundland. ◆

Thick-billed murre

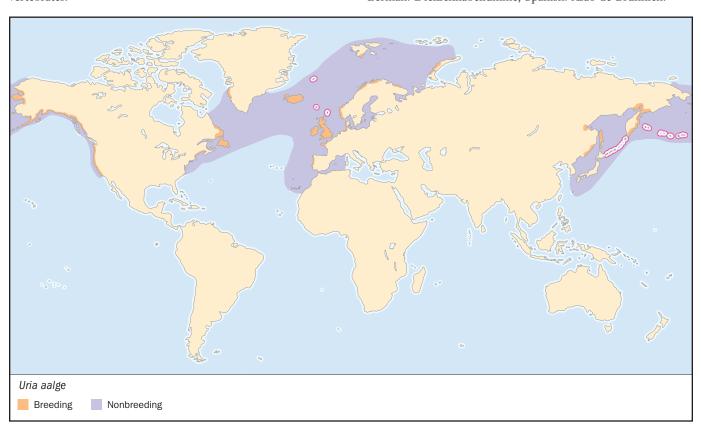
Uria lomvia

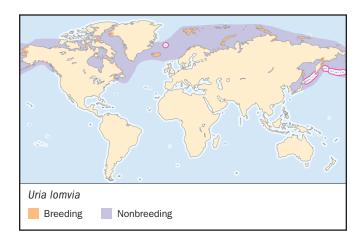
TAXONOMY

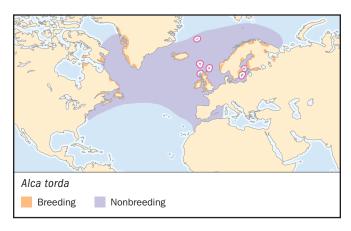
Uria lomvia Linnaeus, 1758, Greenland. Four subspecies.

OTHER COMMON NAMES

English: Brunnich's guillemot; French: Guillemot de Brünnich; German: Dickschnabellumme; Spanish: Asao de Brunnich.







PHYSICAL CHARACTERISTICS

15–17 in (38–43 cm); 28–38 oz (800–1,080 g). Largest living alcid. Blackish head and upperparts; whitish underparts. Black bill is shorter and heavier than *U. aalge* and has a whitish line along the edge of the upper mandible near the gape.

DISTRIBUTION

North American coast from Maine to Baffin Island and the southern half of the Greenland coasts. Also coastlines in northwestern Canada, most of Alaska, the Aleutians, Kamchatka, and northern Japan, plus Arctic islands and the Arctic coast of Norway.

HABITAT

Rocky cliffs and adjoining seas.

BEHAVIOR

Generally a more oceanic bird than the common murre. Their ranges are similar, although the thick-billed tends to stay further north. At sea, they are found in small groups or alone, but they congregate in thousands at established breeding cliff sites.

FEEDING ECOLOGY AND DIET

Fish, especially Arctic cod (*Boreogadus saida*), comprise most of the diet. A variety of crustaceans are also eaten.

REPRODUCTIVE BIOLOGY

Thick-bills brood in huge rookeries. Brooding is done on bare rock, often on narrow ledges of cliffs, with incubation lasting an average of 32 days. Thick-bills are one of several alcid species in which a replacement egg may be laid if the first is broken or fails to hatch. When the chick is fledged, it follows the male parent out to sea.

CONSERVATION STATUS

Widespread and numerous: at least two million breeding pairs in Iceland alone. No special concern.

SIGNIFICANCE TO HUMANS

The thick-billed murre is hunted legally in large numbers in Newfoundland. $lack \bullet$

Razorbill

Alca torda

TAXONOMY

Alca torda Linnaeus, 1758, Baltic Sea. Two subspecies.

OTHER COMMON NAMES

English: Razor-billed auk; French: Petit Pingouin; German: Tordalk; Spanish: Alca Común.

PHYSICAL CHARACTERISTICS

14.5–15.5 in (37–40 cm); 18–32 oz (515–900 g). Blackish head and upperparts; whitish underparts. Black bill is larger than *Uria* and appears rectangular; broken transverse white line across both mandibles and another white line extending from base of culmen to eye.

DISTRIBUTION

Winters in the open sea on the North Atlantic. Breeds on the both coastlines of the North Atlantic.

HABITAT

Rocky coastlines and adjoining seas.

BEHAVIOR

The adults are silent at sea, while the juveniles give a whistling call. At the breeding sites, the adults are very vocal. When members of mated pairs approach each other, they will bow, then growl, and then put on a show of "billing," in which the head is tossed about, the bill swung all around, and the mandibles clicked together.

FEEDING ECOLOGY AND DIET

More than 90% of a razorbill's diet is fish, although the bird will ingest some invertebrates.

REPRODUCTIVE BIOLOGY

Razorbills most often breed in breed in small groups, usually together with murres. The single egg is white or light cream-colored with brownish spots and streaks. Young razorbills are born after about 35 days and get their second down coat 17–22 days after that, when they have reached a quarter of the adult weight. At that time, they leave the nest to go to sea with their male parents.

CONSERVATION STATUS

Some razorbills are killed during legal hunts for murres. Razorbills are the least numerous of North American Atlantic auks, and the population declined significantly in the 1960s and 1970s. However, the species is not in imminent danger.

SIGNIFICANCE TO HUMANS

None known. ◆

Black guillemot

Cepphus grylle

TAXONOMY

Cepphus grille Linnaeus, 1758, Baltic Sea. Five subspecies.

OTHER COMMON NAMES

English: Tystie; French: Guillemot à miroir; German: Gryllteiste; Spanish: Arao Aliblanco.

PHYSICAL CHARACTERISTICS

11.8–13 in (30–33 cm); 1.6–3.9 oz (325–550 g). Overall black plumage except for white wing patches and underwing-coverts. Black bill is slender and pointed; mouth lining, legs, and feet are red.

DISTRIBUTION

Circumpolar distribution, with breeding grounds from the Gulf of Maine intermittently spaced across the top of North America to Alaska and across the Arctic coast of Asia. Winters in the North Atlantic, venturing as far south as France, although they generally stay closer to shore than many auks.

HABITAT

Rocky shores, including islands, and adjoining seas.

BEHAVIOR

Strongly territorial concerning nesting sites, to which they return year after year. Rarely nests in mixed colonies with other species. Engages in courtship displays involving bowing, whistling, etc. Uses a variety of calls, mostly high-pitched, while at the breeding grounds. Swimming in line, apparently for cooperative feeding, has been observed.

FEEDING ECOLOGY AND DIET

Primarily eats fish, but will take many kinds of invertebrates, including sponges and barnacles.

REPRODUCTIVE BIOLOGY

Normally broods in small groups, and sites may be either very close to the surf or 1.2–1.9 mi (2–3 km) off. Will use artificial cover, such as buildings, for nesting sites. Young leave the nest after 35–39 days. Clutch size is usually two eggs, deposited under rocks or in deep crevices in cliffs.

CONSERVATION STATUS

Population appears stable, but local threats arise from oil spills and commercial fishing.

SIGNIFICANCE TO HUMANS

Some subsistence hunting takes place, but greatly reduced from the level of a century ago. ◆

Puffin

Fratercula arctica

TAXONOMY

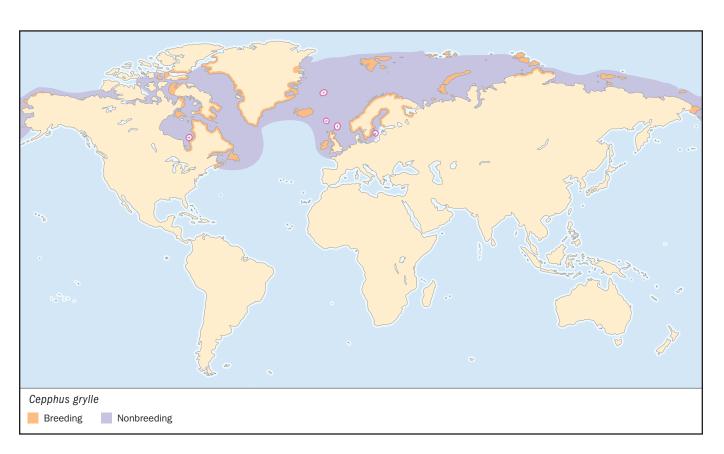
Fratercula arctica Linnaeus, 1758, Norway. Three subspecies.

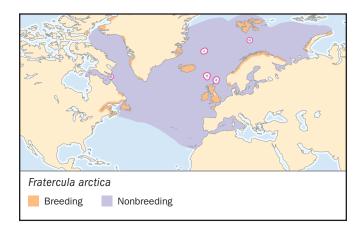
OTHER COMMON NAMES

English: Atlantic puffin; French: Macareux moine; German: Papageitaucher; Spanish: Frailecillo Atlántico.

PHYSICAL CHARACTERISTICS

11–14.6 in (28–37 cm); 10.6–21.1 oz (300–600 g). Distinctive large, triangular, mostly yellow and orange bill with bluish gray base; yellowish mouth and tongue. White to grayish face, black





band from forehead to nape, grayish chin. Mostly black upperparts; snowy white underparts; orange to yellowish orange legs and feet.

DISTRIBUTION

The puffin winters at sea in the North Atlantic and breeds on the American and European coasts. Range includes the Baltic Sea and eastern Mediterranean.

HABITAT

Marine areas near rocky coasts and islands with suitable conditions for digging burrows.

BEHAVIOR

A strong flier, the puffin is rarely seen near land except during the breeding season. The adults give moaning or bellowing calls. While at sea, puffins have been known to gather in groups with murres and razorbills, although the puffins tend to stay on the periphery of any mixed gatherings.

FEEDING ECOLOGY AND DIET

Puffins eat mainly fish. The species is known for its habit of packing dozens of small fish crossways in its bill to bring back to its young.

REPRODUCTIVE BIOLOGY

Couples engage in mating displays in which they tap their prominent bills together. Mating takes place at sea. Puffins nest at the far end of long passageways, which they dig with their beaks and talons into the loose earth covering the rocks. Breeding places may be on crags close to the sea, or several hundred meters removed from the coast. The single egg shell is white and has almost invisible dots. The nestling wears a "furry" down that is dense and soft. Fledglings leave the nest after 36–47 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

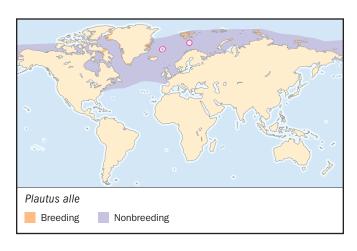
None known. ◆

Dovekie

Plautus alle

TAXONOMY

Alle alle Linnaeus, 1758, Scotland. Two subspecies.



OTHER COMMON NAMES

English: Little auk; French: Mergule nain; German: Krabbentaucher; Spanish: Mérgulo Atlántico.

PHYSICAL CHARACTERISTICS

7–8 in (17–20 cm); 4.6–6.7 oz (130–190 g). Small, chubby bird with black head and neck, black upperparts, and white underparts. Short black bill and blackish gray legs and feet.

DISTRIBUTION

The breeding territory includes all North Atlantic and Arctic coastlines. Outside the breeding season, dovekies are scattered far over the northern Atlantic; some winter amid the drifting ice.

HABITAT

Rocky coastlines and adjoining seas.

BEHAVIOR

Silent while at sea as an adult, although the young birds have a high-pitched, peeping call. Adults give vent to a short, high-pitched trill while at breeding grounds.

FEEDING ECOLOGY AND DIET

Primarily small invertebrates and plankton.

REPRODUCTIVE BIOLOGY

Greenland and Spitsbergen have colonies of dovekies consisting of thousands, possibly numbering in the hundreds of thousands. Nesting occurs within stretches of shingle or in rock clefts near the ocean, as well as at distances of from four to eight kilometers inland on mountain slopes. The single chick stays in the nest for approximately a month, after which it reaches adult size.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

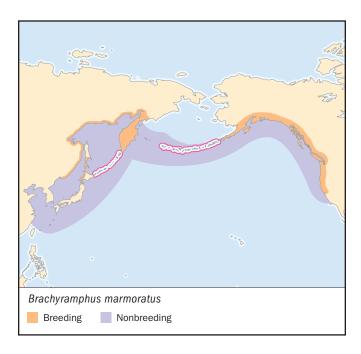
None known. ◆

Marbled murrelet

Brachyramphus marmoratus

TAXONOMY

Brachyramphus marmoratus Gmelin, 1789, Alaska. Two subspecies.



OTHER COMMON NAMES

English: Atlantic murre, long-billed murrelet; French: Guillemot marbré; German: Marmelalk; Spanish: Mérgulo Jaspeado.

PHYSICAL CHARACTERISTICS

9.5–10.5 in (24–27 cm); 6.7–9.5 oz (220–270 g). Dark brown crown and upperparts, back feathers tipped in rusty brown; mottled brown and white underparts. Black bill is slender and pointed; flesh-colored legs and feet with dark webs.

DISTRIBUTION

Pacific coast of North America from the Bering Sea to central California, and in similar latitudes on the western side of the Bering Strait.

HABITAT

Nests in coastal forest, preferring large old-growth areas offering heavy cover, or on rocky ground in the northernmost sections of its range.

BEHAVIOR

Marbled murrelets spend most of their time at sea, although individuals are occasionally still seen in the forests. Non-breeding birds spend the nights a few miles from shore, moving in closer during the day to feed. Mated pairs are often sighted together at sea throughout the year. Never seen in large flocks.

FEEDING ECOLOGY AND DIET

Fish and marine invertebrates.

REPRODUCTIVE BIOLOGY

The murrelets build small, cup-shaped nests, flying to and from them at dawn and dusk. They nest solitarily or, in some areas, in small, loose aggregations. Accordingly, studies of nesting behavior remain limited. Egg is incubated for 27–30 days. After hatching, the chick is fledged and on its own after 27–40 days.

CONSERVATION STATUS

Not threatened. There is some concern, especially in the Pacific Northwest, about the effects of increasing nest predation, the reduction in old-forest habitat, and the effects of commercial fishing nets.

SIGNIFICANCE TO HUMANS

None known. ◆

Great auk

Pinguinus impennis

TAXONOMY

Pinguinus impennis. Formerly known as Aka impennis Linnaeus, 1758.

OTHER COMMON NAMES

English: Garefowl, penguin (the original bird to be so named); French: Grand pingouin; German: Riesenalk; Spanish: Alca Gigante.

PHYSICAL CHARACTERISTICS

30.5 in (78 cm); 11 lb (5 kg).

DISTRIBUTION

The great auk ranged across the North Atlantic, south of the Arctic Circle as far as New England and the British Isles.

HABITAT

Rocky coastlines and adjoining seas. Restricted to a few locations where the nesting sites could be reached without flying.

BEHAVIOR

The great auk was the most dependent of the alcids on the ocean because, unlike its relatives, it had lost the power of flight. Because most observations were made during hunts, little is known about the species' normal behavior. We do know that great auks spent the winters at sea.

FEEDING ECOLOGY AND DIET

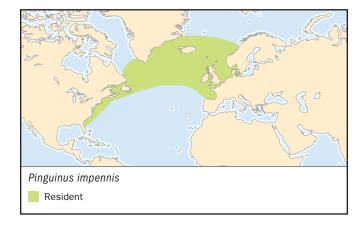
Presumed to have fed mainly on fish.

REPRODUCTIVE BIOLOGY

Bred in enormous rookeries on a handful of islands: St. Kilda, the Orkneys, islands off Newfoundland, and islands off the southern coast of Iceland. A single pear-shaped egg, which weighed approximately 14 oz (400 g), was laid on rock. Each egg carried a unique pattern of spots and blotches, which probably aided the parents in identifying their own egg.

CONSERVATION STATUS

Extinct. By the beginning of the nineteenth century, 300 years of reckless human predation of the easily-captured auks seri-



ously diminished their numbers. Hunting and egg-collecting continued at an unsustainable rate, exacerbated by a volcanic eruption in 1830 which destroyed one of the bird's last breeding grounds. In 1844, the last two auks known to exist were killed on the island of Eldey, off the southwest coast of Iceland, and their egg was collected and sold.

SIGNIFICANCE TO HUMANS

When the great auk was discovered by mariners, it was looked upon as an excellent source of provisions. The easily-caught birds soon became the focus of an unrestrained industry, in which their feathers were plucked and their bodies were boiled alive for their high oil content. This havoc continued until it became uneconomical due to the lack of auks. •

Resources

Books

Fuller, E. The Great Auk. New York: Harry N. Abrams, 1999.

Gaston, A. J., and I. L. Jones. *Bird Families of the World: The Auks (Alcidae)*. Oxford: Oxford University Press, 1998.

Elphick, Chris, John B. Dunning, Jr., and David Allen Sibley. *The Sibley Guide to Bird Life and Behavior*. New York: Alfred A. Knopf, 2001.

Periodicals

DeSanto, Toni L., and S. Kim Nelson. "Comparative Reproductive Ecology of the Auks (Family Alcidae) with Emphasis on the Marbled Murrelet." *USDA Forest Service General Technical Report* 152 (1995): 33–47.

Friesen, V. L., A. J. Baker, and J. F. Piatt. "Phylogenetic Relationships Within the Alcidae (Chadriiformes: Aves) Inferred from Total Molecular Evidence." Molecular Biology and Evolution 13, 2 (1996): 359–367.

Hipfner, J. Mark. "Timing of Nest Departure in the Thickbilled Murre and Razorbill: Tests of Ydenberg's Model." *Ecology* 80 (1999): 587–596.

Hunter, F. M., and I. L. Jones. "The Frequency and Function of Aquatic Courtship and Copulation in Least, Crested, Whiskered, and Parakeet Auklets." *The Condor.* 101 (1999): 518–528.

Other

IUCN-The World Conservation Union. "Alcidae." The 2000 IUCN Red List of Threatened Species. http://www.redlist.org>

Matthew A. Bille Cherie McCollough

Pterocliformes Sandgrouse (Pteroclididae)

Class Aves

Order Pterocliformes

Family Pteroclidae

Number of families: 1

Thumbnail description

Medium-sized, pigeon-like birds, with a stocky body, small head, short bill and legs, and camouflaged plumage

Size

9.8-19 in (25-48 cm); 0.7-1.2 lb (130-550 g)

Number of genera, species

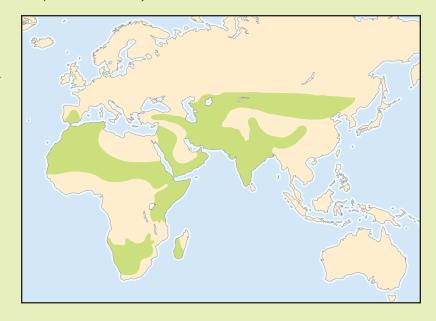
2 genera; 16 species

Habitat

Desert, semi-desert, open steppe, and dry savanna, always within flying range of drinking

Conservation status

Not threatened



Distribution

Africa, Madagascar, Iberian and Arabian peninsulas, Middle East to Indian subcontinent, China, and Mongolia

Evolution and systematics

Sandgrouse are known as fossils of the genus Archaeoganga from the Upper Eocene of France, some 35 million years ago, one species of which is estimated to have been about three times the size of the largest living sandgrouse species, weighing perhaps 3 lb (nearly 1.5 kg). Other fossil genera occur into the Lower Miocene, about 20 million years ago. The general consensus, based on morphological, behavioral, and chromosomal evidence, is that sandgrouse are derived from the shorebirds (order Charadriiformes) and are sometimes grouped in that order under the suborder Pterocli. However, even the earliest fossil sandgrouse show marked divergence from the ancestral shorebird. They are no longer regarded as closely related to doves and pigeons (order Columbiformes), with which they were placed for many years.

Sandgrouse probably evolved in the arid zone of North Africa and the Middle East, spreading to southern Africa and central Asia. They are more closely associated with the Afro-Asian deserts than any other family of birds. The 14 species of the genus Pterocles retain a rudimentary hind toe; this toe has been lost in the two species of Syrrhaptes that are likely to be more recent offshoots of the ancestral sandgrouse stock. Four species of sandgrouse (Lichtenstein's, double-banded, four-banded, and painted) share the habit of crepuscular or nocturnal drinking and may constitute a separate genus (or at least a subgenus) Nyctiperdix on the basis of this and the possession of a strongly barred abdomen in both sexes.

Physical characteristics

Sandgrouse are stocky terrestrial birds with dense, beautifully camouflaged plumage. They are covered with an underdown even between the main feather tracts. Their lower legs are feathered in front in the genus Pterocles, whereas the whole lower leg and the toes are feathered in Syrrhaptes, possibly as an adaptation to cold climates. Despite their short legs, sandgrouse walk and run well. The nostrils of all species are covered with fine feathers. Their wings are long and pointed, giving them exceptional powers of flight. The sexes differ markedly in plumage pattern, the females being more cryptically colored than the males.

Distribution

Sandgrouse occur from South Africa and Namibia through the drier parts of East Africa to North Africa, Spain, the Arabian peninsula, central Asia, Mongolia, and India.

Habitat

Desert, semi-desert, dry savanna, and short-grass steppe.

Behavior

Sandgrouse are the most terrestrial of birds, feeding, roosting, and nesting on the ground. They fly to water almost every day, covering up to about 75 mi (120 km) round-trip,



A male Burchell's sandgrouse (*Pterocles burchelli*) wets his front feathers to take drinking water to his chicks. (Photo by Nigel J. Dennis. Photo Researchers, Inc. Reproduced by permission.)

depending on the location of feeding areas. All species are gregarious, except when breeding: flocks may number hundreds or thousands of birds. They call to each other in flight and sometimes when flocking on the ground.

Adaptations of sandgrouse to arid zones include: seeking shade in hot conditions, flying and feeding in the cooler hours

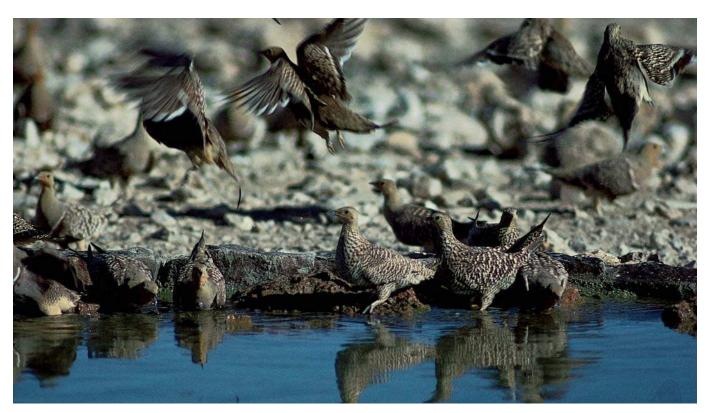
of the day, insulation against overheating by dense plumage, and huddling together under extreme conditions. Some species of sandgrouse also may limit their frequency of drinking to conserve energy, though this may not be possible in hot conditions.

Feeding ecology and diet

Sandgrouse feed almost exclusively on small seeds picked up from the surface of the soil; the birds also use their bills to flick loose sand sideways to uncover buried seed. Because of the dry diet, they must drink often, especially in hot weather when drinking may occur daily. Most species drink an hour or two after sunrise, but some drink only at dusk or at night. Sandgrouse drink by dipping the bill, sucking a draft of water, and raising the head to swallow, taking several drafts at each bout of drinking.

Reproductive biology

Sandgrouse are monogamous, solitary nesters, though nests may be fairly close together, giving the appearance of a loose colony. The nest is a shallow scrape, often under a plant, but also in the open; it is usually lined with fragments of soil, stone, or plants. Clutches usually contain three rather elongated, spotted eggs. Each clutch is incubated by the female during the day and by the male at night, at least in those species which have been studied. The chicks hatch after about 21–31 days, depending on the species. They feed themselves but are given water by the male parent, which soaks his belly



Namaqua sandgrouse (*Pterocles namaqua*) at a watering hole in the Namib Desert in Namibia. (Photo by M.P. Kahl. Photo Researchers, Inc. Reproduced by permission.)



Chestnut-bellied sandgrouse (*Pterocles exustus*) in flight over Samburu Game Reserve, Kenya. (Photo by Peter Davey. Bruce Coleman Inc. Reproduced by permission.)

feathers at a drinking place and flies back to the chicks, which take the water from his plumage. This method of providing the chicks with water is unique among birds. Sandgrouse young fly at about four to five weeks, after which they accompany their parents on flights to the watering hole.

Conservation status

Sandgrouse are abundant throughout their distribution and are not in need of special conservation measures. How-

ever, where they are hunted for sport, the shooting season needs to be regulated to avoid overexploitation.

Significance to humans

In many parts of their range, sandgrouse are considered good eating and are hunted at watering points. Because most species inhabit remote areas, they generally suffer little human disturbance away from their drinking places.



1. Male chestnut-bellied sandgrouse (*Pterocles exustus*); 2. Male black-bellied sandgrouse (*Pterocles orientalis*); 3. Male Lichtenstein's sandgrouse (*Pterocles lichtensteinii*); 4. Male Namaqua sandgrouse (*Pterocles namaqua*); 5. Male spotted sandgrouse (*Pterocles senegallus*); 6. Male Pallas's sandgrouse (*Syrrhaptes paradoxus*). (Illustration by Emily Damstra)

Species accounts

Namaqua sandgrouse

Pterocles namaqua

TAXONOMY

Tetrao namaqua Gmelin, 1789, Namaqualand, South Africa. Monotypic.

OTHER COMMON NAMES

French: Ganga Namaqua, ganga de Namaland; German: Namaflughuhn; Spanish: Ganga Namaqua.

PHYSICAL CHARACTERISTICS

9.4–11 in (24–28 cm); 5–8.5 oz (143–240 g). Medium-sized; tail wedge-shaped; central, elongated tail feathers. Male has yellowish olive head, breast and mantle; double breast-band white, bordered below with maroon; belly and back brown; back spotted pearl-gray. Female mostly barred brown and buff; streaked brown and buff on head and neck.

DISTRIBUTION

Southern Africa from extreme southwestern Angola through Namibia to Botswana and western South Africa.

HABITAT

Open desert and semi-desert, usually stony with low shrubs; sandy desert with scattered grass tufts.

BEHAVIOR

Gregarious, except when nesting. Flocks may number several hundred or thousands of birds at watering points. Usually drinks in the morning up to three hours after sunrise; some birds may drink only every three to five days. Feeding grounds



may be 35 mi (60 km) from nearest palatable drinking water. Flies up to 45 mi (70 km) per hour; birds in flock keep contact with an intermittent, three-note call.

FEEDING ECOLOGY AND DIET

Feeds mainly on small, dry seeds picked up from surface of soil. Drinking water needed to augment lack of water in food and for evaporative cooling in hot weather.

REPRODUCTIVE BIOLOGY

Nests solitarily on open ground, which is usually stony and shrubby. Nest is shallow scrape lined with some pebbles and bits of dry vegetation. Clutch of three well camouflaged eggs incubated by female during day and by male at night for about three weeks. Chicks leave nest within 24 hours of hatching; can fly at about a month. Chicks dependent on male parent for water for two to three weeks until able to fly to water.

CONSERVATION STATUS

Common to abundant throughout limited range; not threatened.

SIGNIFICANCE TO HUMANS

Important gamebird, hunted for food and sport. Presently under intensive study as subject for game management. ◆

Spotted sandgrouse

Pterocles senegallus

TAXONOMY

Tetrao senegallus Linnaeus, 1771, "Senegal" = Algeria. Monotypic.

OTHER COMMON NAMES

English: Saharan sandgrouse; French: Ganga tacheté; German: Wüstenflughuhn; Spanish: Ganga Moteada.

PHYSICAL CHARACTERISTICS

About 14 in (36 cm); 8.8–12 oz (250–340 g). Both sexes mainly sandy, pinkish, or a rust-colored buff with yellowish orange throat. Female spotted blackish brown above and below; male mostly plain but lightly mottled brownish on wings, looking fairly uniform in the field. Both sexes have black center of belly and elongated, central tail feathers.

DISTRIBUTION

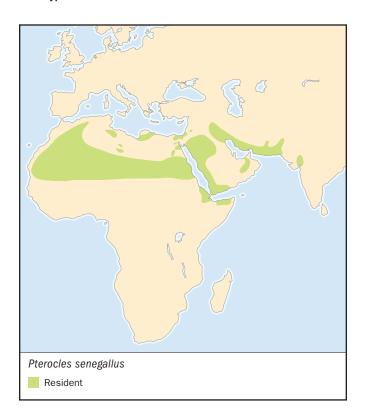
From southern Morocco, much of Sahara, through Arabian Peninsula to Iraq, Iran, Pakistan, and northwestern India.

HABITAT

Desert and semi-desert, usually where stony and flat with isolated patches of vegetation; sometimes in completely bare desert.

BEHAVIOR

Gregarious in flocks of up to about 60, but birds congregate to drink at watering sites in flocks of several hundred about two hours after sunrise. Some birds may drink again in evening. Birds call to each other with a bubbling sound. In Egypt, may gather with flocks of crowned sandgrouse (*Pterocles coronatus*) to feed on grain spilled by trucks traveling from Nile to Red Sea ports. Nonbreeding flocks roost on ground in open desert, each bird making a shallow scrape.



FEEDING ECOLOGY AND DIET

Mainly small, hard seeds, including fallen grain. May feed on insects, but this needs verification.

REPRODUCTIVE BIOLOGY

Nests in solitary pairs; makes small unlined scrape, usually among stones for camouflage. Breeds mostly March to July. Three camouflaged eggs incubated by female by day and male by night for up to 31 days. Chicks take water from male's soaked belly plumage but feed by themselves on food shown by parents. When disturbed, chicks may dig themselves into soft sand for concealment or may hide among stones.

CONSERVATION STATUS

Common to abundant over most of range; extreme arid habitat means little contact with humans, and therefore, there is little threat to most populations. Said to be increasing in Somalia.

SIGNIFICANCE TO HUMANS

Generally small but may be hunted occasionally ◆

Chestnut-bellied sandgrouse

Pterocles exustus

TAXONOMY

Pterocles exustus Temminck and Laugier, 1825, Senegal. Six subspecies.

OTHER COMMON NAMES

English: Common Indian sandgrouse, common sandgrouse, Indian sandgrouse, Kenyan pin-tailed sandgrouse, lesser pintailed sandgrouse, singed sandgrouse, small pin-tailed sandgrouse, Somaliland pin-tailed sandgrouse, chestnut-

breasted sandgrouse; French: Ganga à ventre brun; German: Braunbauchflughuhn; Spanish: Ganga Moruna.

PHYSICAL CHARACTERISTICS

About 12.5 in (28 cm); 6–10 oz (170–284 g). Medium-sized; plumage mostly rich golden-buff; central, elongated tail feathers. Male has narrow, black breast-band; chestnut belly and underwing; and mottled back and wings. Female streaked and barred blackish; center of belly and underwing blackish brown; two or three narrow, brown breast-bands.

DISTRIBUTION

African Sahel from Senegal to Sudan and Ethiopia, northern Tanzania, Somalia, southern Arabian Peninsula, and most of Indian subcontinent.

HABITAT

Desert, semi-desert, dry steppe, arid scrub, and fallow fields.

BEHAVIOR

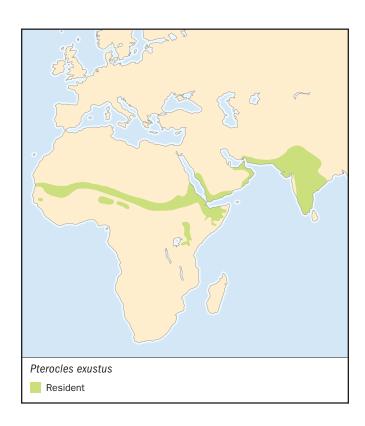
Gregarious unless breeding, flocks are comprised of tens of thousands at favored drinking places. Birds forage mostly morning and evening, flying to water two to three hours after sunrise. Roost at night on ground in compact groups in open country.

FEEDING ECOLOGY AND DIET

Hard seeds, mostly grains and legumes; also said to feed on ants in Chad. Up to 10,000 seeds counted in one bird's crop.

REPRODUCTIVE BIOLOGY

Breeds mostly May to December in Tanzania, but seasons vary in other parts of Africa according to rainfall and food supply. Breeding in India also variable but mostly February to August. Nest is shallow scrape in open, arid habitat. Clutch of three eggs incubated by male at night and female by day for about 23 days. Male waters chicks from his wet belly feathers.



CONSERVATION STATUS

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One of the most common sandgrouse in Africa and India; in no danger of decline.

SIGNIFICANCE TO HUMANS

May be hunted for food but not on large scale. ◆

Black-bellied sandgrouse

Pterocles orientalis

TAXONOMY

Tetrao orientalis Linnaeus, 1758, "In Oriente" = Anatolia. Two subspecies generally recognized.

OTHER COMMON NAMES

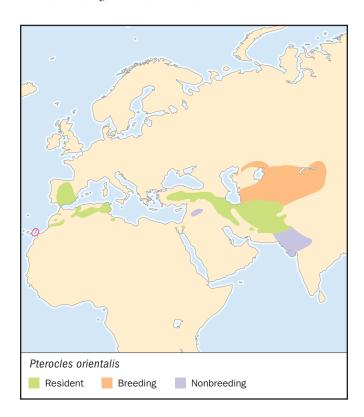
English: Imperial sandgrouse, large sandgrouse, oriental sandgrouse; French: Ganga unibande; German: Sandflughuhn; Spanish: Ganga Ortega.

PHYSICAL CHARACTERISTICS

About 15 in (39 cm); female 10.6–16.4 oz (300–465 g), male 14.1–19.4 oz (400–550 g). Largest sandgrouse; robustly built, without elongated, central tail feathers. Male rust-colored buff above, mottled grayish on back and wings; throat a bright rusty color with triangular black patch; breast gray, bordered with narrow, black band and broad, pinkish band; belly black. Female similar to male but less strongly tinged rust coloring; lacks rust coloring and black on throat; breast spotted black; narrow black collar on throat and below breast. Underwing white in both sexes.

DISTRIBUTION

North Africa from Canary Islands and Morocco to Libya; Iberian Peninsula; discontinuously from Turkey to southwestern Russia, Iran, Afghanistan, Pakistan, and northwestern India.



HABITAT

Grassy steppe and semi-desert with scattered clumps of grass and herbs.

BEHAVIOR

Gregarious except when breeding; flocks may number thousands at drinking sites but usually not more than about 30 birds on feeding grounds. Usually drinks a couple of hours after sunrise. Normally lands a small distance from water's edge before running down to drink, then takes off directly from water's edge and returns to feeding areas.

FEEDING ECOLOGY AND DIET

Mostly seeds, especially legumes. May also eat termites. Up to 30,000 seeds taken from single crop.

REPRODUCTIVE BIOLOGY

Solitary nester, mostly from March to September. Nest is scrape on ground, often under a shrub. Three well camouflaged eggs incubated by female during day and by male at night for about 23–28 days; male provides young with water from soaked belly feathers.

CONSERVATION STATUS

Abundant over most of range but may be increasingly scarce in Spain and Portugal. Becoming increasingly scarce on Fuerteventura in the Canaries.

SIGNIFICANCE TO HUMANS

Highly prized by sportsmen. ◆

Lichtenstein's sandgrouse

Pterocles lichtensteinii

TAXONOMY

Pterocles lichtensteinii Temminck, 1825, Nubia. Four subspecies usually recognized.

OTHER COMMON NAMES

English: Abyssinian sandgrouse, close-barred sandgrouse, Somaliland sandgrouse, Suk sandgrouse; French: Ganga de Lichtenstein; German: Wellenflughuhnl; Spanish: Ganga de Lichtenstein.

PHYSICAL CHARACTERISTICS

About 9.8 in (25 cm); 6.2–8.8 oz (175–250 g). Smallish, without elongated, central tail feathers. Both sexes strongly barred black on buff above and below; male distinguished by black-and-white forehead pattern, yellow bill, and two broad breastbands of buff, each bordered black below. Downy chick, unusual in being almost plain brown; other sandgrouse chicks boldly patterned above.

DISTRIBUTION

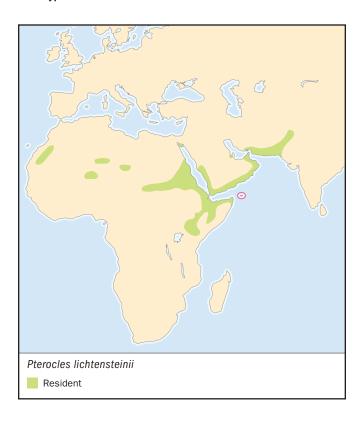
Discontinuous from Mauritania to Ethiopia and Somalia, central Kenya, southern Arabian Peninsula, Socotra Island, and North-West Frontier province of Pakistan.

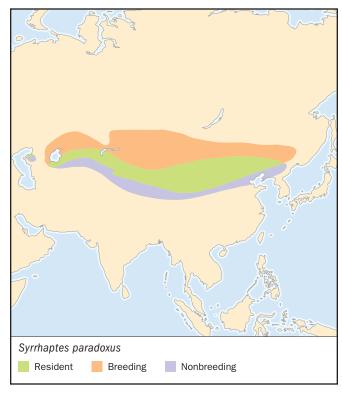
HABITAT

Extreme rocky or scrubby desert hillsides and dry washes; avoids open desert and cultivated fields.

BEHAVIOI

Most desert-adapted sandgrouse. Normally in pairs or small groups by day, gathering into larger flocks at dusk to fly to water. Lands a few yards from water, then runs down to drink.





Kidney structure is especially well adapted to water conservation; water-carrying capacity of male's belly plumage is greatest for any sandgrouse studied. Largely nocturnal, roosting by day in shade of rocks or plants.

FEEDING ECOLOGY AND DIET

Small, hard seeds, especially of Acacia sayal and other legumes.

REPRODUCTIVE BIOLOGY

Breeds mainly May to July, rarely to September. Nest is shallow scrape among scattered rocks and vegetation. Two or three camouflaged eggs form usual clutch but little else known.

CONSERVATION STATUS

Common over most of range. Very arid habitat provides best protection from humans.

SIGNIFICANCE TO HUMANS

Probably very little contact with humans because of extreme habitat preference. ◆

Pallas's sandgrouse

Syrrhaptes paradoxus

TAXONOMY

Syrrhaptes paradoxus Pallas, 1773, southern Tartarian Desert. Monotypic.

OTHER COMMON NAMES

French: Syrrhapte paradoxal; German: Steppenhuhn; Spanish: Ganga de Pallas.

PHYSICAL CHARACTERISTICS

15–16 in (38–40.6 cm); male 8.8–10.6 oz (250–300 g), female 7.1–9.2 oz (200–260 g). Medium-sized with very long, central

tail feathers and white underwing in both sexes. Male mostly rich orange-buff above, coarsely barred with black on back; throat rich tawny; breast buffy gray with scalloped band of black and white in center; belly black. Female buff above, heavily barred with black; below mostly buffy gray; belly black. Hind toe absent; legs and feet feathered, except for soles of toes.

DISTRIBUTION

Southern Russia from Caspian Sea to China, including Tibet, and Mongolia. Irrupts sporadically into Europe and British Isles, most recently in 1908.

HABITAT

Open steppe and sandy desert, often with wormwood (Artemisia) scrub. In summer, mostly between 4,300 and 10,500 ft (1,300 and 3,200 m) but may move to lower elevations in winter.

BEHAVIOR

Gregarious when not breeding; sometimes in flocks of hundreds, especially on migration, though most populations are sedentary or locally nomadic. Wings have specialized outermost primaries that produce whistling in flight. Flies to water at any time of day but mostly before mid-morning.

FEEDING ECOLOGY AND DIET

Seeds, mostly of legumes. Some green shoots may also be taken.

REPRODUCTIVE BIOLOGY

Nesting occurs mostly from April to June; nesting pairs generally solitary, but adjacent nests may be only 13–20 ft (4–6 m) apart. Nest scrape is on ground among vegetation or in open. Three eggs incubated for 22–26 days. The roles of the sexes unknown in the wild, but in captivity only female incubates both day and night; male sits near female most of time but not on nest. Nothing known of care of the young.

CONSERVATION STATUS

Highly adaptable. Seems to be able to maintain numbers, even in agricultural areas; in no need of special conservation measures.

SIGNIFICANCE TO HUMANS

Possibly hunted for food but appears not to be considered important game bird. $lack {f }$

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Organizations

African Gamebird Research, Education and Development (AGRED). P.O. Box 1191, Hilton, KwaZulu-Natal 3245 South Africa. Phone: +27-33-343-3784. E-mail: plloyd@botzoo.uct.ac.za

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Gordon Lindsay Maclean, PhD, DSc

• Columbiformes

(Pigeons, doves, and dodos)

Class Aves

Order Columbiformes

Number of families 2

Number of genera, species 40–45 genera; 300–320 species

Photo: A blue-crowned pigeon (*Goura cristata*) with nesting material in New Guinea. (Photo by Helen Williams. Photo Researchers, Inc. Reproduced by permission.)



Evolution and systematics

This order consists of two families—the pigeons and doves (Columbidae) and the extinct dodos (Raphidae) of the Indian Ocean Mascarene Islands. It is a homogenous group of arboreal and terrestrial birds with several unique anatomical and physiological features. The order is generally agreed to be monophyletic (derived from a single common parent form) and does not appear to have clear affinities with any other. At various times it has been considered close to the gamebirds (Galliformes), parrots (Psittaciformes), or shorebirds (Charadriiformes). Anatomically the Charadriiformes appear to be the closest. They have similar features of the palate, nostrils, wings, voice boxes, and skull. They differ, however, in biology, behavior, the type of young, and by the fact that pigeons have a specialized backbone and a long hindtoe. DNA analysis has shown that the Columbiformes have no close relationships with any other birds and their similarities are due to convergence or the retention of primitive characteristics.

Sandgrouse (Pterocliformes) have been often considered to be Columbiformes having similar feather structure and musculature but in other respects they are midway between the Columbiformes and the Galliformes. They are now considered to be closest to the shorebirds.

The order has a somewhat poor fossil history and the oldest species is *Columba calcaria* from the Miocene of France. Miocene material is also known from Australia and recently from Japan.

Physical characteristics

The Columbidae is the only surviving family in the order. They are generally compact birds with small- to medium-sized heads held on short but graceful necks. The smallest is

the Australian diamond dove (*Geopelia cuneata*) which weighs about 1.1 oz (30 g) and the largest the Victoria crowned-pigeon (*Goura victoria*) of Papua New Guinea at 3.7–6.6 lb (1.7–3 kg). The sexes are similar with males being marginally larger than females. Generally they possess similar plumage, but some tropical species are sexually dimorphic—the males having quite brilliant plumage. Pigeons are generally very similar in body form although some species resemble quail, partridges, or small turkeys. The unique pheasant pigeon (*Otidiphaps nobilis*) of Papua New Guinea looks and acts like a pheasant and is considered by local people to be megapode and not a pigeon at all.

The wings are usually broad with rounded tips and pigeons are strong direct flyers. They can glide and often incorporate this into display flights, but they cannot soar. They have proportionally more wing muscle (31–44% of body weight) compared to most other birds. The wings have 11 primary feathers, although the first is very reduced, and 10–15 secondaries and tertials, the two being indistinguishable. Primary feathers are often modified by being variously emarginate (narrowed in their outer sections), but nobody seems to know why they are this shape. Pigeons take off and often fly with a characteristic clapping of wings. The tails are of varying lengths, usually shortish, and there are 12–14 tail feathers (up to 18 in *Goura* and *Otidiphaps*).

Body feathers are unique. The shaft is generally flattened, strong, and broad then tapers abruptly to a fine point. There is generally no aftershaft, although small ones may be present on some wing and tail feathers. Body feathers have very dense fluffy bases, are loosely attached into the skin, and drop out easily. This may be a predator avoidance mechanism. If grabbed by a predator large numbers of feathers come out in the attacker's mouth and the bird can make its escape. Pigeons

Order: Columbiformes Vol. 9: Birds II



Feral pigeons are a common sight in cities, such as these being fed in Trafalgar Square, London, United Kingdom. (Photo by Ernest James. Bruce Coleman Inc. Reproduced by permission.)

have no or only rudimentary oil glands, glands possessed by most birds which exude an oil used for preening. Powder downs are dispersed over the entire body. These feathers disintegrate to produce a talcum-like powder that the pigeon uses to maintain plumage condition. This gives a beautiful soft silky feel to pigeon plumage unmatched by most other birds. Two kinds of domestic pigeon produce very peculiar curled "fat quills." These special feathers contain yellow fat that derives from the same cells as powder down.

The generally dull plumage of the domestic pigeon is not representative of the huge range of color schemes the order presents. Combinations of delicate grays, browns, and creams complement the soft plumage. Many species, particularly in the Indo-Pacific, are spectacularly clothed in greens, reds, purples, pinks, blues, and oranges. The gorgeous golden doves of Fiji (genus *Ptilinopus*) are fiery orange or metallic green and gold. Some pigeons have crests or naked skin around the eyes. Pigeons only have one adult plumage—they do not alternate breeding and nonbreeding plumages and so have a complete post-breeding molt.

Most pigeons have short weak bills, often with a characteristic expanded tip and the nostrils are under a thin plate, which is covered by an often brightly colored, cushion-like

structure called a cere. A dove's legs are generally short with small rounded or hexagonal scales at the sides and rear, and it has three front and a long, functional hind toe.

The backbone, usually of 37–39 vertebrae, is very rigid. The vertebrae are strongly amalgamated with the synsacrum (the back plate), and the fused vertical spines on the vertebrae form a low ridge that contrasts abruptly with the coccygeal (tail) vertebrae with their normal spines. The pelvis is peculiarly shaped so as not to form an interpelvic space. The sternum (breast bone) has an internal spine. The skull has small basipeterygoid processes (where the palate joins the braincase).

Internally the caeca (long appendix like pouches of the gut) are absent or very small. The crop is very large with two lobes. To make room for the crop, the muscles of the syrinx (voice box) are modified being larger on one side. Most species have a thick, muscular gizzard, which, with the help of grit the bird swallows, grinds up hard seeds and fruit. Over one-third of the species in the order—the fruit pigeons (genera *Ptilinopus*, *Ducula*, and *Lopholaimus*)—have thin-walled gizzards and do not ingest grit. These birds are specialist frugivores and their gizzards massage the nutritious flesh off the rainforest fruits they eat—the hard seeds are passed out whole. These birds

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A white-winged dove (*Zenaida asiatica*) displaying in south Texas. (Photo by John A. Snyder. Bruce Coleman Inc. Reproduced by permission.)

act as effective seed dispersers and are common components of the rainforest ecosystems of Indonesia, Melanesia, the Pacific islands, and Australasia.

Distribution and habitat

Pigeons occur in all terrestrial habitats from deserts to forest, although most species are forest dwellers, particularly rainforests. There are no aquatic or wading species. They occur all over the world being absent only from the Arctic, the Antarctic, and very high mountains. The order is generally well distributed on islands, with over 60% of species occurring only on islands away from continental land masses. They have radiated most prolifically in terms of species, plumage, and body form in the tropics, particularly in the Indian and Pacific ocean regions.

Some doves (*Columba*, *Streptopelia*) have unique adaptations to control their temperature in very hot conditions. There is a plexus or mass of blood vessels forming a collar inside the neck and around the esophagus. In very hot weather the birds pant, rhythmically bringing the esophagus and the plexus into contact. Heat is transferred from the blood to the moist wall of the gullet where it is lost by evaporation. Some doves have a similar plexus behind the ear coverts that keeps the brain cool.

Behavior

Social behavior varies widely in the order ranging from solitary species to ones that form small to large permanent

flocks or are colonial. Most species are gregarious. Many species, even the solitary ones, readily gather at abundant food sources such as fruiting trees or grain crops. Single fruiting trees in tropical rainforests may attract seven or more species of fruit pigeons at the same time. Rock doves (Columba livia), wood pigeons (Columba palumbus), and stock doves (Columba oenas) gather in huge numbers in grain fields—a flock of 100,000 wood pigeons has been recorded in Germany, and the eared dove (Zenaida auriculata) of South America breeds in colonies of up to five million. The extinct passenger pigeon (Ectopistes migratorius) of North America was possibly the most abundant bird on Earth and flocks of hundreds of millions were recorded. One flight of birds in Ontario seen during 1866 was 300 mi long by 1 mi wide (480 km by 1.6 km) and lasted for 14 hours—there were up to perhaps three billion birds!

Pigeons have a fairly consistant set of breeding displays—all species have a range of bows, stretches, and display flights. No species has complex songs and their calls are generally "coos" and "oohs," often quite deep and sonorous. Several species have clicks, soft whistles, and soft grunts, or are almost completely silent.

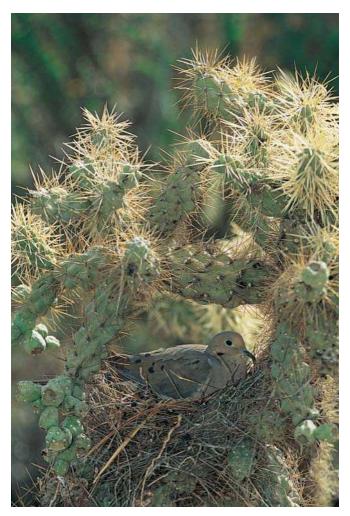
Feeding ecology and diet

All species in the order eat mostly seeds, fruits, and leaves. Invertebrates are eaten occasionally, but only rarely do they make up a large portion of the diet. An exception is the atoll fruit-dove (*Ptilinopus coralensis*), which takes a lot of insects and even lizards on the generally barren Pacific coral islands it inhabits.



A white dove in flight. (Photo by Kim Taylor. Bruce Coleman Inc. Reproduced by permission.)

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An American mourning dove (*Zenaida macroura*) on its nest in a Cholla cactus, Arizona. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)

A supposedly unique feature is a pigeon's capacity to drink by sucking water up directly, but several other birds can do this and pigeons sometimes do not suck—it seems to depend upon how much of a hurry they are in. Drinking was also one of the features that supposedly related pigeons to sandgrouse, but the latter do not drink like pigeons at all.

Reproductive biology

The crop of all pigeons is specialized to an extent unknown in any other birds. This organ has a glandular lining that, during the breeding season and in both sexes, enlarges and produces a soft, nutritious, cheesy secretion called crop milk, which is fed to the chicks. This feature is probably unique to pigeons, although some parrot breeders claim that in the first few hours after hatching young parrots are also fed a crop milk by their parents. Crop milk gives pigeons a distinct advantage in that the chicks need not starve if food is scarce. So long as the parents are fat and healthy the young can continue to receive nutritious food in hard times.

Most pigeons form monogamous pairs at least for one breeding season. They do not put much effort into nest building: a few twigs woven together form a flimsy platform or, for terrestrial species, the egg is laid in a scrape in the ground. Clutch size is usually one or two white, rarely cream or buff, eggs, although some temperate species occasionally have clutches up to four eggs. As a generality the one-egged species tend to be either fruit eaters that live in rainforests and are large or are colonial. Pigeon young, called squabs, are helpless and generally nearly naked with only a few lax yellow, brown, or gray down feathers. Both parents care for the young, which fledge at between 7 and 28 days depending upon the species. Chicks grow very fast and those of some species leave the nest when wing feathers are only half grown. Young of the Torresian imperial-pigeon (Ducula spilorrhoa) are particularly precocial. This pigeon from Australia and New Guinea breeds in colonies in mangroves, usually on off-shore islands. If a person walks through a colony, the tiny chicks leap from their nests and attempt to scramble away. Once the danger is passed, however, they laboriously climb back to the nests using their necks and little stubby wings.

Young pigeons quickly develop a distinct, generally brown juvenal plumage, and start to molt and develop adult plumage before the juvenal plumage itself has fully grown.

The dodos

The family Raphidae appears at first sight quite different from the Columbidae. It consists of three extinct species from the Indian Ocean—the famous dodo (*Raphus cucullatus*) on Mauritius, the Rodrigues solitaire (*Pezophaps solitaria*) on Rodrigues, and the solitaire (*Raphus solitarius*) on Réunion. (The existence of *R. solitarius* is based on contradictory traveler's accounts. No illustrations or physical remains currently exist, so its taxonomic position is less certain than the other two species in this family.) They were all exterminated in the sixteenth to eighteenth centuries mostly by European sailors visiting the islands and killing the trusting animals en masse for food and fun. The sailors also released pigs, monkeys, and rats, which preyed on eggs and young.

The Raphidae were very large, flightless birds—the Rodrigues solitaire weighed as much as 62 lb (28 kg). Early illustrations and skeletal remains suggest they had large distended bellies, short thick legs, and big heads with massive bills that had a big expanded tip. The dodo's bill was 8 in (20 cm) long and heavily hooked. Their plumage was lax and soft, they had a peculiar short curly tail set high on the back, and they had tiny wings.

While apparently so dissimilar, they were anatomically very close to pigeons. The dodo's big hooked bill is fore-shadowed by the enlarged bill tips of most pigeons. This is obvious in the green pigeons (genus *Treron*) of Africa and Asia, several of which have enlarged bills. *Treron pembaensis* from the East African island of Pemba and *T. sanctithomae* from the West African island of São Tomé have particularly hooked bills. The thick-billed ground-pigeon (*Trugon terrestris*) of New Guinea has a large bill, heavily expanded at the tip, while the tooth-billed pigeon (*Didunculus strigirostris*) of Samoa has a bill intermediate in character between pigeons and dodos.

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Dodo's feathers were identical to pigeon feathers and the looseness of the plumage is like that seen in young squabs. Indeed the whole appearance of the dodos is very similar to a pigeon squab. Most of their other features are the same as pigeons—the skeletons are similar given the specializations of flightlessness; they laid a single white egg on the ground; they had muscular gizzards and enlarged crops; and, like many pigeons, they were specialized fruit eaters. What is not known is the extent to which physiological and behavioral features were shared. Did they produce crop-milk, for example?

It is now generally agreed that the dodos are an example of neotony or paedomorphosis—the retention of juvenile characters into adulthood. Derived from pigeon-like stock, the dodos lost their wings, developed gigantism, and retained juvenile body form and plumage. Paedomorphosis and gigantism are common in island birds and may be a particular way in which Columbiformes adapt to the harsh life on islands. Like the rails (Rallidae) the strong flying, adaptable Columbiformes have been spectacularly successful in reaching and adapting to island life. Continuing fossil discoveries on Pacific islands reveal that there was a large fauna on these islands, including many pigeons, that was exterminated by Melanesian and Polynesian settlers before Europeans arrived and carried out their own exterminations. Most fascinating of all is the recent discovery on Viti Levu (Fiji) of fossils of a dodo-sized pigeon. Perhaps dodos were not so unique and the ones known of in the Indian Ocean may just have been the last "giant baby pigeons" of a range of island specialists exterminated by man over the last thousand years.

Extinction

Extermination is perhaps the saddest feature of the order. It contains the two most famous avian extinctions attributable to man—the dodos and the passenger pigeon—the former one of the rarer and the latter the most abundant bird ever known. In addition, eight other species and subspecies of pigeons are known to have been exterminated in historical times following European expansion. The toll is even higher when the extinctions brought about by pre-European peoples in the Pacific Oceans are included.

The dodos and to some extent the passenger pigeon, are used as the prime examples of evolution's losers, that there was somehow something wrong with how they lived and fitted into the world—adapt or die. Nothing could be further from the truth. Dodos were beautifully adapted to their island habitats. They simply couldn't adapt to a determined war of attrition waged by people and to predation by introduced species. War of attrition is not an overstatement when applied to the passenger pigeon either—how else would one describe the killing in Michigan during 1874 of 700,000 passenger pigeons a month from one breeding colony alone? The reason for this killing was market hunting and whole train loads of dead pigeons were carried to market in Chicago.

The extinction of dodos is not an example of evolutionary incompetence. It is just another example of blaming the victims. Evolutionarily the dodos, and the Columbiformes in general, are or were some of the best-adapted species on Earth.

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Francis Hugh John Crome

Pigeons and doves

(Columbidae)

Class Aves

Order Columbiformes

Family Columbidae

Thumbnail description

Small to medium-sized birds; they generally have small heads and full-breasted bodies, and soft but very dense plumage

Size

5.9-31.5 in (15-120 cm); 1.1-4.4 lb (0.5-2 kg)

Number of genera, species

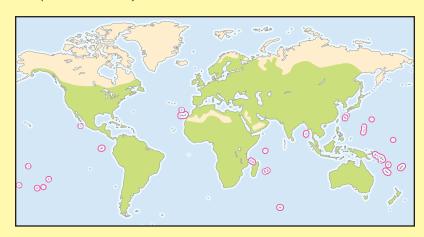
42 genera; 316 species

Habitat

All terrestrial habitats, from desert to rainforest, and mangrove to high alpine mountains

Conservation status

Extinct: 11 species; Endangered: 14 species; Critically Endangered: 12 species; Vulnerable: 34 species; Near Threatened: 34 species



Distribution

Cosmopolitan, except the Arctic and Antarctica

Evolution and systematics

Pigeons (Columbidae) form, along with the extinct dodo family (Raphidae), the order Columbiformes. Formerly pigeons were placed close to sandgrouse (Pterocliformes), which are related to waders (Charadriiformes), or to parrots (Psittaciformes), but DNA hybridization showed no close relation between pigeons and parrots. Pigeons and waders share some characteristics, such as the form of palate and nares, the type of tracheobronchial syrinx (vocal organ), and the configuration of toe flexor tendons. Therefore, an ancestral wader is the common ancestor of Columbidae.

Until now, all fossil pigeons that date from the late Eocene belong to modern members of Columbidae.

All five subfamilies of Columbidae occur in tropical southeast Asia. This part of the world is inhabited by 21 columbid genera and 175 species, and characterized as a center of radiation at least in modern times, but also concerning the dynamic geological history of southeast Asia. Sibley and Monroe place Columbidae by DNA hybridization in the superorder Passerimorphae, which also contains Gruiformes, Ciconiformes, and Passeriformes, but this classification is questioned.

Today Columbidae is composed of 316 species divided into five subfamilies—Columbinae (29 genera, 187 species), Otidiphabinae (pheasant pigeon: 1 species), Treroninae (fruit doves: 10 genera, 124 species), Gourinae (crowned pigeons: 3 species), and Didunculinae (tooth-billed pigeon: 1 species).

Physical characteristics

Pigeons have compact bodies and rather small heads on short necks. In most species the external sexual dimorphism

is poorly developed. The wings are long and broad in many species, and consists of 10 primaries with the first reduced and 10–15 secondaries. Flight muscles are about 40% of total body mass; in poor fliers this is 14%. Columbid tails are usually long and broad, but some species have long, pointed tails. Twelve to 14 feathers build the tail. Crowned pigeons have 16–18 tail feathers. Pigeons lack down tracts, but all body feathers exhibit downy barbs at the base. Many pigeons have no oil gland at all, others have a small and naked oil gland. Preen oil is not used during preening. Powder-downs replace the function of preen oil.

The legs of arboreal pigeons are shorter than those of terrestrial pigeons. Tarsi (legs) are covered in front by large scales but laterally and behind with small ones; in *Staroenas* and *Goura*, front scales are also small. Feet are the perching type, with three toes in front and a large hind toe.

Pigeons have short bills. The basal portion is swollen and covered with soft skin, the cere. The middle portion of the bill is constricted, giving it a plover-like appearance. Eyes are surrounded by bare skin that varies in color and may be red, blue, yellow, or white.

Two large lobes form the crop, which plays an important role in nutrition, when feeding young, and in vocalization. Caeca—cul-de-sac-like structures at the lower end of the gastrointestinal tract—are rudimental. The gall bladder is missing in most species.

Distribution

Fossil remains of some pigeons have been found from the Miocene in Europe, the Pliocene in North America, and the

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Ice Age in many parts of the world. Asia, especially southeast Asia, is considered a center of radiation for pigeons; the many archipelagos and most islands are inhabited by pigeons. Here we find more than half the total number of genera. The Americas follow with three monotypic genera, three genera containing less than five species, and five polytypic genera. Africa and Australia are inhabited by 10 genera each; two of these are monotypic genera. The New Zealand pigeon belongs to the monotypic genus *Hemiphaga*.

A strong power of flight lets pigeons colonize distant ocean islands. Most islands of the Pacific Ocean, Polynesia, and Melanesia are inhabited by pigeons, often by several species on one island. The wood pigeon colonized the Azores, 780 mi (1,260 km) from the next inhabited place, and formed a subspecies. Forerunners of the Galápagos dove also had to cross more than 560 mi (900 km) of ocean to reach the Galápagos archipelago.

Habitat

There is considerable ecological differentiation. Most species are arboreal, with a few exceptions concerning the terrestrial forms of humid tropics and species bound to rock cliffs. True arboreal forms are the specialized pure fruit-eating fruit doves living in tropical rainforests. The savannas of America, Africa, and Australia are occupied by preferentially tree-bound species. Some species breed in colonies in the mangroves of the Caribbean, Australia, and Malaysia.

Cliff-nesting species occur mostly in Eurasia, but also in the Andes. The snow pigeon (Columba leuconota) is a close relative of the rock pigeon, which inhabits the high mountains of Asia from Afghanistan to western China, and often breeds in colonies nesting in cliff recesses and crevices. During summer the species inhabits great mountain heights, and in winter feeds at lower altitudes. Ernst Schäfer reports, "These large pigeons (0.6 lb; 280 g) never sleep at lower altitudes. In the evening they form great flocks and by the thousands, in groups of 100-200, fly up the valley cliffs to reach their sleeping quarters 15,100–16,400 ft (4,600–5,000 m) high, and some 6,600 ft (2,000 m) above the feeding grounds. As soon as the sun appears in the morning the same spectacle can be observed, only reversed. The pigeons always maintain the same flyway, and fly rapidly down into the valleys in great masses to feed to their satisfaction and return to the rough heights for night."

In California deserts the American mourning dove may breed at air temperatures to 111°F (44° C); in Australian deserts the common bronzewing (*Phaps chalcoptera*) lives in dry, hot conditions. Australian spinifex pigeons also live in a very hot habitat; they forage in morning shade and rest hidden in crevices during the hottest time of day. This species has a lower basal metabolic rate and a high upper critical temperature. At 113°F (45°C), ambient temperature gular (an area directly under the bill) fluttering starts. Otherwise, heat is dissipated through the skin by evaporative water loss.



American mourning dove (Zenaida macroura) with week-old nestlings in Baton Rouge, Louisiana. (Photo by C.C. Lockwood. Bruce Coleman Inc. Reproduced by permission.)

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Behavior

Many species show social behavior; we distinguish flocks, colonies, and aggregations. The flock is a small unit often formed for evident functional purposes such as foraging, commuting, roosting, or predator avoidance. The colony is a larger social unit characterized by spatial cohesion in connection with nesting or winter roosting behavior. The aggregation is a large social unit often composed of several flocks. An environmental feature such as a rich food source may cause an aggregation to form. Feral pigeons, for example, undertake foraging, flight, loafing, and roosting in flocks or aggregations of flocks. An individual pigeon in a flock may be safer from most forms of predation. Flocks provide the advantage of extra eyes for spotting predators and offering escape tactics, especially relative to high-speed predators such as falcons. Stable social hierarchies are demonstrated in roosting and feeding flocks. Birds observed in the center of a feeding group obtained more food. Those birds had heavier weights than peripheral, subordinate individuals.

Intraspecific aggression occurs over nesting territories, nesting places, or roosting perches. The aggressor pecks at the head and especially against the orbital skin, and strong wing beats occur; seldom are fights over food.

Pigeons drink by immersing the bill and sucking—a most unusual method in birds. Only sandgrouse, buttonquails, mousebirds, and some finches drink this way. This behavior lets pigeons take water from the most meager sources.

The gait of pigeons is peculiar because of bobbing head movements, so the head stays on the same level while the body moves.

The post-breeding molt is a complete descendant one. Molt is very slow, sometimes taking up to 10 months, and is not suspended during breeding. In the domestic pigeon, the wing molt starts before breeding and is interrupted when the nestlings hatch; it ends in autumn and may be interrupted by winter. In the European turtledove, the post-breeding molt starts in July, but is interrupted by the onset of the migratory disposition (new feathers complete their growth and old feathers will not fall). Therefore, the wing will be complete during migration. The rest of the molt, especially that of the tail feathers, occurs in the winter quarter.

Preening with the bill rearranges feather vanes and disposes of ectoparasites. Mites, ticks, flies, bugs, lice, and fleas can be found on pigeons. The birds may disperse down-powder over the feather. After the first filling of the crop with food, pigeons use food-digestion time for preening.

Doves, in general, have songs that are used in three contexts, corresponding with territorial or sexual drives. The *advertising* or *perch-coo*, the *nest-coo* delivered at the nest or potential nest site, and the *bow-coo*, when the male is displaying to the female. The advertising role of coos may be demonstrated in caged pairs of American mourning doves by counting coos of the males before and after the females are removed: a 10-fold increase in cooing has been noted in males bereft of their mates. Cooing rates dropped to previous levels if the females were returned and pair bond was restored.



A bleeding-heart pigeon (*Gallicolumba luzonica*) fluffs its feathers to conserve body heat. (Photo by Tom McHugh. Photo Researchers, Inc. Reproduced by permission.)

The sexual role of dove song has been demonstrated by playing tape-recorded coos to captive African collared doves: the ovaries of female doves grew at a faster rate when exposed to tape recordings than in females not exposed to playback. Females respond to conspecific sound alone, independent of visual stimuli produced by the live male. Although songs are generally associated with male doves, many female doves also sing. A male song may stimulate the female to produce nest calls, and it is her own song that stimulates gonadotrophic hormone production in the hypothalamus; the male coo thus sustains the female's cooing, which in turn stimulates production of pituitary hormones that stimulate ovulation. Playback has also been used to demonstrate that juvenile American mourning doves may recognize the male parent by characteristics in his individual song: the male sings to nestlings during his nest visitations, and so enables his progeny to learn the characteristics of his voice.

Feeding ecology and diet

Frugivorous (fruit-eating) and granivorous (grain- and seed-eating) species show special adaptations of the digestive tract. In seasonal climates pigeons are forced to switch among different food types. The nutmeg or pied imperial pigeon picks nutmegs directly from trees. Delacour and Mayr note that the pigeons can ingest extremely large fruits with huge pits; pits are regurgitated after the pulp is worked off. Fruit doves feed on nutmegs as soon as the brownish shell has cracked open. The nut itself, often as large as the bird's head, is taken out of the shell and swallowed completely. There is usually room for only one hard-pitted fruit in the stomach. The stomach wall rubs off the thin layer around the nut by

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A golden-heart pigeon (*Gallicolumba rufigula*) feeds its young by regurgitation. (Photo by Tom McHugh. Photo Researchers, Inc. Reproduced by permission.)

the action of two antagonistic muscle pairs, and only this envelope is digested; the large pit passes out unharmed.

Seeds are mostly pecked from the ground surface. Especially soft grass seeds are stripped off the stem. The Galápagos dove digs with its long decurved bill for very hard seeds in the soil. The persistence and eagerness in collecting seeds is remarkable. Gasow found in a crop of a wood pigeon 8,050 capsules and 6,479 seeds of stitchwort (Stellaria sp.), with 30 cherries, 72 fragments of clover leaves, and 10 scale insects. Leaves, grass stems, buds, and flowers are a substantial part of the diet of granivorous pigeons when seeds and mast are not in season. Small snails are often found in crops and stomachs, but it is not clear if this supplements the calcium demand or is eaten directly as animal food. Eberhard Curio published a figure of a Negros bleeding heart (Gallicolumba keayi) with grasshoppers in its bill. The atoll fruit dove (Ptilinopus coralensis) can live on treeless coral atolls of the Toamotu archipelago in the Pacific Ocean far east of Australia. The diet may be purely animal, consisting of insects and even small lizards. The Wonga pigeon (Leucosarcia melanoleuca) from Australia is unusual among pigeons. Invertebrates (Blattodea and worms) form an important part of the diet. It has been observed scratching in leaf-litter like a gallinaceous bird and investigating lyrebird Menura display mounds in search of small snails, insects, and their larvae.

Domestic pigeons will lower their body temperature under conditions of extreme hunger after reducing locomotion. They store a small remainder of food in the crop and digest it before they awake in the morning to use the digestive heat (special dynamic adaptation) to warm their bodies.

Reproductive biology

Most pigeons form monogamous pairs at least for one breeding period. Photoperiod triggers in some species the recrudescence of the gonads, but some species breed through the whole year in spite of molt. In most birds molt and reproduction exclude each other, but in migratory turtle doves a refractory period prevents them from breeding when the premigratory fattening starts. In desert-living pigeons, photoperiod will activate the gonads, but breeding begins only when rain has fallen.

Aerial display occurs in many species. In the wood pigeon it serves as advertisement and defense of a territory. Territories space the nesting, but feeding occurs mostly outside the territory. The male wood pigeon flies several feet (meters) upward and, reaching the summit, claps up to nine times with its wings. Murton writes that the sound of the clap is made during the down stroke by a whip-like crack. A gliding phase follows, and this is repeated up to five times. The territory is also marked by the advertising call. In the rock pigeon a similar display flight starts from a cliff or building. The wing beats are slow and exaggeratedly deep. The wing claps initiate a gliding phase with the wings held in a "V" and tail spread. The Papua mountain pigeon (Gymnophaps albertisii) begins the display flight almost straight up, spiraling up to 100 ft (30 m) above the canopy. It then folds the wings and plunges down like a stone. Forest-living and ground-living pigeons usually perform no aerial displays.

Pigeons have one element of the courtship ritual, the bow-coo, in common. It is the key behavior of a courtship display that consists of a series of patterns ending in copulation. The name "bow-coo" is given because of the peculiar combination of bowing posture and cooing vocalization; it is seemingly a very important element maintaining species distinctiveness. The call and posture as a unit are species specific, or characteristically given a certain way by a certain species. Konrad Lorenz has shown that hybridization between species of the turtledove group does not take place when intended partners exhibit a bow-coo, which is different and not mutually appropriate. However, one can cross "good" species under forced-cage conditions.

Pigeons build weak and flimsy platform nests of twigs, straw, or similar nest materials. The female sits in place and tucks the material around and under her body, while the male collects nesting material and gives it to the female. There are hole nesters and ground nesters among pigeons, and those that nest in trees or bushes.

Most species lay two eggs, but some pure fruit-eating doves lay only one egg. Nearly all pigeons lay white eggs. Hole nesters lay relatively larger, typically white eggs. Smaller birds lay proportionally larger eggs up to 8.3% of body weight; in the wood pigeon (1.2 lb [539 g]), one egg (0.65 oz [18.5 g]) corresponds to 3.4% of body weight. The western crowned-pigeon (*Goura cristata*) (4.4 lb [2,000 g]) lays one egg weighing 1.4 oz (40 g). Open nests of many pigeons are subject to predation because white eggs are visible to potential predators, even though pigeons continuously cover their eggs.

The male incubates preferentially from morning to afternoon, the female from afternoon to the next morning. Incubation time ranges from 11 days in the South American ruddy quail dove (*Geotrygon montana*) (0.25 lb [115 g]), to 30 days for the Victoria crowned-pigeon (*Goura victoriae*) (4.4 lb [2,000 g]) of New Guinea. The changeover of pair partners occurs



Cape turtledoves (*Streptopelia capicola*) drink at a waterhole in Kalahari Gemsbok National Park, South Africa. (Photo by G.C. Kelley. Photo Researchers, Inc. Reproduced by permission.)

when one leaves the nest by walking a short distance away, then flying off. Pigeons do not have brood patches. The hatched altricial (a relatively undeveloped stage) young are naked or covered by yellow hairy down and open their eyes in three to five days. In domestic pigeons, the eye that was covered by the wing in the egg is less developed than the eye exposed to light through the egg shell. The nestling's bill is grayish, with a terminal white spot that may serve as a releasing stimulus for feeding by the parents. The nestling's lower bill is boat-shaped to help gather crop milk regurgitated by the parents in the first days. Nestlings introduce their bills into a parent's crop to feed.

African collared doves (0.33 lb [150 g]) increase body weight by 7% during incubation, but only 1% is due to weight increase of the crop gland. The rest is explained by increased water content of body tissue; water is used for crop milk. Crop milk is unique in birds and consists of fatty degenerated crop cells. Crop milk contains no carbohydrates, but is 76% water, 12% protein, 6% fat, and 1.5% minerals. Consistency is quite different from mammalian milk, but production is under the control of the pituitary hormone prolactin in male and female pigeons. Prolactin plays the same role in mammals.

Fruit doves have a nutritional problem because fruit contains little protein compared with insects and some seeds. This may explain why fruit doves lay only one egg and feed crop milk to the young throughout the nestling period. In other pigeons, after day three to five, more and more adult foods

are added until finally no crop milk is included. The advantage is reduced nestling time. A black woodpecker (0.66 lb [300 g]) needs 27 days nestling time, a stock pigeon (Columba oenas) (0.74 lb [337 g]) only 18 days. The American mourning dove (Zenaida macroura) (0.31 lb [140 g]) has a nestling period of 13 days, but the rose-ringed parakeet (Psittacula krameri) (0.26 lb [120 g]) needs 49 days. Laura Kaufman found that in nestlings of domestic pigeons the intestines (digestive tract, liver, and pancreas) grow very rapidly and constitute about 30% of body mass between days four and five after hatching, when both parents feed them crop milk. But in the late nestling phase, until day 21, when they fledge, these organs shrink (absolutely and relatively) to 11% of body weight. Thus the nestling phase of the pigeon can be described as a feeding stage or larval period. Pigeons undergo a breaking of the voice at seven to eight weeks, along with the first aggressive behavior. Juvenile peeping stops and deep whoo calls start. Under favorable conditions, females reach sexual maturity at three months, males at four months.

Conservation status

About a third of all species are threatened according to the IUCN. Most problems occur with inhabitants of small, distant oceanic islands, where small populations exist that are put at risk by destruction of natural forested habitat. An exception to this was the passenger pigeon (*Ectopistes migratorius*), which was found in North America from the great plains eastward to the Atlantic, and from southern Canada

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to northern Mississippi. It lived in forest and open lowland. Owing to well-developed social tendencies, the species normally congregated in large numbers all year, and stories from early North American settlers suggest that millions of these birds roamed the great eastern forests in spring, summer, and fall. They were well known for a southward migration in dense masses of billions of individuals.

Dense breeding colonies in forests extended over miles (kilometers). Clutch of one egg. Breeding season in the wild extended from April to September, and in captivity beginning in February.

The cause of the rapid extinction of this species is a subject of contention. Some researchers believe passenger pigeons were relatively inefficient at reproduction, and persisted only by maintaining enormous flocks because their reproductive rate was so slow. The only seeming explanation for the passenger pigeon's decline and fall is that more died each year than were produced. Major causes of mortality did not include men with guns and large appetites for squab and sport shooting.

In migration the birds made a great impression on watchers. The classic report of this spectacle is from famed American observer, John James Audubon: "I spotted a flock of passenger pigeons, and I realized that the number of pigeons in the flock was greater than I had ever seen before, and I decided to count them. I got off my horse, sat down and began to pencil a dot on a piece of paper for each bird that I saw. Soon I discovered that it was impossible to continue, for the birds were coming in huge groups. In 21 minutes I had made 163 dots. As I departed, the flocks grew still denser, and the air was literally filled with pigeons; they darkened the sun as in an eclipse, and their droppings fell like snowflakes. The whistling of their beating wings could practically make one fall asleep. During the entire time I waited for my lunch in Young's Inn, and I saw legion after legion fly by; the width

of the group measured from Ohio to the forested areas as far away as one could see."

Audubon tried to estimate the number of pigeons that flew by and came up with an astronomical figure: 1.1 billion birds. Passenger pigeons flew together, fed together, and roosted together. They were subject to shooting and other forms of collecting especially at roosts, and it is as much a result of this inordinate tendency to flock as anything else that they were so easy to kill.

Decline in numbers was noted in the late 1700s and considered marked by 1850. Probably to this point the decline represented the pigeons' response to cutting forests. The well-documented great slaughters occurred only after the railroad had pushed into the central part of the continent, making it possible to ship birds reasonably rapidly to the great consumer markets of the east. Millions of adults and young were taken in the 1860s and 1870s, and hundreds of thousands in the early 1880s, but by the mid-1880s the species was showing that the end was near. Predictably, exploitation of nesting and roosting colonies continued into the 1890s, apparently being profitable at least to the small operator. The last wild passenger pigeon was killed in Ohio, in March 1900; the last captive, a bird hatched in captivity named Martha that enjoyed great popularity, died in September 1914, at the Cincinnati Zoo.

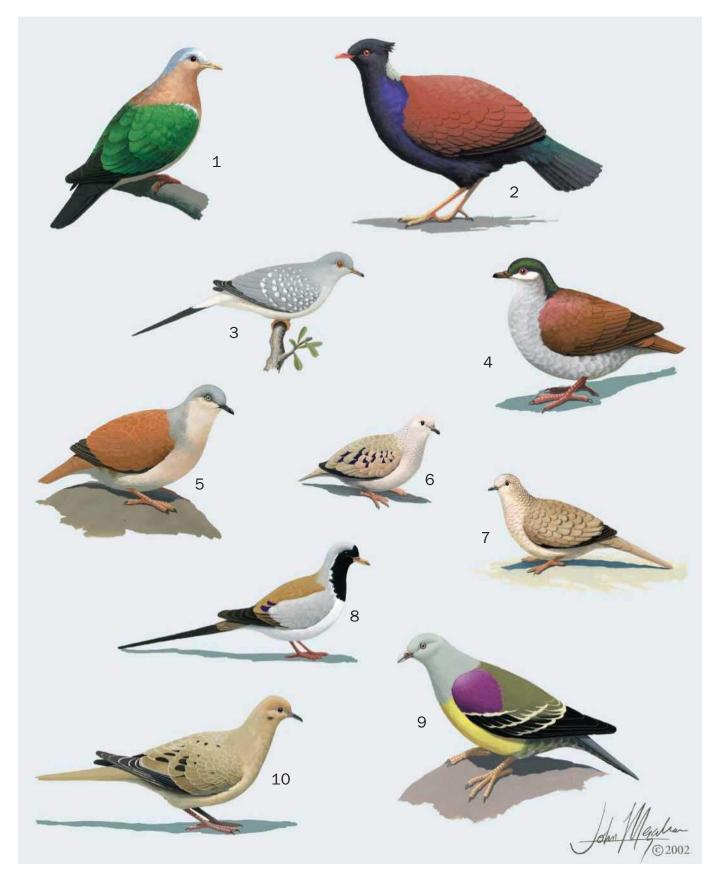
Pigeons as a game bird were hunted mostly by snare, by lime twigs, or by netting; eggs and nestlings also were collected. Pigeons as domesticated birds used for food, as pets, or for other purposes have played an important role in human history.

Significance to humans

Since ancient times pigeons have been domesticated and used as food and to transport messages.



1. Luzon bleeding heart (*Gallicolumba luzonica*); 2. Barred cuckoo-dove (*Macropygia unchall*); 3. Western crowned-pigeon (*Goura cristata*); 4. European turtledove (*Streptopelia turtur*); 5. Rock pigeon (*Columba livia*); 6. Snow pigeon (*Columba leuconota*); 7. White imperial pigeon (*Ducula luctuosa*); 8. Tooth-billed pigeon (*Didunculus strigirostris*); 9. Crested cuckoo-dove (*Reinwardtoena crassirostris*); 10. Wompoo fruit dove (*Ptilinopus magnificus*). (Illustration by John Megahan)



1. Emerald dove (*Chalcophaps indica*); 2. Pheasant pigeon (*Otidiphaps nobilis*); 3. Diamond dove (*Geopelia cuneata*); 4. Key West quail dove (*Geotrygon chrysia*); 5. Gray-headed dove (*Leptotila plumbeiceps*); 6. Common ground dove (*Columbina passerina*); 7. Inca dove (*Scardafella inca*); 8. Namaqua dove (*Oena capensis*); 9. Bruce's green pigeon (*Treron waalia*); 10. American mourning dove (*Zenaida macroura*). (Illustration by John Megahan)

Species accounts

Rock pigeon

Columba livia

SUBFAMILY

Columbinae

TAXONOMY

Columba livia Gmelin, 1789, southern Europe. Thirteen subspecies.

OTHER COMMON NAMES

English: Rock dove; French: Pigeon biset; German: Felsentaube; Spanish: Paloma Bravia.

PHYSICAL CHARACTERISTICS

Male, 12.2–13.4 in (31–34 cm), 6.3–12.5 oz (180–355 g). Plumage generally bluish gray with relatively short tail and long, strong wings.

DISTRIBUTION

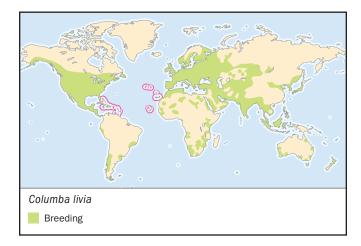
Including feral pigeons, worldwide.

HABITAT

Breeds in cliffs and human structures from sea level to high alpine Himalayas. Feeds in unwooded areas.

BEHAVIOR

The rock pigeon has a rather fast and long step. It is a skillful flyer. Flight velocities of 115 mph (185 kph) have been recorded. Günther Niethammer notes that rock pigeons in the Ennedi mountains of Africa fly down cliff walls almost vertically when a falcon is spotted, and with surprisingly great velocity into cliff crevices. They are also able to start vertically and use this ability when returning after drinking in narrow and deep wells in the desert. Oskar Heinroth considers rock pigeons to be more clever and resourceful than other wild pigeons. This may be the consequence of adapting to its socioecological niche. The social organization—the hierarchy within the flock—is not well understood. Their curiosity is similar to that of ravens. They pick at every button, and at all things their caretaker handles. They quickly learn the time of day they will be fed, and become accustomed to sounds that initially frighten them, such as vacuum cleaners.



The alarm call is a short "ruh," and the nesting call is a "ruu-ruu." which can be heard at a distance.

Rock pigeon courtship behavior has been thoroughly described by Oskar and Katharina Heinroth: "Courtship is initiated when each partner rapidly rubs its beak across its back and under the wings in a characteristic manner; it looks as if each bird is preening its back. Occasionally the male during courtship feeds the female; the female sticks her beak inside that of the male, much like the motion of feeding young. They mutually preen each other on the head and neck. Soon the female assumes the copulatory position and is mounted by the male, and generally the female flies away immediately thereafter."

At sundown or earlier, rock pigeons begin roosting. They sleep in recesses and under roofs, but not in trees, and awaken immediately with the onset of dawn. In most regions they are permanent residents.

FEEDING ECOLOGY AND DIET

The rock pigeon is a typical seed eater, preferring weed seeds, and peas over wheat, barley, and corn.

REPRODUCTIVE BIOLOGY

Particular stimuli evoke egg laying. A captive female will not lay an egg until a caretaker simulates male courtship behavior by stroking the back of the female with his finger or preening neck feathers. Generally a female lays two white eggs that weigh 0.6 oz (17 g). Young hatch after 17–18 days and are initially fed with crop milk by both parents; later, seed that has been soaked is added to the diet. Young make loud peeping sounds, and can fly after 4–5 weeks.

CONSERVATION STATUS

Interbreeding with feral pigeons seriously threatens the species.

SIGNIFICANCE TO HUMANS

The rock pigeon, which has a wide geographical range, has been domesticated several times and in different locales. There are three theories on domestication. According to one theory, the rock pigeon was domesticated in connection with the start of agriculture 10,000 years ago in the region of the near-East "fertile crescent." A second theory holds that they were domesticated as people collected nestlings for food, and a third from the fact that temples were erected near cliffs and colonized by rock pigeons. The pigeon was transformed into the accompanying bird of Ishtar, and later of Venus.

Carrier pigeons deserve special mention. Pigeons have been used to send communications since earliest times. In ancient Egypt, Pharaoh Djoser (2600–2550 B.C.) released house pigeons at the borders of his empire to mail the news that enemies were attacking the frontiers. Today's carrier pigeon was created about 1850 in Belgium by breeding various races. Carrier pigeons can cover up to 621 mi (1,000 km) in a single day, and were trained to live with two lofts 12.4 mi (20 km) apart. In one they were fed, in the other they roosted. If they were released in a place in between, hungry pigeons flew to the feeding loft and fed pigeons flew to the roosting loft. They navigated with the help of an internal map.

Urban predators have become rare. The number of unhealthy pigeons in cities is relatively high, and a lack of predators and availability of food allows sick feral pigeons to

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withstand poor weather conditions. Pigeons and their nests, especially in crowded situations, are subject to parasites, including bird mites, bed bugs, ticks, and others, which can gain entry to human habitations from pigeon nests. Some feral pigeons carry the parrot disease, psittacosis, which can be fatal in humans. *Salmonella* organisms, which propagate typhus, have also been found in pigeons. Playgrounds are dangerous if they become soiled with pigeon droppings. ◆

Snow pigeon

Columba leuconota

SUBFAMILY

Columbinae

TAXONOMY

Columba leuconota Vigors, 1831, Himalayas. Two subspecies.

OTHER COMMON NAMES

English: White-bellied pigeon, Tibetan dove; French: Pigeon des neiges; German: Schneetaube; Spanish: Paloma Nival.

PHYSICAL CHARACTERISTICS

12.2–13.4 in (31–34 cm); 9–10.8 oz (255–307 g). Dark slategray head; white and grayish brown upperparts; white underparts. Three black bars across folded wing. Black tail with broad white "V."

DISTRIBUTION

High mountains of central Asia.

HABITAT

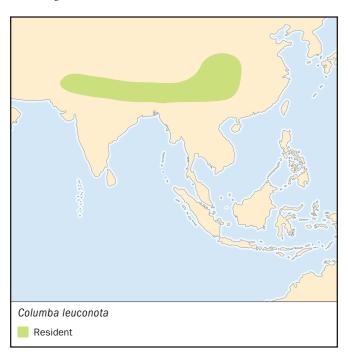
Cliffs at 9,800–16,400 ft (3,000–5,000 m).

BEHAVIOR

Advertises in bowing the head down and lifting the rear with closed tail. Display flight with spread wings and wing-claps.

FEEDING ECOLOGY AND DIET

Feeds on seed, crocus bulbs, and roots; also grain near mountain villages.



REPRODUCTIVE BIOLOGY Similar to rock pigeon.

CONSERVATION STATUS Not threatened.

SIGNIFICANCE TO HUMANS

European turtledove

Streptopelia turtur

None known. ◆

SUBFAMILY

Columbinae

TAXONOMY

Columba turtur Linnaeus, 1758, India, error = England. Four subspecies.

OTHER COMMON NAMES

English: Common turtledove; French: Tourterelle des bois; German: Turteltaube; Spanish: Tortola Europea.

PHYSICAL CHARACTERISTICS

Old World turtle doves are generally medium to small in size, around 12 in (30 cm) and 5.3 oz (150 g). They have long tails and fairly well-developed display plumage on the neck, which is shown in characteristic bow-coo displays. Plumage mostly chestnut. Tips of tail feathers and outer rim of the tail white, otherwise grayish. Display plumage is a patch of black tipped with blue, and in the center nearly white.

DISTRIBUTION

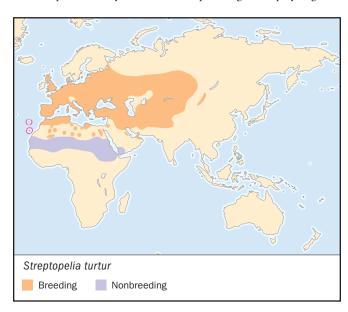
Europe, North Africa, western Asia.

HABITAT

Park landscape with woody patches in agricultural areas.

BEHAVIOR

Long-distance migrant and, during migration, social. The bow-coo includes half a dozen bobs in succession, with crop inflated and bill pointing vertically down, with the courtship note "coo" repeated many times without phrasing. A display flight



involves the male rising up steeply and going back to the perch in a circular flight 100 ft (30 m) in diameter.

FEEDING ECOLOGY AND DIET

Forages on the ground, mostly seed from furmitory, plantain, chickweed, and persicary.

REPRODUCTIVE BIOLOGY

Breeding starts in Europe mid-May, nests are placed in shrubs. Pairs tend to aggregate in small colonies. Clutches are two eggs incubated by the female at night and by the male during the day for 13 days. Young remain in the nest for about 18 days. Turtledoves tend to be double brooded.

CONSERVATION STATUS

Not threatened, but population decline in some countries during 1970–1990 of 50%. Use of chemical herbicides seems to be a serious factor in that they cause the decline or elimination of some food plants.

SIGNIFICANCE TO HUMANS

Hunted, especially during migration and in winter range. ◆

Barred cuckoo-dove

Macropygia unchall

SUBFAMILY

Columbinae

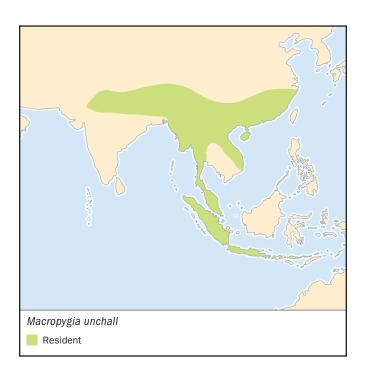
TAXONOMY

Columba unchall Wagler, 1827. Three subspecies.

OTHER COMMON NAMES

English: Long-tailed cuckoo dove, larger Indian cuckoo dove; French: Phasianelle onchall; German: Bindenschwanztaube;

Spanish: Tortola-Cuco Unchal.



PHYSICAL CHARACTERISTICS

16 in (41 cm); 6 oz (170 g). Long tail and upright stance gives a cuckoo-like appearance. Upper parts barred black with chestnut. Display plumage iridescent green and violet.

DISTRIBUTION

Southeast Asia.

HABITAT

Dense broad-leaved forest.

BEHAVIOR

Defends fruiting trees by chasing competitors. While displaying, the male inflates his crop so that it reaches the ground, but the rear is held straight. In display, the bird flies up steeply with clapping wings and glides down in a spiral.

FEEDING ECOLOGY AND DIET

"May hang upside down from a tree and swing out towards a berry, otherwise out of reach. A wide variety of seeds, berries and drupes." (del Hoyo et al., 1999).

REPRODUCTIVE BIOLOGY

The nest is a large platform of twigs in a tree. Lays one egg, slightly glossy or cream-colored, occasionally with a small number of olive-yellow speckles and spots. Incubation 16 days, fledging after 19 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Crested cuckoo-dove

Reinzvardtoena crassirostris

SUBFAMILY

Columbinae

TAXONOMY

Turacoena crassirostris Gould, 1856, Guadalcanal, Solomon Islands. Monotypic.

OTHER COMMON NAMES

English: Crested pigeon; French: Phasianelle huppee; German: Helmtaube; Spanish: Paloma Rabuda Crestada.

PHYSICAL CHARACTERISTICS

15.7–16.1 in (40–41 cm). A unique combination of gray head and underparts, blackish upperparts, crest, long tail, and hooked stout bill.

DISTRIBUTION

Solomon Islands.

HABITAT

Evergreen forest.

BEHAVIOR

Possibly nomadic. While giving the display call, the male throws the head forward with each call in fairly slow motion.

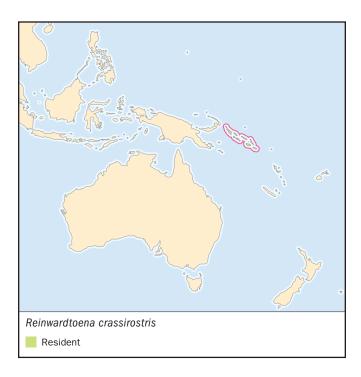
FEEDING ECOLOGY AND DIET

Feeds on fruit in trees.

REPRODUCTIVE BIOLOGY

Extensive research required.

Family: Pigeons and doves Vol. 9: Birds II



CONSERVATION STATUS

Near Threatened.

SIGNIFICANCE TO HUMANS

None known.

Namaqua dove

Oena capensis

SUBFAMILY

Columbinae

TAXONOMY

Columba capensis Linnaeus, 1766, Cape of Good Hope, South Africa. Two subspecies.

OTHER COMMON NAMES

English: Cape dove, long-tailed dove; French: Tourtelette masquee; German: Kaptäubchen; Spanish: Tortolita Rabilarga.

PHYSICAL CHARACTERISTICS

11 in (28 cm); 1-1.9 oz (28–54 g). Sexual dimorphism. The male has an orange bill and a black mask-like marking on face and throat.

DISTRIBUTION

Sub-Saharan Africa, Madagascar, and parts of Arabia. At the northern border it expands to Israel. In 1961, first bred in the Negev.

HABITAT

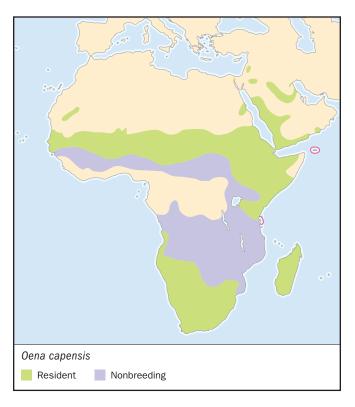
Savannas.

BEHAVIOR

Intertropical migrant.

FEEDING ECOLOGY AND DIET

Feeds on the ground; various seeds and fallen fruits, also insects and snails.



REPRODUCTIVE BIOLOGY

Nest in low bushes lined with grass.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Frequently kept as pets. ◆

Emerald dove

Chalcophaps indica

SUBFAMILY

Columbinae

TAXONOMY

Columba indica Linnaeus, 1758, Ambon. Nine subspecies.

OTHER COMMON NAMES

English: Little green pigeon; French: Colombine turvert; German: Glanzkäfertaube; Spanish: Palomita Esmeralda Dorsiverde.

PHYSICAL CHARACTERISTICS

9.1--10.6 in (23–27 cm); 3.8--5.6 oz (108–160 g). Wings and mantle metallic green.

DISTRIBUTION

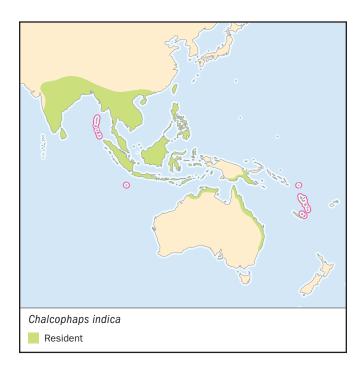
From Indian subcontinent to China, south through Southeast Asia and to Australia.

HABITAT

Forest.

BEHAVIOR

The silent male displays by bowing the head and lifting the closed wings and tail while sitting on a branch.



FEEDING ECOLOGY AND DIET

Seed and fallen fruits.

REPRODUCTIVE BIOLOGY

Clutch of cream-colored or buffish eggs.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Diamond dove

Geopelia cuneata

SUBFAMILY

Columbinae

TAXONOMY

Columba cuneata Latham, 1801, New Holland-Sydney, New South Wales, Australia. Monotypic.

OTHER COMMON NAMES

English: Little turtledove; French: Geopelie diamant; German: Diamanttäubchen; Spanish: Tortolita Diamante.

PHYSICAL CHARACTERISTICS

7.9 in (20 cm), weight less than 1.4 oz (40 g). Very small, gray long-tailed dove.

DISTRIBUTION

Australia.

HABITAT

Species of outback Australia.

BEHAVIOR

The male bobs rapidly with wings partly opened to show the white markings and class loudly. No display flight.



FEEDING ECOLOGY AND DIET

Seeds, mainly from grass.

REPRODUCTIVE BIOLOGY

Rainfall and food availability govern breeding. Juveniles can breed at three months old.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

The diamond dove and zebra dove (Geopelia striata) are popular as pets. ◆

American mourning dove

Zenaida macroura

SUBFAMILY

Columbinae

TAXONOMY

Columba macroura Linnaeus, 1758, West Indies. Five subspecies.

OTHER COMMON NAMES

English: Carolina dove; French: Tourterelle triste; German: Carolinataube; Spanish: Zenaida Huilota.

PHYSICAL CHARACTERISTICS

12 in (30 cm), 4.2 oz (120 g). Olive-gray above, brownish gray beneath. Display plumage of the neck is iridescent pink and violet.

DISTRIBUTION

Common in North America.







Savanna and hot and dry areas, also in agricultural land.

BEHAVIOR

The male stands behind the female with his head up and inflated crop and utters the coos. The iridescent areas of the neck are exposed by inflating the crop, but no bowing is shown. At the nest site, the male calls with the tail spread just to show the white feather tips.

FEEDING ECOLOGY AND DIET

Chiefly seeds.

REPRODUCTIVE BIOLOGY

Birds have four or five breeding attempts, but pairs rarely try more than twice.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Extensively pursued as game bird in the United States and Mexico. lacktriangle

Inca dove

Scardafella inca

SUBFAMILY

Columbinae

TAXONOMY

Chamaepelia inca Lesson, 1847, Mexico. Monotypic.

OTHER COMMON NAMES

French: Colombe inca; German: Aztekentäubchen; Spanish: Tortolita Mexicana.



PHYSICAL CHARACTERISTICS

Very small; 8 in (20 cm), 1.4 oz (40 g). Plumage appears scaly. Every grayish brown feather is subterminally margined with black.

DISTRIBUTION

From southern United States to Costa Rica.

HABITAT

Dry and open areas.

BEHAVIOR

Upon trespass by an intruder, the territorial male utters a guttural call of great complexity and takes a horizontal posture in which the tail is vertically raised and partly fanned. Because females look like males, the territorial male always challenges an intruding female. Courtship begins with the male bobbing his head at the female and attempting to take her neck feathers in his bill (heteropreening or billing). If the female is receptive she will bob in return and follow the male's lead in heteropreening. The incipient pair may remain together for a week or more before undertaking the next stages.

During cold weather, to conserve heat at night, they sometimes form pyramids of five to 12 birds in two to three rows, roosting on each other's backs. May be become hypothermic, body temperature drops 9–22°F (5–12°C) below normal.

FEEDING ECOLOGY AND DIET

Forage on the ground for seeds and small berries.

REPRODUCTIVE BIOLOGY

The precopulatory ritual is a capsule summary of the ritual in pair formation, but takes 15–20 minutes rather than two weeks or so. Males bob and preen and females respond; males go into the bow-coo, standing horizontally with tail raised and widely fanned and giving a call of moderate complexity. Females ultimately beg for ritual feeding. Males feed females, then females

stand horizontally with wings slightly raised; males then mount, and copulation occurs. Copulation almost never occurs in pigeons and doves without the courtship feeding first being given. Clutch of two eggs. Incubation for 14 days. Nestlings brooded for eight days, fledging in 14 days; two days after fledging, renesting may start.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Common ground dove

Columbina passerina

SUBFAMILY

Columbinae

TAXONOMY

Columba passerina Linnaeus, 1758, South Carolina, USA. Eighteen subspecies.

OTHER COMMON NAMES

English: Tobacco dove; French: Colombe a queue noire; German: Sperlingstäubchen; Spanish: Columbina Comun.

PHYSICAL CHARACTERISTICS

Very small; 7.1 in (18 cm), 1.2 oz (35 g). Rufous inner webs of the primaries form a panel in flight. Scaly plumage pattern.



DISTRIBUTION

From southern United States through Central America to Brazil.

HARITAT

Savanna, cultivated land, settlements.

BEHAVIOR

The male sings from a low branch the whole day. When he displays, he bobs his head and flicks his wings.

FEEDING ECOLOGY AND DIET

Forages on the ground; grass seeds and berries.

REPRODUCTIVE BIOLOGY

Nest a shallow cup sometimes on the ground. Clutch of two eggs incubated for 14 days. Young at hatching with hair-like gray down, may fledge in 11 days. Juveniles mature sexually in 79 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

In villages and towns, common ground doves eat bread. ◆

Gray-headed dove

Leptotila plumbeiceps

SUBFAMILY

Columbinae

TAXONOMY

Leptotila plumbeiceps Sclater and Salvin, 1868, Vera Paz, Guatemala. Two subspecies.



Family: Pigeons and doves Vol. 9: Birds II

OTHER COMMON NAMES

French: Colombe a calotte grise; German: Bonapartetaube; Spanish: Paloma Montaraz Cabecigris.

PHYSICAL CHARACTERISTICS

9.8 in (25 cm), 6.0 oz (170 g). Forehead bluish gray. Olivebrown above, white pinkish buff beneath.

DISTRIBUTION

Central America, from Mexico to Colombia.

HABITAT

Humid forest.

BEHAVIOR

Not known.

FEEDING ECOLOGY AND DIET

Not known.

REPRODUCTIVE BIOLOGY

Not known.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Key West quail dove

Geotrygon chrysia

SUBFAMILY

Columbinae

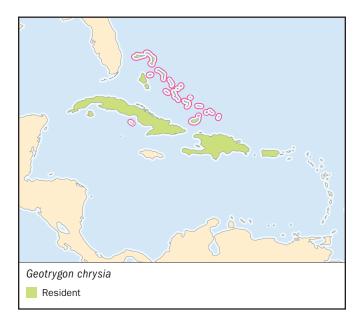
TAXONOMY

Geotrygon chrysia Bonaparte, 1855, Florida. Monotypic.

OTHER COMMON NAMES

French: Colombe ajoues blanches; German: Bahamataube;

Spanish: Paloma-Perdiz Barbiqueja.



PHYSICAL CHARACTERISTICS

11 in (28 cm), 6.2 oz (175 g). White face, chestnut brown above, grayish white beneath.

DISTRIBUTION

Greater Antilles, Cuba, Hispaniola, and Puerto Rico. Formerly bred in Florida keys.

HABITAT

Wooded areas.

BEHAVIOR

Not known.

FEEDING ECOLOGY AND DIET

Feeds in leaf-litter seeds, small fruits, insects, grubs, and caterpillars.

REPRODUCTIVE BIOLOGY

Not known.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Hunting pressure exists. ◆

Luzon bleeding heart

Gallicolumba luzonica

SUBFAMILY

Columbinae

TAXONOMY

Columba luzonica Scopoli, 1786, Luzon Philippines. Three subspecies.



OTHER COMMON NAMES

English: Blood-breasted pigeon; French: Gallicolombe poignardee; German: Dolchstichtaube; Spanish: Paloma Apunalada de Luzon.

PHYSICAL CHARACTERISTICS

11.8 in (30 cm), 6.3 oz (180 g). Orange-red breast spot.

DISTRIBUTION

Philippines, partly.

HABITAT

Forest.

BEHAVIOR

"A courting male chases the female over the ground, then suddenly stops and, with tail raised and feathers puffed out, he may lower his head and arch his wings to display the wing bars or squat back on his tail, strike an upright posture, throw back his head and fluff out his breast facing the female to show to best effect the brilliant breast spot. He may then bow his head forward while uttering the display coo." (Gibbs et al., 2001).

FEEDING ECOLOGY AND DIET

Forest floor; seeds, berries, invertebrates.

REPRODUCTIVE BIOLOGY

Scarcely known.

CONSERVATION STATUS

Near Threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Pheasant pigeon

Otidiphaps nobilis

SUBFAMILY

Otidiphabinae

TAXONOMY

Otidiphaps nobilis Gould, 1870. Four subspecies.

OTHER COMMON NAMES

English: Green-collared pigeon, magnificent ground pigeon; French: Otidiphaps noble; German: Fasantaube; Spanish: Paloma Faisan.

PHYSICAL CHARACTERISTICS

17.7–19.7 in (45–50 cm); 1.1 lb (500 g). A clumsy pigeon with long legs and a unique, laterally compressed pheasant-like tail built by 20–22 tail feathers.

DISTRIBUTION

The hills of New Guinea and the neighboring islands of Waigeeo, Batanta, Yapen, Aru, and Ferguson.

HABITAT

Rainforest and partly monsoon forest.

BEHAVIOR

The pheasant pigeon behaves like a gallinaceous bird and is terrestrial. The male performs a display flight and the wingclap is a loud crack like a gun shot.

FEEDING ECOLOGY AND DIET

Seeds and fallen fruit.



REPRODUCTIVE BIOLOGY

The nest is on the ground and forms a platform of a few sticks. One egg is brooded for 28 days. In the first week of nestling time, the male brings food to the female on the nest, and the female passes it to the squab.

CONSERVATION STATUS

Not globally threatened. Subspecies *Otidiphaps nobilis insularis* from Fergusson Island may be endangered. Deforestation negatively affects this species.

SIGNIFICANCE TO HUMANS

None known. ◆

Bruce's green pigeon

Treron waalia

SUBFAMILY

Treroninae

TAXONOMY

Columba waalia F. A. A. Meyer, 1793, near Lake T'ana, Ethiopia. Monotypic.

OTHER COMMON NAMES

English: Yellow-bellied green pigeon; French: Colombar waalia; German: Waaliataube; Spanish: Vinago Waalia.

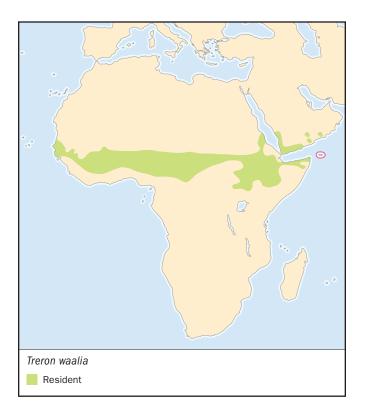
PHYSICAL CHARACTERISTICS

A medium-sized compact pigeon, 11.8 in (30 cm), 9.2 oz (260 g). Head, neck, and breast greenish gray, belly yellow, wings olive-green.

DISTRIBUTION

Africa, in a small belt from Gambia to Somalia.







HABITAT

Forest, associated with figs (Ficus).

BEHAVIOR

Not known.

FEEDING ECOLOGY AND DIET

Feeds on figs in the canopy.

REPRODUCTIVE BIOLOGY

Nest is a frail platform of twigs in a tree or shrub, 8–26 ft (2.5–8 m) above ground. One to two glossy white eggs are laid.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Uses fig trees in cities. ◆

Wompoo fruit dove

Ptilinopus magnificus

SUBFAMILY

Treroninae

TAXONOMY

Columba magnifica Temminck, 1821, New South Wales. Eight subspecies.

OTHER COMMON NAMES

English: Magnificent fruit dove, purple-bellied fruit dove; French: Ptilope magnifique; German: Purpurbrust-Fruchttaube; Spanish: Tilopo Magnifico.

PHYSICAL CHARACTERISTICS

Large, length up to 20 in (50 cm), up to 1.1 lb (500 g). Ashgray head, green upperparts with yellow spots on wing-coverts, throat and breast deep purple, long tail (up to 7.1 in [18 cm]).

DISTRIBUTION

Papua New Guinea and eastern Australia.

HABITAT

Rainforest and secondary forest.

BEHAVIOR

No display flight. When advertising the breast is inflated and the bill is pressed against the upper breast pointing downwards; at each coo the body is inclined very slightly forward; the male bows from an upright posture with the neck slightly inflated forward slowly to about 20° from the horizontal, the bill pressed against the upper breast and the tail raised only slightly from its starting position uttering a low coo.

FEEDING ECOLOGY AND DIET

Various fruits of figs, laurels, and areca palms.

REPRODUCTIVE BIOLOGY

The single-egg clutch can be seen through the nest. Incubation lasts 21 days. If a brooding bird is disturbed it falls vertically from the nest and flies away close to the ground.

CONSERVATION STATUS

Not threatened, but nesting success in Papua New Guinea very low.

SIGNIFICANCE TO HUMANS

None known. ◆

White imperial pigeon

Ducula luctuosa

SUBFAMILY

Treroninae

TAXONOMY

Columba luctuosa Temminck, 1825, Sulawesi. Monotypic.

OTHER COMMON NAMES

English: Celebes pied imperial pigeon, nutmeg pigeon, white fruit pigeon; French: Carpophage luctuose; German: Elster-fruchttaube; Spanish: Ducula Luctuosa.

PHYSICAL CHARACTERISTICS

Large, 16.1 in (41 cm), 14.5 oz (410 g). All white, but flight feathers and end of tail black.

DISTRIBUTION

Sulawesi (Celebes) and adjacent small islands.

HABITAT

Forest.

BEHAVIOR

Not known.

FEEDING ECOLOGY AND DIET

Not known.

REPRODUCTIVE BIOLOGY

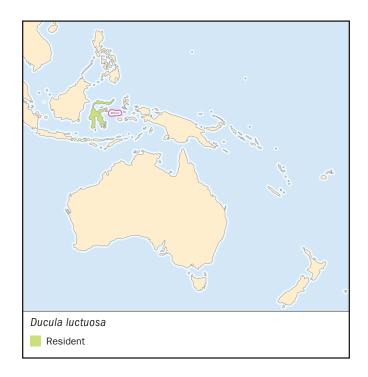
Not known.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆



Western crowned-pigeon

Goura cristata

SUBFAMILY

Gourinae

TAXONOMY

Columba cristata Pallas, 1764, Banda, error = Fak-fak on Onin Peninsula, New Guinea. Two subspecies.

OTHER COMMON NAMES

English: Goura; French: Goura couronne; German: Krontaube; Spanish: Gura Occidental.

PHYSICAL CHARACTERISTICS

Largest pigeons (up to 4 lb [2 kg]), with delicate gray plumage and a fan-like crest.

DISTRIBUTION

Crowned pigeons are confined to New Guinea.

HABITAT

Lowland rainforest.

BEHAVIOR

In display the male spreads and erects his tail, partly opens his wings, then bows his head quickly into an inverted position. In precopulatory display, the male bows and dances with upstretched wings. No display flight.

FEEDING ECOLOGY AND DIET

Food includes fruits, berries, and probably large seeds. Birds forage on the ground in groups of two to 10, according to Gilliard and Lecroy. When disturbed they fly noisily up into nearby trees and characteristically look back down at a passerby.

REPRODUCTIVE BIOLOGY

A large nest built from strong sticks is made up to 33 ft (10 m) in a tree. One egg is laid and incubated for 28 days. Nestling time lasts up to 36 days. The male will feed young much longer.



Family: Pigeons and doves Vol. 9: Birds II

CONSERVATION STATUS

Vulnerable. Danger comes from logging, and hunting for meat, plumes, and trading. Crowned pigeons are protected by law.

SIGNIFICANCE TO HUMANS

Local people use feathers for decoration. Esteemed as an aviary bird. lacktriangle

Tooth-billed pigeon

Didunculus strigirostris

SUBFAMILY

Didunculinae

TAXONOMY

Gnathodon strigirostris Jardine, 1845, Australia, error = Upolu, Samoa. Monotypic.

OTHER COMMON NAMES

French: Diduncule strigirostre; German: Zahntaube; Spanish: Paloma Manumea.

PHYSICAL CHARACTERISTICS

12.2–15 in (31–38 cm); 14.1 oz (400 g). Stout hook-like bill with tooth-like notches in the lower mandible.

DISTRIBUTION

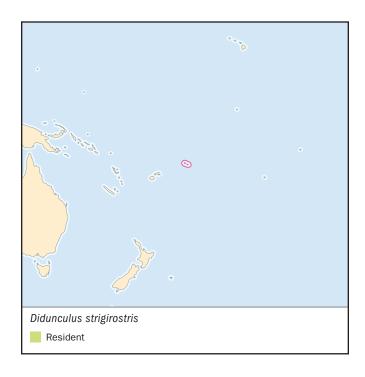
The islands Savai'i, Upolu, and Nu'utele of the Samoa archipelago.

HABITAT

Undisturbed primary forest. Dependent on a mahogany tree *Dysoxylum* (Meliaceae).

BEHAVIOR

Secretive bird that lives in small parties. The advertising call of the male given from the top of a tree lasts about 1.5 seconds.



FEEDING ECOLOGY AND DIET

Hooks out the hard pea-sized seed of *Dysoxylum* and removes the viscous flesh with a sawing movement of the lower mandible. No competition for food.

REPRODUCTIVE BIOLOGY

Not known.

CONSERVATION STATUS

Endangered. This species has a small fragmented range and population; both are declining due to deforestation. More than 50% of the population was probably lost over the past decade due to the effects of severe cyclones.

SIGNIFICANCE TO HUMANS

Hunting may occur. ◆

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Michael Abs, Doctor rerum naturalium

Dodos and solitaires

(Raphidae)

Class Aves

Order Columbiformes

Family Raphidae

Thumbnail description

Large, stocky, flightless birds

Size

40 in (100 cm); 24-40 lb (10.5-17.5 kg); some estimates up to 50 lb (22.5 kg)

Number of genera, species

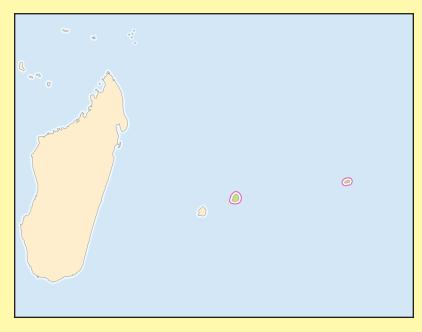
2 genera; 3 species

Habitat

Woodlands

Conservation status

Extinct



DistributionMascarene Islands

Evolution and systematics

The Mauritius dodo (*Raphus cucullatus*), Rodrigues solitaire (*Pezophaps solitaria*), and the Réunion solitaire (*Raphus soliatrius*) were three very large, flightless birds usually treated taxonomically as constituting the family Raphidae within the order Columbiformes. In their isolation on the Mascarene Islands, 500 mi (800 km) east of Madagascar, these aberrant pigeons evolved gigantism and flightlessness in the absence of native ground predators. Their existence has been documented in journal accounts and, in the case of the dodo and Rodrigues solitaire, in illustrations made by eyewitnesses as well as from skeletal material that has been excavated and examined in detail.

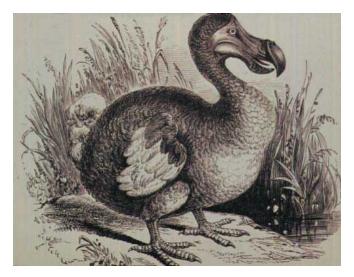
Masauji Hachisuka, in his extensive monograph on these species, reports about 20 firsthand accounts that mention the dodo, and evidence exists of 16 live dodos that were exported to Europe, India, or Japan. The dodo first appeared in the journals of Dutch Admiral Jacob Cornelius Van Neck in 1598 (published in 1601), who described dodos (in translation) as "larger than the swan, having the body of an ostrich, the feet of an eagle, few feathers on the body, the wings like a teal's." Among the more extensive accounts of the dodo, and perhaps also the last report of this species in the wild, is that of Volquard Iversen, who was shipwrecked on Mauritius for five days in 1662. Skeletal remains of dodos have been found in alluvial outwashes in bogs on the island. One mounted specimen reached Europe and was mentioned in a 1656 publication, but this specimen was burned in 1755 and only its head and right foot were saved. The left foot of another individual exists in the British Museum and another head in the Zoological Museum of Copenhagen.

More is known of the Rodrigues solitaire. The journal of François Leguat describes this species' behavior in a rather extensive account written when he and eight others inhabited Rodrigues for two years, from April 3, 1691 until May 21, 1693. Specimen records of solitaires are more extensive than those of dodos; over 2,000 solitaire bones were found in caves on the island between 1864 and 1875.

The existence on Réunion of another species of solitaire has been inferred only from contradictory travelers' accounts; no illustrations exist of this bird, nor have any raphid skeletal remains been found. This "solitaire" may actually have been an ibis (genus *Threskiornis*), as arguments attempt to reconcile skeletal remains found in the 1990s with the meager description of Réunion's "solitaire" by Sieur DuBois in 1669. This Réunion bird was described as a solitary bird, rarely seen, that inhabited remote mountain forests, fed on worms and soil insects, flew "but very little," and had a bill "like that of a Woodcock but larger." Nothing is known of its breeding. It was considered frequent in 1705 but disappeared suddenly thereafter and was last reported being seen in 1708.

While, at first glance, the Raphidae appear unlike pigeons, they are actually very close to them anatomically. Hence, both the pigeons (Columbidae) and the Raphidae are placed in the order Columbiformes. The dodo's big hooked bill is foreshadowed by the enlarged bill tips seen in most pigeons, and the skeletons of the dodos and pigeons are similar given the

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Early illustration of a dodo (*Raphus cucullatus*). (Illustration by George Bernard/Science Photo Library. Photo Researchers, Inc. Reproduced by permission.)

dodo's adaptation to flightlessness. Dodo feathers were identical to pigeon feathers and the loose plumage is like that seen in young squab. In fact, it is now generally agreed that the dodos are an example of neotony or paedomorphosis—the retention of juvenile characters into adulthood. Derived from pigeon-like stock, the dodos lost their wings, developed gigantism, and retained juvenal plumage and body form.

Physical characteristics

These birds were all about the size of a turkey, were heavily built, and possessed much reduced wings, strong feet, and a strong bill. The dodo had a featherless face, and its plumage was represented as bluish or brownish gray in paintings. Its bill was heavy and hooked and bore transverse ridges; possibly the bill's rhampotheca (horny sheath) was molted seasonally. Compared with the dodo, the Rodrigues solitaire was taller and more slender, with a smaller head and a slighter bill, metacarpal wing spurs, and largely brownish plumage.

John Tenniel's illustrations of the dodo in Lewis Carroll's Alice's Adventures in Wonderland express the traditional image of a dodo: a fat bird with a clumsy shape, a very large head, a heavy hooked bill, and a little tail of curly feathers. This characterization of the dodo may not be accurate. In 1993, Andrew Kitchener presented several arguments for a thinner dodo. He noted that drawings made before 1620 (by individuals who had seen these birds on the islands) showed thinner birds than did illustrations made after 1620 (which were done mostly in Europe). The very fat birds depicted in illustrations likely represent individual captives in Europe. Traditional descriptions of size emphasize Thomas Herbert's estimate (in 1634) of dodo body mass at 50 lb (22.7 kg), but estimates of body mass based on scale models, skeletal mass, and various scaling relationships show the dodo as a normally "thin" bird (about 23-39 lb; 10.5-17.5 kg). Scaling relationships suggest that the Rodrigues solitaire may not have been

as large as Leguat's estimate (in 1708) of a body mass of 45 lb (20.4 kg).

Distribution

Extinct, known only from Mauritius, Rodrigues, and possibly Réunion islands in the Indian Ocean

Habitat

Woodlands; no journal account associates either species with shore or river banks

Behavior

Despite the attention the birds received as curiosities by early seventeenth century visitors, nothing was recorded of the dodo's habits. The habits of the Rodrigues solitaire were better documented by Leguat and another later, brief account. Rodrigues solitaires, at least, were territorial. They produced wing sounds in apparent courtship displays and made use of wing spurs in agonistic encounters.

Feeding ecology and diet

The dodo diet was described as fruit and that of the Rodrigues solitaire as seeds, fruit, and foliage. Gizzard stones have been found in association with skeletal remains of both species. A marked annual fat cycle, common for many Mascarene species, has been postulated for the dodo. Such a cycle had been reported by Legaut for the Rodrigues solitaire: fat from March to September and thin the remainder of the year.

Stanley Temple postulated a close mutualistic relationship between the dodo and the tambalacoque tree (*Sideroxylon grandiflorum*; also known as *Calvaria major*) in that germination of the tree's hard seeds was promoted (or assisted) by passage through the dodo's gut. However, evidence for this relationship is tenuous.

Reproductive biology

There is very little information of undisputed acceptance. These species probably laid clutches of a single egg in nests on the ground. Young were probably altricial (hatched helpless and requiring considerable care), but no information exists to describe either their appearance or development. Leguat described Rodrigues solitaire adults bringing young together to a vacant territory as an arranged "marriage," but this behavior may represent formation of creches of young.

Conservation status

Extinct; dodo by 1670, Rodrigues solitaire by 1770, Réunion solitaire by 1750. Primary cause of extinction attributed to predation on eggs and young by pigs (*Sus scrofa*), rats (*Rattus rattus* and *R. norvegicus*), and, on Mauritius, monkeys (*Macaca fascicularis*). Cats (*Felis catus*) may have also have

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played a role. Introduced herbivores—cattle (*Bos taurus*), goats (*Capra* spp.), and, on Mauritius, deer (*Cervus timorensis*—likely altered native habitat, but this impact on dodo and solitaire populations was probably not as severe as that caused by predation by pigs, rats, and monkeys. Early extinctions of other native species on the Mascarene Islands are also attributed to introductions of exotic species.

Significance to humans

Dodos and solitaires were killed for food and to restock supplies of ships visiting the islands. While still extant, these species were presented to Europe as curiosities of exotic islands. The very short time between their European discovery and their extinction has enhanced their cultural significance as symbols of extinction.

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Species accounts

Dodo

Raphus cucullatus

TAXONOMY

Struthio cucullatus Linne, 1758, Mauritius (the name Didus ineptus Linne, 1766, used in older literature).

OTHER COMMON NAMES

French: Dronte de Mourice; German: Dronte; Spanish: Dronte de Mauricio.

PHYSICAL CHARACTERISTICS

Large turkey-like bird. Contemporary paintings of this species, based on live birds or traveler's descriptions, show grayish plumage, darker above and lighter below, vellowish white wings with five to six larger feathers, and a tail with five curled feathers. The hooked bill was deep yellow with a horny sheath on the upper and lower mandibles. The skin on the face

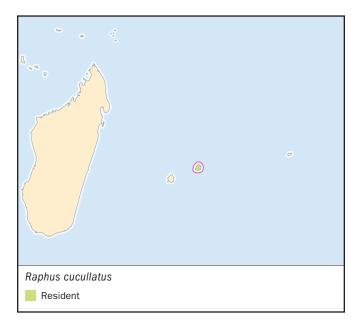


Raphus cucullatus

and around the bill was dull gray and bare of feathers.

DISTRIBUTION

Mauritius, a small (720 mi²; 1,865 km²) volcanic island about 500 mi (800 km) east of Madagascar in the Indian Ocean.



HABITAT Woodlands.

BEHAVIOR

The most extensive record of the dodo comes from Volquard Iversen, who was shipwrecked on Mauritius for five days in 1662 (not in 1669 as indicated in some accounts). Iversen did not find the dodo on the mainland but did see it on an islet that was isolated from pigs and monkeys but that was still accessible by foot at low tide. Iversen wrote: "Amongst other birds were those that men in the Indies call doddaerssen; they were larger than geese but not able to fly. Instead of wings they had small flaps; but they could run very fast." He wrote that after catching them, other dodos would run up when the captive screamed ("When we held one by the leg he let out a cry, others came running forward to help the prisoner, and were themselves caught"). One Dutch sailor described dodos in 1631 as "very serene or majestic, they showed themselves to us with an extremely dark face with open beak, very dapper and bold in their walk, would hardly move out of our way."

FEEDING ECOLOGY AND DIET

Dodos reportedly ate fruit. Dodos swallowed stones apparently to aid the breakdown of food in the crop. This species apparently had a seasonal fat cycle. A possible mutualistic relationship existed between dodos and the tambalacoque tree, with passage of the tree's seed through the dodo's gut promoting the seed's germination.

REPRODUCTIVE BIOLOGY

Dodos nested on the ground and laid a one-egg clutch. The egg was described by François Cauche in 1651 as being the same size as a half-penny roll. Cauche used this same comparison for the egg of the great white pelican (*Pelecanus onocrotalus*), which has a 6.3 oz (180 g) egg. The general relationship between egg mass and incubation period suggests that the dodo's incubation period was about 37 days.

CONSERVATION STATUS

Extinct. The Mascarene Islands had been known to Arab navigators prior to European contact but nothing of their exploration of these islands is known other than the appearance of the islands on their maps. For Europeans, the existence of Mauritius was first recorded in 1507 by Portugese sailors, and until 1598 it remained uninhabited except for pigs, goats, and fowl that were stocked on the island. The primary cause of extinction of the dodo is likely to have been egg predation by introduced pigs, monkeys, and cats, even though dodos were slaughtered in large numbers by sailors. Dodos were very rare by 1640, although some survived to 1662, at least, on offshore islets. The last sighting of a dodo was recorded somewhere between 1665 and 1670, but it is an unconfirmed report.

SIGNIFICANCE TO HUMANS

Dodos were a source of fresh meat for crews and passengers of ships traveling in the Indian Ocean. The dodo is the first species to be counted as becoming extinct because of human activity. •

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Rodrigues solitaire

Pezophaps solitaria

TAXONOMY

Didus solitaria Gmelin, 1789, Rodrigues.

OTHER COMMON NAMES

French: Dronte de Rodriguez; German: Einsiedler; Spanish: Solitario de la Rodríguez.

PHYSICAL

CHARACTERISTICS

These large birds were strongly sexually dimorphic in size; males were larger than females and possessed metacarpal spurs the size of "musketballs."

DISTRIBUTION

Rodrigues, a small (40 mi²; 104 km²) volcanic island about 220 mi (350 km) east of Mauritius in the Indian Ocean.





Pezophaps solitaria

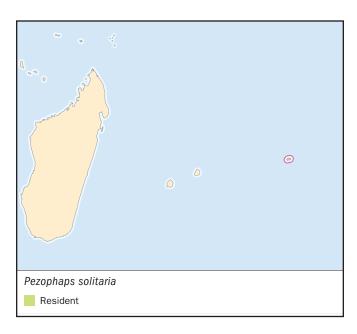
BEHAVIOR

Better known than the dodo from contemporary accounts. François Leguat described their behavior in 1692: solitaires lived in pairs, were territorial, laid clutches of a single egg, and their young joined a creche. Skeletal remains show mended fractures in the metacarpus that suggest a pugilistic function. Wings were vigorously flapped "when angry" and produced "a great noise...something like thunder in the distance" or "very like that of a rattle;" this display was likely an aspect of courtship behavior. Their voice had been described as similar to that of a gosling's squeak.

This solitaire was an apparently territorial species. During incubation or while caring for their young during the time "which [it] is not able to provide for its self in several Months, they will not suffer any other Bird of their Species to come within two hundred yards round of the Place;" males responded to intruding males and females to other females. This stated measure suggests maintenance of a 25-acre (10-ha) territory.

FEEDING ECOLOGY AND DIET

This solitaire was reported to have fed on seeds, *Latania* palm fruit, and foliage. Like dodos, Rodrigues solitaires appeared to



have had a marked annual fat cycle in which they were fat from March to September and thin for the remainder of the year. Gennes de la Chancelière described two young birds as each having a fat layer 1-in (2.5-cm) thick over the body. Gizzard stones have been found with skeletal remains.

REPRODUCTIVE BIOLOGY

Rodrigues solitaires laid a single egg in a nest constructed of palm leaves. Nests were built on the ground and were about 16 in (40 cm) in height. Both sexes incubated eggs. Leguat reported a seven-week incubation period, but based on estimated egg size, models predict a 37-day incubation period. Young apparently joined creches after a period with parents, although Leguat described this social amalgamation of broods as "marriages."

CONSERVATION STATUS

Extinct. Portuguese sailors reached Rodrigues in 1507, but the island was not inhabited by humans until May 1, 1691, when Leguat and eight others arrived. Introduced pigs were especially devastating predators of young solitaires and eggs. A few solitaires were reported in the wild in 1755 and 1761, but these seem to be the last sightings. Individuals who speculate that the solitaire disappeared in the 1750s blame feral cats and possibly dry season fires for the solitaire's demise.

SIGNIFICANCE TO HUMANS

Rodrigues solitaires were a source of fresh meat for crews and passengers of ships traveling in the Indian Ocean. ◆

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Peter E. Lowther, PhD

Psittaciformes Parrots

(Psittacidae)

Class Aves

Order Psittaciformes

Family Psittacidae

Number of families 1

Thumbnail description

Very small to large, often brightly colored birds with hooked bill and zygodactyl feet (two toes facing forward and two backward)

Size

3.2-39.4 in (8-100 cm); 0.02-6.6 lb (0.01-3 kg)

Number of genera, species

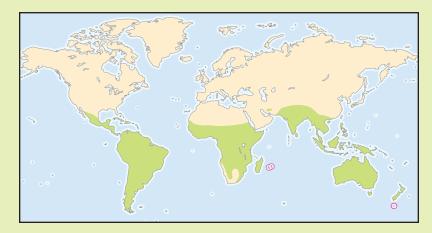
84 genera; 353 species

Habitat

Forests, woodlands, and savanna

Conservation status

Critically Endangered: 15 species; Endangered: 34 species; Vulnerable: 45 species; Lower risk: 30 species; 10 species extinct since 1600



Distribution

Mainly Southern Hemisphere and predominantly in tropical or subtropical regions, but north to latitude 34° north in eastern Afghanistan and south to latitude 55° south at Tierra del Fuego

Evolution and systematics

Parrots are an ancient group but significant gaps in their fossil history have raised questions about their evolution. The earliest fossil dates from the late Cretaceous, 70 million years ago (mya), and comes from Wyoming, but some doubt that the fragment found there is from a parrot. Dating from the early Miocene, some 25 mya, the fossil parrot Archaeopsittacus verreauxi found near Allier, France, and, with similarities to the modern gray parrot (Psittacus erithacus), seems the earliest record that can unquestionably be referred to as Psittaciformes. Confirming a widespread existence of parrots at this time is a northwestern Queensland, Australia, fossil indistinguishable from modern cockatoo (Cacatua) species. Another representative of a modern genus is Conuropsis fratercula from the upper Miocene, approximately 10-15 mya, and described from remains found in Nebraska. In 1998, G. Mayr and M. Daniels concluded that parrots appear to be a very ancient group possibly diverging from other birds in the Palaeocene, at least 60 mya.

The homogeneity of parrots has caused difficulties for systematists attempting to determine taxonomic arrangements. In 1900, D. Thompson followed the classification based entirely on external features and proposed almost 10 years earlier by T. Salvadori, who recognized seven families, one of which, Psittacidae, was divided into six subfamilies. For almost 70 years the work of these pioneers formed the basis for taxonomy of the Psittaciformes, though higher categories were downgraded to produce six or seven subfamilies in a single family. In 1975, a major essay detailing anatomical, morphological, and behavioral characters was presented by G. A. Smith, who recognized a single family divided into four sub-

families, with one subfamily, Platycercinae, being further divided into four tribes, and another, Loriinae, divided into five tribes. In a revised edition of his *Parrots of the World*, published in 1989, J. M. Forshaw redistributed Smith's tribes among three subfamilies—Loriinae (no tribes), Cacatuinae (three tribes), and Psittacinae (eight extant tribes)—and similar or variably modified arrangements were adopted by other workers until the advent of biochemical techniques. Peters Checklist lists 81 genera and 340 species, but by 2000, there emerged a general consensus, emanating principally from biochemical and chromosomal studies, that cockatoos are quite distinct from other parrots and should be separated at family level. The 353 species of parrots are generally placed in 84 genera, which, in turn, are grouped in nine or more tribes in three or up to five subfamilies and one or two families.

Physical characteristics

Parrots retain a strong structural homogeneity, but vary in size from the pygmy parrots of New Guinea—less than 3.5 in (9 cm) in length and weighing only 0.35 oz (10 g)—to the giant macaws of South America and the bulky kakapo (*Strigops habroptilus*) of New Zealand. Up to 40 in (100 cm) from bill to tail, the hyacinth macaw (*Anodorhynchus hyacinthinus*) is the largest parrot, while the kakapo, weighing up to 6.6 lb (3 kg), is the heaviest. Plumage color is variable, and, although most are brilliantly colored, with green, red, and yellow predominating, there are uniformly dull-colored species like the two *Coracopsis* parrots from Madagascar. Colors can be structural, pigmentary, or a combination of both. Blue and green are



Little corellas (*Cacatua sanguinea*) grasp each other's legs in a game they use for social interaction. (Photo by Wayne Lawler. Photo Researchers, Inc. Reproduced by permission.)

structural colors, due principally to back-scattering of light from the texture of the feathers. Named after its discoverer, Danish ornithologist Jan Dyck, this Dyck-texture is not present in feathers of cockatoos, hence the absence of green and blue from their plumage. A capacity to produce abnormal or mutant plumages, particularly among neotropical species, is well-known in captive parrots. There are numerous color variants of domesticated budgerigars (Melopsittacus undulatus) and cockatiels (Nymphicus hollandicus). Only two species, the Papuan lory (Charmosyna papou) of New Guinea and the St. Vincent Amazon (Amazona guildingii) of the Lesser Antilles, have distinct morphs in wild populations. Sexual dichromatism is common in parrots from Australasia and Asia, but uncommon in African and neotropical species. Females of sexually dichromatic species normally are duller than males and lack some prominent markings. Two exceptions are the eclectus parrot (Eclectus roratus) from Australasia and Rüppell's parrot (Poicephalus rueppellii) from southwest Africa. So different are sexes of the eclectus parrot that for nearly a century the green males and red females were considered separate species. Juveniles generally resemble, or are duller than, females.

Apart from erectile headcrests of cockatoos, structural modifications in plumage are uncommon. Tails may be long, narrow, and pointed, broad and rounded, or short and squarish. Markedly elongated central tail feathers are found in the Papuan lory, while long central tail feathers of racket-tailed parrots are subterminally bare and tipped with flag-like spatules. Narrow, pointed wings usually are associated with swift, direct flight, and are prevalent in lories, while broad, rounded wings often denote slow, labored flight.

The unique and specialized bills of parrots enable the birds to crush seeds and nuts, which constitute the diet of many species. Minor modifications in bill shape are associated with different foraging techniques. An elongated, less-curved upper bill facilitates digging of roots and corms or the extraction of seeds from hard, woody fruits. Narrow, protruding bills are used for probing into blossoms when gathering pollen

or nectar. The thick, fleshy tongue generally has a dense, horny epithelium towards the tip, but in nectar-feeding species it is tipped with brush-like papillae, an adaptation for gathering pollen and nectar. Both the hooked bill and zygodactyl feet are used when climbing amidst foliage, the former to grasp a branch as the bird steps higher, and the foot to hold a fruit while seeds are extracted.

Distribution

Parrots are distributed mainly in the Southern Hemisphere, and are most prevalent in tropical regions. Following extinction of the Carolina parakeet (Conuropsis carolinensis) in North America, the slaty-headed parakeet (Psittacula himalayana) is the most northerly species, reaching latitude 34° north in the Safed Koh area of northern Afghanistan. Occurring south to latitude 55° south in Tierra del Fuego, the Austral conure (Enicognathus ferrugineus) occupies the southernmost range, though the red-fronted parakeet (Cyanoramphus novaezelandiae) formerly ranged farther south to Macquarie Island. The order is most strongly represented in South America and Australasia, but the marked diversity in Australasia has prompted speculation that parrots originated in the Old World, with dispersal being facilitated by interconnections of the southern continents in the Cretaceous and early Tertiary, some 70-90 mya. Parrots occur in Asia, mainly on the Indian subcontinent, and in Africa, but representation in these regions is much less than what might be expected.

Habitat

Although found in a variety of habitats, parrots are most prevalent in lowland, tropical, or subtropical rainforest, where they seem to prefer forest margins or clearings. Species that inhabit open country also show a strong attachment to trees, especially along watercourses, and seldom are encountered far from cover. Parrots are less common at higher altitudes, and those that do occur there are absent from, or are rare in, neighboring lowlands. There are distinctive highland forms, including the highly inquisitive kea (*Nestor notabilis*), which commonly frolics in snow high up in the Southern Alps of New Zealand.

One of the few species confined to specialized habitats is the terrestrial ground parrot (*Pezoporus wallicus*), which occurs only in coastal and contiguous mountain heathlands in southern Australia, a very restricted habitat that is rapidly disappearing. Along the seaboard of southern Australia, the rock parrot (*Neophema petrophila*) frequents coastal sand-dunes and offshore islets, where it nests in rock crevices. Dependence on particular plants or vegetation communities, usually as sources of food or nest sites, can be evident in the dispersal of some species.

Behavior

Being predominantly green and living in the rainforest canopy, most parrots are difficult to observe, and often the only sighting is a momentary glimpse of a screeching flock in swift overhead flight. Species that inhabit open country or are plentiful near urban centers tend to be conspicuous, and there is more information on their habits, but as a group parrots are not well-known.

Vocalizations are used to maintain pair-bonds and to reinforce flock cohesion. The distinctly metallic call-notes typically are harsh and unmelodic, generally based on a simple syllable or combination of simple syllables. Variation comes primarily from the timing of repetition. Calling is prevalent in early morning and early evening, especially during flights from and to roosts. Daytime foraging or resting normally is undertaken in relative silence. Solitary species such as the kakapo and night parrot (*Pezoporus occidentalis*) tend to be less vocal than highly social species, who normally exhibit dueting within pairs. Although well-known in captive parrots, vocal mimicry rarely has been reported from the wild.

The flight of most parrots, especially small species, is swift and direct. In larger species flight is variable; macaws are fairly fast, their long tails streaming behind to give a distinctive flight silhouette, but the buoyant flight of black cockatoos is slow and labored. It has been estimated that galahs (*Eolophus roseicapillus*) can maintain for many minutes a flight speed of 44 mi (70 km) per hour, thereby covering long distances in a short time, and speeds of up to 50 mi (80 km) per hour probably are reached by migrating swift parrots (*Lathamus discolor*).

Regular seasonal migration is known only from southeast Australia, where blue-winged (*Neophema chrysostoma*), orangebellied (*N. chrysogaster*), and swift parrots cross the 187-miwide (300-km-wide) Bass Strait between breeding areas in Tasmania and mainland wintering sites. Altitudinal movements occur in some areas, but the extent to which highland sites are vacated is influenced by severity of winter conditions. Seasonal patterns have been identified in movements of some nomadic parrots.

Feeding ecology and diet

The diet of most parrots includes seeds and fruits procured in treetops or on the ground. These parrots are adept at dehusking seeds to extract nutritious kernels. With the thick tongue, a seed is held against the broad, ridged underside of the upper bill while the front cutting edge of the lower bill efficiently peels away the seed-coat. Use of a foot, usually the left one, to hold food up to the bill is prevalent among arboreal species, but less common or even absent in predominantly ground-feeding species.

Minor modifications in bill structure are associated with different feeding techniques. For example, elongated, less-curved upper bills of slender-billed (*Cacatua tenuirostris*) and Western corellas (*C. pastinator*) are used to dig up roots, bulbs, and corms, while the broad, blunt bill of the red-tailed black cockatoo (*C. banksii*) is ideal for crushing seeds or hard nuts.

Apart from occasionally dropping to the ground a few viable seeds or undamaged fruits, parrots play no role as dispersal agents, and their feeding can significantly impact local levels of seed production. Field studies reveal that red-lored



A rainbow lorikeet (*Trichoglossus haematodus*) extracts nectar from a flowering swamp bloodwood in Queensland, Australia. (Photo by Mitch Reardon. Photo Researchers, Inc. Reproduced by permission.)

Amazons (*Amazona autumnalis*) can destroy entire seed crops from poorly fruiting *Stemmadenia* trees or up to 33% of crops from heavily fruiting trees. A flock of 100 orange-chinned parakeets (*Brotogeris jugularis*) was estimated to have taken 15% of the seed crop of a fig tree during just one morning feeding session.

Because the arboreal lories and lorikeets feed on pollen, nectar, and soft fruits, their gizzards are weak and less muscular than those of seed-eating species. Constantly on the move in search of flowering trees or shrubs, these specialists use the protruding, sharply pointed bill and "brush-tipped" tongue to gather pollen and nectar. Rainbow lorikeets (*Trichoglossus haematodus*) probe into *Eucalyptus* flowers at a rate of 35 flowers per minute, and in two or three hours one can gather nectar from up to 5,000 flowers, sufficient to satisfy its daily needs. Pygmy parrots also are specialist feeders, using the stiffened, projecting shafts of their short tail feathers and their long, curved claws to move woodpecker-like up and down tree trunks or stout limbs, gleaning lichen from the surface.



Green-winged (Ara chloroptera) and scarlet macaws (A. macao) at a clay lick in Manú National Park, Peru. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)

Reproductive biology

Most parrot species appear to be monogamous and remain paired for long periods, perhaps for life. A notable exception is the kakapo, a flightless, lek-display species whose males take no part in incubation or care of the young. Pairs and family groups are discernible within flocks of gregarious parrots, with paired birds usually perching or foraging together and regularly indulging in mutual preening.

Our knowledge of the nesting habits of parrots is patchy, and much of the available information comes from captive birds. Breeding takes place when climatic conditions produce reliable food supplies for rearing young; in temperate regions this is during spring-summer months. In the tropics rainfall usually is key to the timing of breeding. In arid regions, where rainfall is highly irregular, availability of surface water, often originating from distant storms, can bring about a prompt onset of breeding. In southern Australia, budgerigars normally breed during spring-summer months, while in the north breeding occurs mainly in the early dry season, during autumn and winter, but in any district nesting may take place at other times in response to drought-breaking rains or a flow of surface water, and rapid sexual development, with males producing sperm within 60 days of fledging, enables the population to increase quickly in response to propitious conditions.

Available information suggests that courtship displays generally are simple, and even the most elaborate consist of a sequence of simple actions such as bowing, wing-drooping,

wing-flicking, tail-wagging, foot-raising, or dilation of eye pupils. Prominently colored parts of the male plumage feature strongly in displays. Prior to copulation, there is considerable bodily contact: bill-nibbling, mutual preening, and courtship feeding. During this feeding, the male feeds regurgitated food to the female in the same manner as parents feed chicks. More spectacular "drumming" displays are undertaken by the palm cockatoo (*Probosciger aterrimus*). These involve outstretching of wings, raising of the crest, and stomping of a foot. Unique is the highly specialized lek display by male kakapos. At bowl-like depressions, up to 12 of which are excavated and meticulously maintained by each male, the male emits loud "booms" from inflated thoracic air-sacs followed by a display featuring an opening of the wings and slight bowing of the head while moving backward.

Nests usually are in hollows in trees or holes in arboreal and terrestrial termitaria, occasionally in holes in earth-banks or in crevices among rocks. If in termitaria, the tunnel and nesting chamber are excavated by the birds, whereas in trees few parrots excavate fresh hollows; most use natural hollows or old cavities of other birds, such as woodpeckers or barbets. Crevices in walls or under eaves of buildings sometimes are used for nesting, especially by the rose-ringed parakeet (*Psittacula krameri*) in India. Keas, kakapos, and the burrowing parakeet (*Cyanoliseus patagonus*) from South America dig burrows in the ground or under rocks; some macaws and the scarlet-fronted parakeet (*Aratinga wagleri*) nest in fissures in cliff-faces; the rock parrot nests in crevices in rocks or in old

burrows of seabirds; and a few Australasian species nest on the ground under or in grass tussocks. Unique are the often huge communal nests of twigs and dead branches built in trees by monk parakeets (*Myiopsitta monachus*), with each pair having its own nest chamber. Lining material normally is not brought to the nest cavity, the eggs being laid on decayed wood dust or crumbled earth that accumulates at the bottom. Some *Agapornis* lovebirds, *Loriculus* hanging parrots, and *Neophema* parakeets line their nests with grass, twigs, or leaves carried by the birds in the bill or thrust among the body feathers, particularly those of the rump.

Eggs are white, and usually one is laid every other day. Clutch sizes vary from one to three for large parrots, three to five for medium-sized species, and up to eight or more for some small parrots. It is difficult to ascertain when incubation begins. As a rule, it begins with or immediately after laying of the second egg. Generally the female alone incubates, and she is fed by the male, but there are many species in which males share incubation. Male lorikeets spend considerable time in the nest with females, but it is doubtful that they participate in incubation. Duration of incubation varies roughly in proportion to the size of the birds; for small parrots it is from 19–23 days; for large macaws it can be more than 30 days.

Newly hatched chicks are blind and naked or with sparse natal down, which is white in most species. Nestling cockatoos are well covered with down; pink in the galah, yellow in other species. Eyes open seven to 14 days after hatching, and in most species the natal white down is soon replaced by, or supplemented with, dense gray down, which gradually gives way to feathers. Newly hatched nestlings are closely brooded and fed by the female, who in turn is fed by the male. When chicks are about five to 10 days old the male assists by feeding them directly. Chicks develop slowly and remain in the nest for three to four weeks in the case of small parrots and up to three months in large macaws. In proportion to size, lories and lorikeets have a long nestling period. A disproportionately long nestling period of up to nine weeks has been recorded for the red-fan parrot (Deroptyus accipitrinus). A relatively short nestling period of 24 days has been recorded for the medium-sized ground parrot; their chicks can run from the nest at 18 days. After leaving the nest, young birds are fed by their parents for varying periods. Post-fledging independence is almost immediate in young budgerigars, while at the other extreme young Calyptorbynchus black cockatoos are fed by their parents for up to four months after leaving the nest. Young birds usually remain with their parents until near onset of the next breeding season, thus forming the family parties often observed.

Juveniles generally resemble females, or are duller than adults of both sexes. A distinctly juvenal plumage is present in some, including the crimson rosella (*Platycercus elegans*) from Australia and some *Psittacula* species. Juveniles usually have shorter tails than do adults; this is especially so in the Papuan lory and some *Psittacula* species, adults of which have elongated central tail feathers, and in *Prioniturus* racket-tailed parrots, where juveniles lack the central rackets. There is a striking difference between adults and juveniles of the vulturine parrot (*Pionopsitta vulturina*); in adults the bare head is sparsely covered with inconspicuous "bristles," but in juve-



Rainbow lorikeets (*Trichoglossus haematodus*) groom each other in a eucalypt forest of coastal southeastern Australia. (Photo by Gregory G. Dimijian. Photo Researchers, Inc. Reproduced by permission.)

niles the head is well feathered. In general, where adults of a species have dark bills, those of juveniles generally are pale, but when adults have pale bills, those of juveniles are dark or have dark markings at the base of one or both bills. If the irides of adults are pale colored, such as orange, yellow, or white, those of juveniles usually are dark. The time taken for juveniles to attain adult plumage varies greatly; it may be within months of leaving the nest, or it may be up to three or four years and sometimes later. Some species acquire adult colors rapidly with the first complete molt, while for others it is a slow, imperceptible process. With certain species, including the red-cheeked parrot (Geoffroyus geoffroyi) and the plumheaded parakeet (Psittacula cyanocephala), the distinct juvenal plumage is replaced in young males by the plumage of adult females before they acquire adult male plumage.

Conservation status

In 2000 more than 90 of the approximately 350 species were in danger of extinction according to the IUCN, making parrots the most threatened of the major bird families. Habitat destruction and trapping for the live-bird trade were identified as the major threats. Another factor threatening these species was their restricted ranges. This was highlighted by the high proportion of island forms among the 18 parrot taxa listed in 1981 as having become extinct between 1600 and 1980.

Of particular concern is the widespread destruction of tropical forest, a habitat favored by many species. Alarming levels of clearing in the developing nations of Amazonia, southeast Asia, and central Africa, regions of strong endemism, are impacting local and regional populations. Protection of habitat in reserves seems inadequate to arrest declining numbers.

In Colombia, almost complete destruction of stands of wax palms (*Ceroxylon quindiuense*) has brought about near extinction of the yellow-eared parrot (*Ognorhynchus icterotis*), which is dependent on the palms for food and nesting sites. In the highlands of Mexico, a probable relative, the thick-billed

parrot (*Rhynchopsitta pachyrhyncha*), is similarly threatened by intensive felling of *Pinus* forest, and no longer can the species wander north into southern Arizona. The highly specialized, terrestrial ground parrot occurs only in coastal or near coastal heathlands in east and southwest Australia, but as these heathlands are claimed for urban development or agriculture, local populations are extirpated.

Much recovery effort has been directed at island parrots, and results are encouraging. Economic benefits derived from ecotourism associated with the occurrence of spectacular Amazona parrots have been promoted successfully in the Lesser Antilles to outweigh short-term gains from logging or hunting. This has resulted in steady increases of four threatened endemic species. Beginning in 1968 and remaining operational at the time of writing (2001), an intensive effort to save the Puerto Rican Amazon (Amazona vittata) from extinction has been conducted under the sponsorship of the U.S. Fish and Wildlife Service, the U.S. Forest Service, the World Wildlife Fund, and the Puerto Rican government. Captive breeding and protection of known nest-sites have improved the previously low fledging success rate. A similar program was initiated on Norfolk Island in 1983 by the Australian National Parks and Wildlife Service to save the critically endangered Norfolk Island parakeet (Cyanoramphus cookii), the population of which at that time was estimated to be between 17 and 30 birds. This program has been successful, and in 2000 the population was estimated to exceed 100 birds. On Mauritius, the almost total loss of native forest, coupled with hunting and predation by introduced macaques, reduced numbers of the endemic Mauritius parakeet (Psittacula echo) to an estimated 10 birds in the 1980s. A recovery program involving captive breeding and protection of known nest-sites has resulted in a steady increase to an estimated 120-130 birds in 2001.

The plight of parrots is acknowledged in legislative protection afforded under international and national statutes. Since 1981, all species, except the cockatiel, the rose-ringed parakeet, and the budgerigar, have been listed on Appendices

to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and the listing in 2001 of 38 species on Appendix I recognized that the endangered status of those species renders their involvement in commercial trade unacceptable. Although domestic legislation may afford additional protection to endangered species in range states, inadequate enforcement often undermines the effectiveness of that protection. In some instances, including the Endangered Species Act, protection is given to non-native endangered parrots through controls on trafficking.

Significance to humans

The popularity of parrots as pets is unequalled in any other group of birds, and one species, the budgerigar, ranks second to the goldfish as the world's most popular pet animal.

Damage to crops by parrots has been reported from some countries, but there has been little objective evaluation of the problem. Losses experienced by farmers locally can be severe, but studies undertaken in Australia have shown that this damage is not economically significant at the national level. It has been demonstrated repeatedly that shooting, trapping, or poisoning parrots are ineffective in reducing damage. Although it is unlikely that damage can be completely eliminated, levels can be reduced by modification of farming practices or by adopting protective measures based on sound ecological principles.

In some parts of their range, parrots are hunted for food or for their feathers, the latter being used as adornments in ceremonial or religious rituals. Tail feathers from large macaws are harvested by indigenous peoples in Central and South America, while in New Guinea there is widespread trading of the highly prized flight feathers from Pesquet's parrot and tail feathers from the Papuan lory. Also in New Guinea, persistent hunting of palm cockatoos for food has extirpated the birds from the environs of most larger towns and villages.



1. Monk parakeet (*Myiopsitta monachus*); 2. Brown-throated parakeet (*Aratinga pertinax*); 3. Rosy-faced lovebird (*Agapornis roseicollis*); 4. Rainbow lorikeet (*Trichoglossus haematodus*); 5. Kea (*Nestor notabilis*); 6. Painted parakeet (*Pyrrhura picta*); 7. Philippine hanging-parrot (*Loriculus philippensis*); 8. Red-breasted pygmy-parrot (*Micropsitta bruijnii*); 9. Pesquet's parrot (*Psittrichas fulgidus*); 10. Yellow-crowned Amazon (*Amazona ochrocephala*). (Illustration by Barbara Duperron)



1. Eastern rosella (*Platycercus eximius*); 2. Gray parrot (*Psittacus erithacus*); 3. Hyacinth macaw (*Anodorhynchus hyacinthinus*); 4. Scarlet macaw (*Ara macao*); 5. Palm cockatoo (*Probosciger aterrimus*); 6. Rose-ringed parakeet (*Psittacula krameri*); 7. Budgerigar (*Melopsittacus undulatus*); 8. Female (left) and male Eclectus parrot (*Eclectus roratus*); 9. Cockatiel (*Nymphicus hollandicus*); 10. Sulphur-crested cockatoo (*Cacatua galerita*). (Illustration by Joseph E. Trumpey)

Species accounts

Palm cockatoo

Probosciger aterrimus

SUBFAMILY

Cacatuinae

TAXONOMY

Psittacus aterrimus Gmelin, 1788, New Holland, Aru Islands, Indonesia. Four subspecies.

OTHER COMMON NAMES

English: Great palm cockatoo, great black cockatoo, Goliath cockatoo, Goliath aratoo, Cape York cockatoo, black macaw; French: Microglosse noir; German: Arakakadu; Spanish: Cacatúa Enlutada.

PHYSICAL CHARACTERISTICS

23.6 in (60 cm); 1.8–2.4 lb (910–1,200 g). Black plumage with red or pink cheeks from bill to eye; large head crest.

DISTRIBUTION

P. a. aterrimus: Aru Islands and Misool, western Papuan Islands, Indonesia. P. a. goliath: western Papuan Islands, except Misool, Indonesia, and central New Guinea. P. a. stenolophus: north New Guinea. P. a. macgillivrayi: south New Guinea and Cape York Peninsula, northernmost Australia.

HABITAT

Lowlands in rainforest, gallery forest, tall secondary growth, monsoon woodland, partly cleared lands and dense savanna woodland; favors rainforest margins adjoining *Eucalyptus* woodland.



BEHAVIOR

Resident. Noisy, conspicuous when active in the morning and late afternoon, but quiet and secretive when resting in forest trees. Singly or in pairs while breeding, but small groups at other times; roosts singly, departing well after sunrise to join other birds at congregating tree, where much greeting is displayed. When alarmed or excited, bare facial patches become deeper red.

FEEDING ECOLOGY AND DIET

Feeds on seeds, nuts, fruits, berries, leaf buds, and probably insects and their larvae, procured mainly in trees, but will come to the ground; on Cape York Peninsula, favored foods are fruits of *Pandanus* and *Parinari nonda*.

REPRODUCTIVE BIOLOGY

Monogamous. Pairs advertise territory occupation from atop dead tree-trunk with spectacular "drumming" display featuring raising of crest, spreading of wings, and striking a hollow trunk with stout stick held in the foot while pirouetting slowly to the accompaniment of loud, whistling call-notes. Breeding recorded most months; nest in tree-hollow, bottom lined with layers of splintered twigs, forming platform for single egg; incubation by female 33 days; chick fed by both parents; fledging at 90 days.

CONSERVATION STATUS

Listed on CITES Appendix I. Affected by logging and forest clearing in parts of New Guinea; hunted for food; widespread capture for live-bird trade.

SIGNIFICANCE TO HUMANS

In vicinity of towns and villages locally extirpated by hunting for food and trapping for live-bird trade; much in demand as aviary bird. ◆

Sulphur-crested cockatoo

Cacatua galerita

SUBFAMILY

Cacatuinae

TAXONOMY

Psittacus galeritus Latham, 1790, New South Wales. Four subspecies.

OTHER COMMON NAMES

English: Greater sulphur-crested cockatoo, white cockatoo; French: Grande Cocatoès à huppe jaune; German: Grosser Gelbhaubenkakadu; Spanish: Cacatúa Galerita.

PHYSICAL CHARACTERISTICS

19.7 in (50 cm); 1.5-1.8 lb (750–900 g). White plumage, yellow crest on the head, blackish bill.

DISTRIBUTION

C. g. galerita: east and southeast Australia. C. g. fitzroyi: north Australia. C. g. triton: New Guinea and adjacent islands. C. g. eleonora: Aru Islands, Indonesia.



HABITAT

Lowlands and foothills; wide variety of forests and woodlands, also lightly timbered grasslands, plantations, and urban parks or gardens; favors forest margins and trees bordering watercourses, but rarely within closed forest.

BEHAVIOR

Resident. Noisy, highly conspicuous; pairs or family parties in breeding season, at other times in flocks, sometimes comprising hundreds of birds. Wary; in open country "sentinel" birds sit in treetops to warn feeding flock of approaching danger; roosts communally, departing at sunrise to drink and fly to feeding grounds, often at some distance; shelters in trees during middle of day, resuming feeding in late afternoon and then drinking before returning to roost.

FEEDING ECOLOGY AND DIET

Feeds on the ground and in trees, taking seeds, nuts, fruits, blossoms, and insects and their larvae; will attack newly planted and ripening grain crops, but destroys seeds of serious weed pests.

REPRODUCTIVE BIOLOGY

Monogamous. Simple courtship display features raising of crest, head bobbing, and swishing of head from side-to-side in "figure 8" movement while uttering soft, chattering notes. In south, breeding is from August to January, and in north from May to September; nest is high up in a tree hollow, usually near water; clutch of two or three eggs incubated by both sexes for 27 days; chicks fed by both parents; fledging at about 70 days.

CONSERVATION STATUS

Generally common; locally abundant in east Australia; in 1990s population estimated at more than 500,000. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Very popular cagebird; in New Guinea, yellow crest feathers used in ceremonial headdress. Can damage grain crops. ◆

Cockatiel

Nymphicus hollandicus

SUBFAMILY

Cacatuinae

TAXONOMY

Psittacus hollandicus Kerr, 1792, New Holland-New South Wales. Monotypic.

OTHER COMMON NAMES

English: Quarrion, cockatoo-parrot, crested parrot, weero; French: Calopsitte èlègante; German: Nymphensittich; Spanish: Cacatúa Ninfa.

PHYSICAL CHARACTERISTICS

12.6 in (32 cm); 2.6–3.5 oz (75–100 g). Slender bird with long wings and tail. Gray plumage, raised yellow crest, orange cheeks, and white wing patch. Males have brighter markings than females.

DISTRIBUTION

Interior of mainland Australia.

HABITAT

Lowlands; most types of dry, open, lightly timbered country, including farmlands and parks or gardens; favors trees bordering watercourses, and avoids dense woodland or treeless plains.



BEHAVIOR

Nomadic in north, migratory in south. Usually in small flocks, but large flocks at isolated waterholes; conspicuous in flight, showing diagnostic white wing patches; silhouette with backward swept wings; inconspicuous when feeding on the ground or perching lengthways on stout limb; roosts communally, departing at or before sunrise to assembly point in nearby tree and then to feeding area; shelters in trees during middle of day, resuming feeding in late afternoon and then drinking prior to returning to roost; more active on cool, overcast days.

FEEDING ECOLOGY AND DIET

Feeds mainly on the ground, sometimes with other parrots, taking seeds of grasses and herbs; also takes berries and will attack grain crops.

REPRODUCTIVE BIOLOGY

Monogamous; mated pairs or family groups probably basic social unit; breeding influenced by rainfall, but in south mainly from August to December and in north from April to September; nest in tree hollow usually near water, and two or more nests sometimes in same tree; clutch of four or five eggs incubated by both parents; fledging at 25–30 days.

CONSERVATION STATUS

Generally common, locally abundant in north; in 1990s population estimated to exceed one million.

SIGNIFICANCE TO HUMANS

Very popular cagebird; domesticated with numerous color mutations well established in captivity. ◆

Eastern rosella

Platycercus eximius

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus eximius Shaw, 1792, New South Wales. Three subspecies.

OTHER COMMON NAMES

English: Rosella, rosella parrot, red rosella, common rosella, golden-mantled rosella; French: Perruche emnicolore; German: Rosellasittich; Spanish: Perico Multicolor.

PHYSICAL CHARACTERISTICS

12 in (30 cm); 3.2–4.3 oz (90–122 g). Bright plumage with scale-like black marking on the back; red head.

DISTRIBUTION

P. e. eximius: southeastern Australia north to northeast New South Wales. P. e. elecica: northeast New South Wales and southeast Queensland. P. e. diemenensis: Tasmania.

HABITAT

Most types of open, lightly wooded country, including farmlands and orchards; favors trees bordering watercourses and has successfully colonized human-made habitats, especially golf courses, but avoids dense, closed forest.

BEHAVIOR

Sedentary. Pairs or small groups familiar in or near urban centers, where often seen perched on telegraph wires or sitting on roadside fences; inconspicuous when feeding on the ground, but easily identified by characteristically undulating flight and



whistling call-notes; more active in cool or wet weather, at other times resting during middle of day.

FEEDING ECOLOGY AND DIET

Feeds primarily on seeds procured on the ground, but also takes seeds, fruits, and blossoms in trees or shrubs, especially eucalypts and acacias; fond of cultivated fruits.

REPRODUCTIVE BIOLOGY

Monogamous, mated pair being the basic social unit. Courtship display features "squaring" of shoulders and agitated sideways wagging of fanned tail to the accompaniment of chattering notes. Defends territory in immediate vicinity of nesting tree; nest in tree hollow, sometimes in crevice in wall of building; clutch of four or five eggs incubated by female for 19 days; chicks fed by both parents; fledging at 32 days.

CONSERVATION STATUS

Abundant throughout most of its range; benefits from landclearing and crop-growing; in 1990s population estimated to exceed 500,000 and stable or increasing.

SIGNIFICANCE TO HUMANS

Popular cagebird; can cause damage in orchards. •

Budgerigar

Melopsittacus undulatus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus undulatus Shaw, 1805, New Holland = south and west Australia. Monotypic.



OTHER COMMON NAMES

English: Budgie, warbling grass-parakeet, lovebird, parakeet; French: Perruche ondulé; German: Wellensittich; Spanish: Periquito Común.

PHYSICAL CHARACTERISTICS

7 in (18 cm): 0.8–1.1 oz (23–32 g). Small bird with light green and yellow plumage, darker wings, and bluish tail.

DISTRIBUTION

Interior of mainland Australia.

HABITAT

Wide variety of open habitats, from arid shrublands or lightly wooded grasslands and *Atriplex* (saltbush) plains to open forest and farmlands; favors eucalypts bordering ephemeral watercourses; capable of surviving long periods without water, but seldom found far from surface water.

BEHAVIOR

Migrant in south, nomad in north, but everywhere numbers influenced by availability of surface water. Gregarious, flocks normally of 10–100 birds, sometimes much larger, even many thousands; swift, erratic flight of flocks with remarkable precision, all birds twisting and turning in perfect unison. Departs communal roost at sunrise, flying directly to feeding areas; peak feeding periods in the morning and afternoon, in interim comes to drink, some members of flock alighting on water and rising into the air by beating wings down against water surface. Displays pre-roosting aerobatics before returning at dusk to nighttime roost.

FEEDING ECOLOGY AND DIET

Specialist feeder dependent on small seeds of groundcover vegetation; all seeds taken on the ground or within reach from the ground.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding influenced by availability of surface water; in south usually during spring-summer and in north during autumn-winter. Nest in tree hollow or hole in stump, fencepost, or log lying on the ground; often communal nesting, and two or more broods reared in succession; clutch of four to six, up to eight eggs incubated by female for 18 days; chicks fledge at about 30 days, and sexually mature within 60 days of leaving nest.

CONSERVATION STATUS

Plentiful, though numbers fluctuate according to seasonal conditions; possibly most numerous Australian parrot, with estimated population more than five million.

SIGNIFICANCE TO HUMANS

Most popular cagebird worldwide; domesticated and numerous color mutations well established. ◆

Rose-ringed parakeet

Psittacula krameri

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus krameri Scopoli, 1769, Senegal. Four subspecies.

OTHER COMMON NAMES

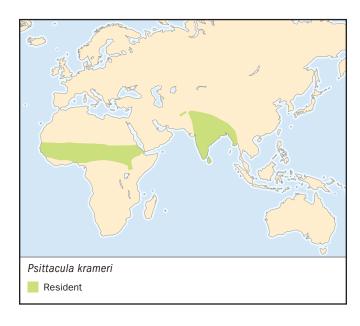
English: Ring-necked parakeet, Indian ringneck parakeet; French: Perruche à collier; German: Halsbandsittich; Spanish: Cotorra de Kramer.

PHYSICAL CHARACTERISTICS

15.7 in (40 cm); 4.1–4.9 oz (116–139 g). Green plumage, red bill, narrow red-and-black necklace, slender tail.

DISTRIBUTION

P. k. krameri: south Mauritania east to western Uganda and southern Sudan. P. k. parvirostris: eastern Sudan, Eritrea, and Ethiopia to northwest Somalia. P. k. borealis: northwest Pak-



istan and north India east to central Myanmar and southeast China. *P. k. manillensis*: Sri Lanka and peninsular India. Feral populations originating from escaped cagebirds established elsewhere.

HABITAT

Lowlands and foothills. Deciduous woodland, secondary growth, and wide variety of open, lightly timbered habitats, including dry scrublands, semidesert savanna, and cultivated farmlands or plantations in and around urban centers; avoids interior of dense, evergreen forest, but present at margins; natural and feral populations have successfully colonized manmade habitats.

BEHAVIOR

Sedentary, but local movements influenced by rainfall. Usually in small groups but very large flocks at concentrated food sources and at nocturnal roosts; noisy, fearless, and highly conspicuous because of constant screeching and squabbling; swift, direct flight, with backward-swept wings and long, pointed tail giving distinctive appearance.

FEEDING ECOLOGY AND DIET

Diet includes seeds, berries, fruits, blossoms, and nectar; fond of cultivated fruits and grain, raiding both standing crops and stockpiles at stores or railway sidings.

REPRODUCTIVE BIOLOGY

Monogamous. In West Africa breeding is from December to April, and is from November to June in India and Sri Lanka. Preceding copulation, elaborate display from male features side-to-side swaying of upward stretching body, repeated raising of one foot, and arching of neck while dilating eye pupils, all to the accompaniment of low, twittering notes. Nest in tree hollow, often in old holes of woodpeckers, or in cavities in walls and under eaves of buildings; clutch of three to four eggs incubated by female for 22 days; young birds leave nest at approximately 30 days.

CONSERVATION STATUS

Uncommon at extremities of range, but elsewhere plentiful and increasing; benefits from agriculture.

SIGNIFICANCE TO HUMANS

Very destructive in croplands and orchards; popular cagebird, with many color mutations established. ◆

Eclectus parrot

Eclectus roratus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus roratus P. L. S. Müller, 1776, Ambon. Nine subspecies.

OTHER COMMON NAMES

English: Red-sided parrot, grand eclectus parrot, red-sided eclectus parrot; French: Grand Eclectus; German: Edelpapagei; Spanish: Loro Eceléctico.

PHYSICAL CHARACTERISTICS

16.5 in (42 cm); 0.88–1.2 lb (440–600 g). Remarkable sexual dimorphism: males green with pale yellow bill; females red and blue with blackish bill.



DISTRIBUTION

E. r. roratus: south Moluccas, Indonesia. E. r. vosnaeri: north and central Moluccas, Indonesia. E. r. cornelia: Sumba Island, Indonesia. E. r. riedeli: Tanimbar Islands, Indonesia. E. r. aruensis: Aru Islands, Indonesia. E. r. biaki: Biak Island, Irian Jaya, Indonesia. E. r. polychloros: New Guinea and adjacent islands. E. r. solomonensis: Admiralty Islands and Bismarck Archipelago to Solomon Islands. E. r. macgillivrayi: Cape York Peninsula, northernmost Australia. E. r. 'westermani': known only from aviary specimens and possibly aberrant roratus.

HABITAT

Lowlands and foothills. Closely associated with tropical rainforest and drier monsoon woodland, but visits variety of timbered habitats, including mangroves, secondary growth, plantations, and gardens.

BEHAVIOR

Sedentary. Noisy and conspicuous in flight, but wary and secretive in forest canopy, keeping very much to treetops; when disturbed circles high overhead, screeching loudly; undertakes long-distance daily flights between communal nighttime roosts and feeding areas, always flying high above canopy, with males in front of females; usually in pairs or small parties, but larger groups may congregate to feed and at nighttime roosts.

FEEDING ECOLOGY AND DIET

Seeds, nuts, fruits, berries, and nectar procured in treetops; particularly fond of *Ficus* and *Parinari* fruits.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding recorded most months, but peak possibly between August and January; nest in tree hollow high above ground, and up to four nests found in same tree; groups of up to eight birds of both sexes in attendance at some nests suggests cooperative breeding, with "helpers," probably offspring from previous years; clutch of two eggs incubated for 26 days; young birds leave nest at approximately 90 days.

CONSERVATION STATUS

Generally common, but locally scarce where captured for livebird trade. On Sumba Island, population of *cornelia* estimated at fewer than 2,000 birds. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Popular cagebird; often kept as pets by local villagers; reported raiding village gardens to take fruit. ◆

Gray parrot

Psittacus erithacus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus erithacus Linnaeus, 1758, Ghana. Two subspecies.

OTHER COMMON NAMES

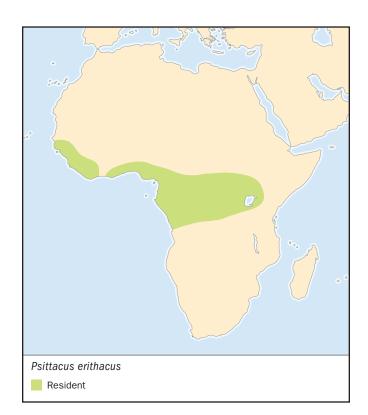
English: African gray parrot; French: Perroquet jaco; German: Graupapagei; Spanish: Loro Yaco.

PHYSICAL CHARACTERISTICS

13 in (33 cm); 08–0.81 lb (402–407 g). Stocky, gray bird with short, red tail.

DISTRIBUTION

P. e. erithacus: Ivory Coast east to Congo River basin. P. e. tim-neb: Sierra Leone to Ivory Coast.



HABITAT

Lowlands and foothills. Primarily moist evergreen forest and tall secondary growth, but commonly visits gallery woodland, mangroves, plantations, and gardens.

BEHAVIOR

Sedentary, but local numbers influenced by food availability. Noisy and highly conspicuous at communal nighttime roosts, where they gather in large numbers; pairs or small groups leave roost at sunrise, flying high above treetops and calling loudly; feeds in canopy during morning and afternoon, resting at midday, but wary and difficult to approach; return flights to roost may continue after nightfall; daily flights follow regular routes.

FEEDING ECOLOGY AND DIET

Feeds arboreally, taking seeds, nuts, fruits, and berries; favors pulp of fruits from cultivated oil palms (*Elaeis guineensis*); reports of damage to maize crops unconfirmed.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding season varies geographically from November to April in West Africa to between July and December in Congo River basin and June–July in East Africa. Nest in tree hollow high above ground; clutch of two or three, rarely four, eggs incubated by female; incubation periods of 21 and 30 days recorded in captivity, and young birds left nest nearly 10 weeks after hatching.

CONSERVATION STATUS

Generally common and locally abundant, but deforestation and capture for live-bird trade have caused dramatic declines in some districts, notably in Sierra Leone and Ghana. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Very popular cage bird with reputation as best "talker;" second most heavily traded parrot species in 1980s, when average annual exports exceeded 47,000 birds. ◆

Hyacinth macaw

Anodorhynchus hyacinthinus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus hyacinthinus Latham, 1790, Brazil. Monotypic.

OTHER COMMON NAMES

English: Hyacinthine macaw; French: Ara hyacinthe; German: Hyazinthara; Spanish: Guacamayo Jacinto.

PHYSICAL CHARACTERISTICS

39 in (100 cm); weight not recorded. Largest and probably most spectacular of all parrots. Deep blue plumage, yellow eye patch and chin, long tapering tail.

DISTRIBUTION

North Brazil to east Bolivia and extreme north Paraguay.

HABITAT

Lightly to moderately wooded country where palm food trees are present; favors gallery woodland traversing semi-open lands, especially seasonally inundated grasslands of the Pantanal; occurs also at margins of moist, lowland forest and in low, dry scrublands or cerrado with scattered clumps of *Mauritia* palms.



BEHAVIOR

At extremities of range seasonal movements influenced by fruiting of palms, but elsewhere largely sedentary. Usually in groups of six to 12, and mated pairs or parents with offspring readily discernible, but singly or in pairs during breeding season. Noisy and conspicuous, especially in flight, and when disturbed rises up from treetops to circle overhead while screaming loudly; rests quietly in uppermost branches during heat of the day, paired birds sitting together and allopreening frequently; long-distance flights between nighttime roosts and feeding areas at great height, pairs normally traveling together, one beside and slightly behind its mate, and long, streamer-like tail giving distinctive appearance.

FEEDING ECOLOGY AND DIET

Principally fruits of palms, procured in trees or on the ground underneath; takes palm seeds from cattle droppings or seeds remaining after pulp has been eaten by foraging mammals. *Ficus* and other fruits sometimes eaten, and recorded taking of *Pomacea* snails from shallow ponds.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding recorded from July to December. In northern Brazil nests commonly in crevices in cliff-faces, but elsewhere in tree hollows, often in dead palm stumps; clutch of two or rarely three eggs, but normally only one chick reared; in captivity incubation by female lasted 28–30 days; young bird fledged at approximately three months.

CONSERVATION STATUS

Endangered and listed on CITES Appendix I. Alarming declines caused by capture of adults and removal of nestlings for live-bird trade, exacerbated by land clearance and hunting for food or feathers. In early 1990s total population estimated at fewer than 3,000.

SIGNIFICANCE TO HUMANS

Very much in demand as aviary bird; also hunted for food and feathers. ◆

Scarlet macaw

Ara macao

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus macao Linnaeus, 1758, South America. Two subspecies.

OTHER COMMON NAMES

French: Ara rouge; German: Arakanga; Spanish: Gaucamayo Macao.

PHYSICAL CHARACTERISTICS

33 in (85 cm); 2.1–2.2 lb (1,060–1,123 g). Brilliant plumage with red, blue, green, and yellow. Bare face patch, yellow wing patch, and long, red tapering tail.



DISTRIBUTION

A. m. macao: northeast Bolivia and central Brazil north to Guianas, north Colombia, Panama, and Costa Rica. A. m. cyanoptera: southeast Mexico to Nicaragua.

HABITAT

Lowlands, on dry ground in evergreen forest and dense gallery woodland traversing savanna, giving way in swampy areas to blue and yellow macaw (*Ara ararauna*); favors riverine forest or woodland, and often visits mangroves or remnant large trees in clearings and cultivation; in parts of Central America occurs in deciduous or *Pinus* forest.

BEHAVIOR

Among the most spectacular of the neotropical birds, brilliant colors and loud calls making them highly conspicuous, especially in flight. Generally in pairs, family parties or small flocks of up to about 20 birds; the strong pair-bonds evident as paired birds fly together, their wings almost touching; daily morning and evening flights along regular routes between nighttime roosts and scattered feeding areas. Can be tame where not molested, but normally extremely wary and at slightest sign of danger rises high into the air while screeching loudly.

FEEDING ECOLOGY AND DIET

Feeds arboreally, taking mainly seeds, nuts, fruits, berries, and flowers, with large, rather soft fruits favored. In Brazil, important foods are *Lecythis* fruits, and fruits of juvia *Bertholletia excelsa* and *Syagrus* palms. With other parrots congregates at clay-licks on exposed banks; purpose unknown, but suggestion that consuming mineralized clays may alleviate effects of toxic alkaloids in unripe fruit.

REPRODUCTIVE BIOLOGY

Monogamous; pair-bond probably lifelong. Breeding season variable over extensive range, but in north nesting recorded in March–April and in south from October–March; nest in hollow in large tree high above ground; reuse of nests in successive years; one clutch of one or two, rarely up to four eggs, but normally only one or two chicks fledge. In captivity, incubation lasts 24–28 days; young birds leave the nest at approximately 14 weeks.

CONSERVATION STATUS

Remains common only in remote areas away from human habitation. Deforestation and capture of birds for live-bird trade have extirpated populations in much of Central America, where total population of *cyanoptera* estimated at about 4,000 in late 1990s; elsewhere declining in accessible localities, but good numbers survive in some national parks and reserves. Listed on CITES Appendix I.

SIGNIFICANCE TO HUMANS

Probably best known of neotropical parrots, and often depicted in travel brochures. Highly prized as aviary bird and as household pet, so nestlings persistently taken; also hunted in some regions for food and for feathers. •

Brown-throated parakeet

Aratinga pertinax

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus pertinax Linnaeus, 1758, Curaçao. Fourteen subspecies.



OTHER COMMON NAMES

English: Brown-throated conure, St. Thomas conure; French: Conure cuivrée; German: Braunwangensittich; Spanish: Aratinga Pertinaz.

PHYSICAL CHARACTERISTICS

10 in (25 cm); 2.6–3.6 oz (75–102 g). Polytypic species with much geographical variation in extent of yellow on face and brown on throat.

DISTRIBUTION

A. p. pertinax: Curaçao, Netherlands Antilles; successfully introduced to St. Thomas, Virgin Islands. A. p. xanthogenia: Bonaire, Netherlands Antilles. A. p. arubensis: Aruba, Netherlands Antilles. A. p. aeruginosa: north Colombia and northwest Venezuela. A. p. griseipecta: Sinú River valley, northeast Colombia. A. p. lehmanni: east Colombia and possibly westernmost Venezuela. A. p. tortugensis: Tortuga Island, Venezuela. A. p. margaritensis: Margarita Island, Venezuela. A. p. venezuelae: much of Venezuela. A. p. chrysophrys: southeast Venezuela and neighboring northern Brazil. A. p. surinama: Guianas and neighboring northeast Venezuela. A. p. chrysogenys: Rio Negro region, and possibly on Rio Solimões, northwest Brazil. A. p. paraensis: Rio Tapajós and Rio Cururu, north-central Brazil. A. p. ocularis: Panama.

HABITAT

Lowlands and less commonly foothills; principally natural savannas and deciduous woodlands, but present in wide variety of open habitats from arid scrublands to plantations and cultivation; avoids dense forest, so distribution patchy.

BEHAVIOR

Sedentary, though local wandering and some seasonal movements in search of food. Generally in pairs or small parties, but

large flocks attracted to concentrated food source; noisy, especially during swift, erratic flight with constant direction change; often calls from conspicuous perch atop emergent leafless branch of dead or deciduous tree; in late evening flies about, screeching almost incessantly before retreating to night-time roost; tame where not persecuted, often present in or around towns and villages.

FEEDING ECOLOGY AND DIET

Seeds, nuts, fruits, berries, flowers, and probably insect larvae taken in trees and bushes; at study site in Venezuela up to 70% of food plants was taken from human cultivation; causes damage to maize crops and in orchards.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding season variable throughout extensive range, and nesting recorded in almost all months, possibly influenced by rainfall. Nest normally in hole excavated by birds in arboreal termitarium, but also in holes in trees, in crevices in rocks or wall of buildings, and in burrows excavated in earth banks; four or five nest-holes excavated in same decayed tree trunk; clutch of two to seven, usually four to five eggs; in captivity incubation of 23 days, probably only by female; young birds vacated nest about 40 days after hatching.

CONSERVATION STATUS

Generally common, locally abundant; often most numerous parrot in district. Probably benefits from landclearing and cultivation, so range may be expanding. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Considered pest in orchards and croplands, so locally persecuted; not popular as cagebird. ◆

Painted parrot

Pyrrhura picta

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus picta P. L. S. Müller, 1776, Cayenne. Nine subspecies.

OTHER COMMON NAMES

English: Painted conure; French: Conure versicolore; German: Rotzügelsittich; Spanish: Cotorra Pintada.

PHYSICAL CHARACTERISTICS

8.7 in (22 cm); 1.9–2.5 oz (54–70 g). Polytypic species with strong geographical variation in plumage patterns of head and breast.

DISTRIBUTION

P. p. picta: Venezuela through Guianas to Amapá, north Brazil. P. p. amazonum: north-central Brazil, north of Amazon River. P. p. microtera: north-central Brazil, south of Amazon River. P. p. lucianii: northwest Brazil and southeast Ecuador to northeast Peru and north Bolivia. P. p. roseifrons: east of range of lucianii in west Brazil and east Peru. P. p. subandina: Sinú River valley, northwest Colombia; probably separate species. P. p. caeruleiceps: western slopes of East Andes, north Colombia; possibly separate species. P. p. pantchenkoi: Sierra de Perijá, Colombia-Venezuela border. P. p. eisenmanni: Azuero Peninsula, Panama; possibly separate species.



HABITAT

Lowlands and foothills. Closely associated with moist, evergreen forest, though occurring also in dense savanna woodland, cloud forest, and partly cleared areas; favors lower stages in interior of forest rather than margins or secondary growth.

BEHAVIOR

Sedentary, but some local altitudinal movements. Pairs, family parties, or flocks of up to 20 birds; inconspicuous while foraging in lower to upper stages of forest; in dry season bathes regularly at favored watering places; emits shrill "eek" call-notes while in swift, direct flight; where sympatric, gives way to larger crimson-bellied parakeet (*Pyrrhura perlata*); nighttime roosting in tree hollows.

FEEDING ECOLOGY AND DIET

Feeds arboreally, taking seeds, nuts, fruits, berries, flowers, and possibly insect larvae; also seen taking algae from surface of deep pools; comes to the ground to take mineralized clay.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding season varies geographically throughout extensive range, but mainly January to June in north and June to September in south. Nest in tree hollow; in captivity, clutch of four or five eggs.

CONSERVATION STATUS

Generally common, but locally scarce and declining because of deforestation; *subandina* possibly extremely rare. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Some localized trapping for live-bird trade. ◆

Monk parakeet

Myiopsitta monachus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus monachus Boddaert, 1783, Uruguay. Four subspecies.

OTHER COMMON NAMES

English: Quaker parrot, gray-breasted parakeet; French: Conure veuve; German: Mönchsittich; Spanish: Cotorra Argentina.

PHYSICAL CHARACTERISTICS

11.4 in (29 cm); 4.5–4.9 oz (127–140 g). Small to mediumsized bird with mostly green plumage and gray or dull white face, cheeks, and throat. Long, green tail feathers; pale orange or yellow bill.

DISTRIBUTION

M. m. monachus: southeast Brazil to Uruguay and northeast Argentina. M. m. calita: western Argentina. M. m. cotorra: northwest Argentina and south Bolivia to Paraguay and south Brazil. M. m. luchsi: central Bolivia; probably separate species. Feral population in many locations, including North America and Europe.

HABITAT

In central Bolivia, in riverine vegetation in arid scrublands near cliff-faces in intermontane valleys (*M. m. luchsi*); elsewhere, dry semi-open lowlands in savanna woodland, gallery forest, dry *Acacia* scrublands, palm groves, pasturelands or cultivation, and urban parks or gardens; often prevalent near human habitation.



BEHAVIOR

Sedentary, but some localized, seasonal movements at fringes of range. Noisy and highly gregarious; flocks of 10–100 or more always in the vicinity of conspicuous communal nests serving as foci for daily activities. Wary when away from shelter; "sentinel" birds sit atop nearby trees to warn feeding flock of approaching danger, and when disturbed all rise into the air, screeching loudly; intruder at nest is watched intently and in silence for some time before birds rise into the air and circle overhead to the accompaniment of loud screeching; swift flight usually low to the ground; daytime resting and nighttime roosting in nests throughout the year.

FEEDING ECOLOGY AND DIET

Diet mainly seeds of grasses and herbs, also nuts, fruits, berries, leaf buds, blossoms, and insect larvae; seeds of thistles important during breeding season; seeds of *Celtis tala* and palm nuts also favored; fond of cultivated grain and fruits.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding season October–March. Nest unique among parrots: large, bulky structure of dry twigs placed in topmost branches of tree, especially introduced eucalypti, or sometimes in transmission tower, pylon, windmill, or under roof of building. Single compartment nests occupied by solitary pairs, but mostly large, communal nests with multiple compartments for many pairs, and probably added to over many years. In central Bolivia, nests of *M. mluchsi* are not communal, but often immediately adjacent to each other, and placed in crevices in cliff-faces. Average clutch seven eggs, but sometimes up to 11 eggs; in captivity incubation lasts 24 days and nestling period about six weeks.

CONSERVATION STATUS

Generally common, locally abundant; benefiting from planting of introduced eucalypts on treeless grasslands; expanding range and increasing numbers. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Widely persecuted as serious pest in orchards and croplands. Exported in large numbers for live-bird market, but potential as pest in importing countries. ◆

Yellow-crowned Amazon

Amazona ochrocephala

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus ochrocephalus Gmelin, 1788, Venezuela. Ten subspecies.

OTHER COMMON NAMES

English: Yellow-crowned parrot, yellow-headed Amazon, yellow-naped Amazon; French: Amazone à front jaune; German: Gelbscheitelamazone; Spanish: Amazona Real.

PHYSICAL CHARACTERISTICS

13.8 in (35 cm); 08–1.1 lb (405–561 g). Stocky, short-tailed species with strong geographical variation; northern birds have entirely yellow head; southern birds have yellow forehead and nape. Juveniles entirely green.

DISTRIBUTION

A. o. ochrocephala: east Colombia through Venezuela to Guianas, Trinidad, and Pará, north-central Brazil. A. o. xantho-



laema: Marajó Island, Amazon River, north Brazil. A. o. nattereri: south Colombia, east Ecuador and east Peru to north Bolivia and west Brazil. A. o. panamanensis: northwest Colombia to west Panama. A. o. auropalliata: northwest Costa Rica to south Mexico. A. o. parvipes: northeast Honduras and north Nicaragua. A. o. caribaea: Bay Islands, Honduras. A. o. belizensis: Belize. A. o. oratrix: Pacific and Caribbean lowlands of Mexico; introduced to Florida and California. A. o. tresmariae: Tres Marías Islands, west Mexico.

HABITAT

Lowlands; variety of wooded habitats, including tropical forest and deciduous woodland, gallery forest in open country, tall scrubland, riverine secondary growth, mangroves, *Pinus* woodland, stands of *Mauritia* palms, remnant woodlots in cultivation, and suburban parks or gardens; in Amazon River basin prefers seasonally inundated forest.

BEHAVIOR

Sedentary, though some local movements with changing food supplies. Large flocks may congregate at nighttime roosts, but during the day small parties of up to 10 usually seen feeding in treetops; quiet while feeding but when disturbed, do not call until well away from tree; strong flier, flying quite high on long-distance flights to and from nighttime roosts; paired birds remain close together and readily discernible within flocks; associates with other parrots at clay-licks on exposed banks.

FEEDING ECOLOGY AND DIET

Feeds arboreally, taking seeds, nuts, fruits, berries, blossoms, and probably leaf buds; uses foot to hold fruit while extracting seeds with bill; fond of maize and cultivated fruits.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding recorded mainly December–May. Nest in tree hollow, often in dead branch or decayed palm stump, also in hole excavated in arboreal termitarium; hollow prepared mostly by female for up to one month before egg-laying; clutch of two to four eggs incubated for 25–26 days by female, male remaining near nest entrance; sitting female fed by male; in captivity, young birds left nest two months after hatching.

CONSERVATION STATUS

Generally common, though locally scarce; yellow-headed subspecies (A. o. oratrix and A. o. belizensis) threatened by capture for live-bird trade and by deforestation; in 1990s population of endangered oratrix estimated at below 7,000. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Reputation as excellent "talker," so popular as pet in all parts of range; yellow-headed subspecies also in strong demand for international trade. Reported to cause damage to maize crops and in orchards. •

Red-breasted pygmy parrot

Micropsitta bruijnii

SUBFAMILY

Psittacinae

TAXONOMY

Nasiterna bruijnii Salvadori, 1875, Arfak Peninsula, New Guinea. Four subspecies.

OTHER COMMON NAMES

English: Rose-breasted pygmy parrot, mountain pygmy parrot; French: Micropsitte de Bruijn; German: Rotbrust-Spechtpapagai; Spanish: Microloro Pechirrojo.

PHYSICAL CHARACTERISTICS

3.5 in (9 cm); 0.42–0.56 oz (12–16 g). One of the smallest parrots. Mostly green plumage with orange-red breasts; bluepurple neck; short tail feathers.

DISTRIBUTION

M. b. bruijni: mountains of mainland New Guinea. M. b. pilata: Buru and Seram, south Moluccas, Indonesia. M. b. necopinata: New Britain and New Ireland, Bismarck Archipelago, Papua New Guinea. M. b. rosea: Bougainville, Papua New Guinea, and Guadalcanal and Kolambangara, Solomon Islands. Undescribed yellow-crowned form recorded from Ok Tedi Mountains, mainland New Guinea.

HABITAT

Mountains and foothills; most upland forests, including cloud forest and moss forest; also forest margins, riparian vegetation, and occasionally coffee plantations.



BEHAVIOR

Possible nomad or altitudinal migrant. Easily overlooked because of diminutive size, and often detected only by shrill "tsee... tsee" calls; pairs or small parties climb about woodpecker-like on surface of tree trunk or sloping limb with stiffened tail propped against surface for support; individuals keep close together; often leaps surprising distances between branches; swift flight slightly undulating and with audible wingbeats; may roost at night in hole excavated in decayed stump.

FEEDING ECOLOGY AND DIET

Diet poorly known; observed eating fungus, lichen, and moss from surfaces of tree trunks and limbs; also seen feeding on fruits and possibly flowers.

REPRODUCTIVE BIOLOGY

Monogamous. Breeding recorded from December–April, but little studied; only *Micropsitta* species excavate nesting hole in decayed tree or stump, other species excavate in arboreal termitaria.

CONSERVATION STATUS

Generally uncommon or sporadically dispersed, but locally common. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

None known. ◆

Kea

Nestor notabilis

SUBFAMILY

Psittacinae

TAXONOMY

Nestor notabilis Gould, 1856, South Island, New Zealand. Monotypic.

OTHER COMMON NAMES

French: Nestor Kéa; German: Kea; Spanish: Kea.

PHYSICAL CHARACTERISTICS

15 in (38 cm); 1.2–1.9 lb (600–960 g). Large bird with dull brown plumage; long, pointed bill.

DISTRIBUTION

South Island, New Zealand.

HABITAT

Mountains; steep-sided wooded valleys and *Nothofagus* forest bordering subalpine scrublands, seasonally visiting scrublands and alpine grasslands; occurs commonly in and around human habitation, notably at ski lodges, tourist hotels, and camping grounds.

BEHAVIOR

Resident, with local altitudinal movements for seasonally available foods; juveniles more mobile than adults; strong fliers, noisy, conspicuous flocks often circling high above mountain valleys, especially in strong winds preceding storm. Tame and highly inquisitive around human habitation, sometimes causing damage to parked cars and tents or cabins when searching for food scraps; attracted to refuse tips and rubbish receptacles, often spilling contents; playful, enjoying rolling in snow or bathing in recently thawed puddles; in summer, regularly active at night.

FEEDING ECOLOGY AND DIET

Forages in trees or shrubs and on the ground; varied diet includes leaf buds, roots, berries, fruits, seeds, blossoms, nectar, and insects. Favored foods include *Podocarpus* and *Coprosma* fruits and nectar from mountain flax *Phormium colensoi*; comes to sheep carcasses or drying skins to feed on fat or decaying flesh and to extract marrow from bones; possibly attacks defenseless, weak, or sick sheep; regularly scavenges for food scraps in refuse tips or rubbish receptacles.



REPRODUCTIVE BIOLOGY

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Breeds mainly July–December, but recorded at other times. Monogamous and apparently at times polygynous; solitary pairs faithful to traditional nest-sites established over number of years and reused annually; also record of one dominant male attached to up to four females. Breeding birds seldom move far from nest-site throughout the year, but not strongly territorial. Nest in crevice under rocks, among roots or trees, or in log lying on the ground; clutch two to four eggs incubated by female for 21–28 days; chicks leave nest some 13 weeks after hatching.

CONSERVATION STATUS

Vulnerable. Formerly persecuted because of alleged killing of sheep, causing decline in numbers and fragmentation of population; now fully protected. In 1990s estimates of total population highly variable, between 1,000 and 5,000 or up to 15,000, with concentrations around human habitation possibly giving false counts. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

For more than a century persecuted as killer of sheep and, despite little supporting evidence, bounty paid to farmers; almost 7,000 birds killed in three years, 1943–46. Now fully protected and, although responsible for damage to vehicles and property, birds popular with tourists because of tameness. •

Pesquet's parrot

Psittrīchas fulgidus

SUBFAMILY

Psittacinae

TAXONOMY

Banksianus fulgidus Lesson, 1830, New Guinea. Monotypic.



OTHER COMMON NAMES

English: Vulturine parrot, bare-headed parrot; French: Psittrichas de Pesquet; German: Borstenkopf; Spanish: Loro Aguileño.

PHYSICAL CHARACTERISTICS

18 in (46 cm); 1.4–1.6 lb (690–800 g). Large bird with grayish black plumage, red underside, bare face, and very broad tail.

DISTRIBUTION

Mountains of mainland New Guinea.

HARITAT

Foothills and lower montane forests, occasionally in adjacent lowland forest; also tall secondary growth near watercourse.

BEHAVIOR

Resident. Singly, in pairs, or small flocks seen in flight or sitting in topmost branches of tall trees; when not feeding retreats to rest in tallest trees, sometimes sitting for hours in rain or sunshine atop emergent dead limbs protruding well above surrounding canopy; does not climb, but jumps from branch to branch with jerky motion and flicking of tail. Noisy and conspicuous in flight, call-notes being heard from afar; shallow wingbeats interspersed with gliding characteristic of flight, and distinctive appearance from short tail, broad wings, and outstretched slender neck; regular flights at dusk to nighttime roosts.

FEEDING ECOLOGY AND DIET

Feeds arboreally, taking soft fruits, particularly figs; also blossoms and probably nectar; seen feeding on large *Freycinetia* flowers. Base of bill becomes caked with fruit pulp, suggesting bare face may have evolved to prevent matting of feathers.

REPRODUCTIVE BIOLOGY

Monogamous. Fledged juveniles recorded in December, adults in breeding condition April–May, laying female observed in February. Nest in cavity excavated by birds in dead tree at 39 ft (12 m) above ground; egg-laying to fledging exceeded 76 days. In captivity, courtship feeding prior to laying of two eggs; incubation by female for 31 days.

CONSERVATION STATUS

Vulnerable. Fairly common in remote areas, but scarce or absent in accessible districts because of persistent hunting; one of the first birds to disappear following local introduction of firearms; also threatened by deforestation. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Hunted intensely for food and feathers; skins highly prized and widely used as "bride price." ◆

Philippine hanging parrot

Loriculus philippensis

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus philippensis P. L. S. Müller, 1776, Luzon, Philippine Islands. Eight subspecies.

OTHER COMMON NAMES

English: Colasisi; French: Coryllis des Philippines; German: Philippinenpapeichen; Spanish: Loriculo Filipino.



PHYSICAL CHARACTERISTICS

5.5 in (14 cm); 1.1–1.4 oz (32–40 g). Polytypic species with geographical variation in head patterns and colors of soft parts.

DISTRIBUTION

L. p. philippensis: Luzon and adjacent islands, Philippines. L. p. mindorensis: Mindoro, Philippines. L. p. regulus: Tablas, Ticao, Masbate, Panay, Guimaras, Negros, and probably Romblon, Philippines. L. p. chrysonotus: Cebu, Philippines. L. p. siquijorensis: Siquijor, Philippines. L. p. apicalis: Mindanao and adjacent islands, Philippines. L. p. dohertyi: Basilan, Philippines. L. p. bonapartei: Sulu Archipelago, Philippines.

HABITAT

Lowlands and foothills. Primarily lowland forest, but occurs in most wooded habitats, including secondary growth, high bushes, plantations, orchards, and remnant woodlots in cultivation.

BEHAVIOR

Resident; local wandering for food. Singly, in pairs, or infrequently in small flocks feeding in middle-to-upper stages of forest or in flowering bushes; difficult to detect amidst foliage, but constant calling betrays presence; associates with other fruit-eating birds in mixed foraging assemblages; shy when disturbed in forest, but bold when feeding in flowering coconut palms; swift flight characteristically undulating.

FEEDING ECOLOGY AND DIET

Fine, protruding bill and "brush-tipped" tongue used to gather nectar and pollen from flowers; also feeds on soft fruits and seeds; takes fermenting coconut nectar harvested by villagers, sometimes becoming intoxicated.

REPRODUCTIVE BIOLOGY

Little known; breeding recorded March–May; nest in hole in dead tree at 39 ft (12 m) height. In captivity, clutch of three eggs incubated by female for 20 days; chicks left nest approximately five weeks after hatching.

CONSERVATION STATUS

Common throughout parts of range, but four subspecies (*mindorensis*, *bournsi*, *regulus*, and *dohertyi*), with combined population estimated in 1990s at probably less than 5,000, threatened by deforestation and capture for live-bird market; another two subspecies (*chrysonotus* and *siquijorensis*) almost extinct because of habitat loss. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Very popular cagebird; commonly traded between islands. ◆

Rosy-faced lovebird

Agapornis roseicollis

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus roseicollis Vieillot, 1818, Goodhouse, Cape Province. Two subspecies.

OTHER COMMON NAMES

English: Peach-faced lovebird; French: Inséparable rosegorge; German: Rosenköpfchen; Spanish: Inseparable de Namibia.

PHYSICAL CHARACTERISTICS

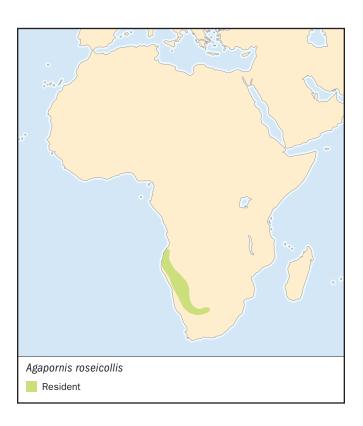
6 in (15 cm); 1.6–2.2 oz (46–63 g). Small bird with mostly green plumage; peach-colored face, forehead, and chin.

DISTRIBUTION

A. r. roseicollis: Namibia and northern Cape Province, Republic of South Africa. A. r. catumbella: southwest Angola.

HABITAT

Lowlands and foothills; in dry open country frequents woodlands, scrubby hillsides, and vegetation bordering watercourses;



also cultivation, gardens, and urban parklands; dependent on surface water.

BEHAVIOR

Resident, wanders locally with changing water availability. Noisy, gregarious, and conspicuous; usually in small flocks, but sometimes flocks of hundreds where food is abundant. In flight, flock twists and turns with remarkable speed and dexterity, showing reddish foreparts on approach and blue rumps when going away; daytime resting and nighttime roosting often in nests of weavers; regular evening flights to drinking pools before going to roost.

FEEDING ECOLOGY AND DIET

Principally seeds gathered from the ground or taken from standing plants; also flowers, buds, and leaf shoots; fond of cultivated grain, especially maize and sunflower seeds.

REPRODUCTIVE BIOLOGY

Monogamous. Breeds colonially, mainly from February–April, but also July in north; cup-shaped nest of grass twigs or leaves placed in rock crevice or sometimes in wall of buildings or underneath bridges, but commonly in communal nests of weavers without addition of new material; nest-building material carried to site by female tucked under rump feathers; four to six eggs incubated by female for about 23 days; young birds fledge at approximately six weeks.

CONSERVATION STATUS

Generally common, locally plentiful; declines in some populations due to heavy trapping for live-bird trade. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

Very popular cagebird worldwide; many color mutations well established in captivity. Causes damage to grain crops. ◆

Rainbow lorikeet

Trichoglossus haematodus

SUBFAMILY

Psittacinae

TAXONOMY

Psittacus haematod (sic.) Linnaeus, 1771, Ambon. Twenty-two subspecies.

OTHER COMMON NAMES

English: Rainbow lory, coconut lory; French: Loriquet à tête bleue; German: Allfarblori; Spanish: Lori Arcoiris.

PHYSICAL CHARACTERISTICS

10 in (26 cm); 3.5–5.8 oz (100–167 g). Brightly colored bird with red, yellow, and green plumage; long, tapering tail. Polytypic species with geographical variation in colors of head and breast.

DISTRIBUTION

T. h. haematodus: south Moluccas, west Papuan Islands, and northwest New Guinea, Indonesia. T. h. mitchelli: Bali and Lombok, Indonesia. T. h. foresteni: Sumbawa, Indonesia. T. h. djampeanus: Tanahjampea, Indonesia. T. h. stresemanni: Kalaotoa, Indonesia. T. h. fortis: Sumba, Indonesia. T. h. weberi: Flores, Indonesia. T. h. capistratus: Timor. T. h. flavotectus: Wetar and Romang, Indonesia. T. h. rosenbergii: Biak Island, Irian



Jaya, Indonesia. T. h. intermedius: north New Guinea. T. h. imicropteryx: east New Guinea. T. h. caeruleiceps: south New Guinea. T. h. nigrogularis: Aru and east Kai Islands, Indonesia. T. h. brooki: Spirit Island, in Aru Islands, Indonesia. T. h. massena: Karkar Island, Bismarck Archipelago, Solomon Islands, and Vanuatu. T. h. flavicans: New Hanover and Admiralty Islands, Papua New Guinea. T. h. nesophilus: Ninigo and Hermit Islands, Papua New Guinea. T. h. deplanchii: New Caledonia and Loyalty Islands. T. h. septentrionalis: Cape York Peninsula, north Australia. T. h. moluccanus: east Australia; introduced to southwest Australia. T. h. rubritorquis: north Australia.

HABITAT

Lowlands to mid-montane elevations. Wide variety of wooded habitats wherever flowering plants are available, ranging from mangroves and coastal heathlands to savanna woodland, gallery forest, secondary growth, and rainforest; colonizes man-made habitats, especially coconut plantations, orchards, and suburban gardens; prefers edges or clearings rather than interior of closed rainforest; tolerates depauperate scrubland or plantations on quite small atolls.

BEHAVIOR

Resident, though pronounced local movements in response to flowering of food plants causes marked fluctuations in numbers. In pairs or flocks of few birds to hundreds depending on food availability; noisy and active, constantly flying back and forth through or above canopy and clambering amidst foliage to get at flowers or fruits; screeching call-notes always betray presence; often in company of other fruit-eating birds; becomes tame in household gardens or at feeders; very swift, direct flight.

FEEDING ECOLOGY AND DIET

Compressed, pointed bill and "brush-tipped" tongue used to extract pollen and nectar from flowers; also fruits, berries, seeds, leaf buds, and insect larvae; in Australia, feeds principally on *Eucalyptus* and *Banksia* flowers; fond of cultivated fruits and unripe "milky" grain; readily comes to garden feeders to take fruit, seed, or artificial nectar mixes.

REPRODUCTIVE BIOLOGY

Monogamous, paired birds staying together and readily discernible within flocks. Breeding season variable in different parts of range, but nesting recorded most months. Courtship display features wing-fluttering to show colorful underwings, side-to-side swaying with neck arched forward and eye pupils dilated; nest in tree-hollow; at times two or more nests in same tree, but hollow entrances defended; nesting on ground recorded from Admiralty Islands, Papua New Guinea; clutch of

two to three eggs incubated by female for about 25 days; young birds fledge at about eight weeks.

CONSERVATION STATUS

Generally common, locally plentiful; in some districts most common parrot; in Australia, benefits from cultivation of native flowering plants in gardens, and numbers increasing. Listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS

In Australia, popular visitor to garden feeders, and major attraction at tourist parks where hundreds come to feed from trays held by visitors. In some regions hunted for food and feathers, latter used in ceremonial headdresses. ◆

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Organizations

- Association for Parrot Conservation. Centro de Calidad Ambiental ITESM Sucursal de Correos J., C.P. 64849, Monterrey, N.L. Mexico.
- Birds Australia Parrot Association, 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
- Loro Parque Fundación. Loro Parque S.A. 38400 Puerto de la Cruz, Tenerife, Canary Islands Spain.
- Research Centre for African Parrot Conservation Zoology and Entomology Department. Private Bag X01, Scottsville, 3201 Natal Republic of South Africa.
- World Parrot Trust. Glanmor House, Hayle, Cornwall TR27 4HB United Kingdom. Web site: http://www.worldparrottrust.org>

Joseph M. Forshaw

Musophagiformes Turacos and plantain eaters

(Musophagidae)

Class Aves

Order Musophagiformes Suborder Musophagae Family Musophagidae Number of families 1

Thumbnail description

Medium-sized to large birds with short, rounded wings, rather long tail and a conspicuous erectile crest

Size

16-30 in (40-76 cm)

Number of genera, species

8 genera; 23 species

Habitat

Forest, woodlands, and savannas

Conservation status

Endangered: 1 species; Vulnerable: 1 species; Near Threatened: 1 species



DistributionSub-Saharan Africa

Evolution and systematics

Turacos are an old family of birds whose ancestry and evolution are undeniably linked to the retraction and subsequent expansion of Africa's forests and savannas. The limited fossil record prevents the simplest reconstruction of turaco evolutionary history. Material from the Oligocene of Bavaria and Egypt, and from the Miocene of France and Kenya, indicates that turacos occurred on both sides of the Sea of Tethys some 25–30 million years ago, prior to the collision of African and European land masses.

The phylogeneric relationships between turacos and other birds have attracted considerable debate over the past 50 years or more, with most authors of modern bird classification giving turacos sister family status with cuckoos. This almost traditional association of the two groups was long based on their shared zygodactyl arrangement of toes, wherein two toes project forward and two toes project backward. However, in turacos the fourth, or outer toe, is normally held at right angles to the main axis of the foot when perched or moving, while in cuckoos, the fourth toe is permanently re-

versed. Recent DNA analyses suggest that turacos have no close living relatives.

Currently 23 species of turacos are recognized, grouped within eight genera and three subfamilies. Corythaeolinae contains the giant monospecific *Corythaeola*, long considered an isolated genus without any close relatives. The Musophaginae contains 17 forest species within four genera, while the remaining five savanna species of the Criniferinae are grouped in three genera.

Physical characteristics

Turacos must surely rank among the most colorful and striking of all African birds. Of the 23 species, the 17 forest and woodland species have lustrous, iridescent green, blue or violet plumage with brilliant red primaries conspicuous in flight. The five savanna species are predominantly gray or brown in color, while the giant of the family the great blue turaco (*Corythaeola cristata*) is largely greenish blue and yellow, with chestnut posterior underparts, but lacks any red in

the wings. With the exception of the great blue, all turacos are medium-sized birds (16-20 in; 40-50 cm), with a fairly long tail and rather short, rounded wings. Most have a prominent erectile crest, the shape, size and color of which is extremely variable. The sexes are alike in all species, though in the white-bellied go-away-bird (Criniferoides leucogaster) the bill color in males is dark, while that of the female varies from pea-green to pale vellow. Most species have a rather short, strong bill with a curved culmen (ridge of upper mandible), that is ridged in a few species. In the two Musophaga species, the culmen extends back to form a brightly colored frontal shield. All species within the genus Tauraco have bright red orbital skin, some with well-developed eye wattles. In nearly all species feathers of the head and breast lack barbules, and are hairy in texture. The two plantain-eaters are somewhat unique in having the elongated feathers that produce the crest present only on the back of the head and on the nape, and that are somewhat bristly and stiff to the touch.

The presence of two copper pigments, red turacin and green turacoverdin is unknown elsewhere in the animal kingdom. Normally such bright colors in birds are produced by melanins and lipochromes, or by diffraction of light from the surface of feathers, but not so in the Musophagidae. Turacoverdin is present in several species that lack turacin, but turacin does not occur in the absence of turacoverdin. The amount of turacoverdin is directly related to the luxuriance of the habitat in which they occur, being most developed in the tropical forest species, and least developed or absent in the savanna species. An earlier belief that these pigments were water soluble and washed out in rainstorms is untrue.

Distribution

Turacos are currently confined to sub-Saharan Africa, being absent only from the dry waterless regions of the central Kalahari, the western Cape, and the Horn of Africa. Being poor fliers, turacos are unable to reach offshore islands, but are present on both Bioko (formerly Fernando Po) and Zanzibar, which were joined to the African mainland in recent geological times.

Habitat

Turacos occupy all arboreal habitats south of the Sahara Desert from sea-level to over 9,800 ft (3,000 m). All types of forest, woodlands, as well as bushed and wooded grasslands, and the semi-arid acacia scrub are home to turacos, go-away-birds, and plantain-eaters. Recently many species have adapted to well-wooded suburban parks and gardens.

Black-billed (*Tauraco schuettii*), Knysna (*T. corythaix*), Livingstone's (*T. livingstonii*), and the great blue turaco are the most ecologically versatile species, occurring in both lowland and montane forests. With the montane forests now recognized as important centers of endemism in Africa, five allopatric turacos: Hartlaub's (*T. hartlaubi*), white-cheeked (*T. leucotis*), Prince Ruspoli's (*Tauraco ruspolii*), Bannerman's (*T. bannermani*), and Ruwenzori turaco (*Ruwenzorornis johnstoni*) are restricted to quite small and in some cases highly threatened habitats. Elsewhere the green (*T. persa*), yellow-billed (*T. macrorbynchus*), and Fischer's turaco (*T. fischeri*) are typi-

cally lowland forest and forest edge species. Schalow's (*T. schalowi*), purple-crested (*Gallirex porphyreolophus*), red-crested (*T. erythrolophus*), white-crested (*T. leucolophus*), violet (*Musophaga violacea*), and Ross's turaco (*M. rossae*) occupy gallery and riverine forests with seasonal periods spent in adjacent and more open woodlands. Outside of these forests and woodlands, the northern savannas of sub-Saharan Africa are occupied by the two plantain-eaters, and the eastern and southern savannas by the three go-away-birds.

Behavior

Most turacos are shy, strongly territorial, and gregarious, often remaining in family groups for long periods. While the forest species are generally highly sedentary, some gallery and riparian turacos are frequently recorded at fruiting trees in areas they are normally absent from for several months. Similarly the plantain-eaters and go-away-birds of the savannas and acacia woodlands regularly undertake local movements in response to fluctuating food and water supplies.

All forest species spend much of their time within a designated core territory, which is itself surrounded by a closely guarded peripheral feeding area. However, they regularly visit forest patches beyond their territory borders for food, often traveling long distances to reach a particularly favored fruiting tree. They invariably approach and leave it in single file and in total silence. Territory size varies considerably, ranging from around 0.7 mi² (2 km²) for the great blue and Ross's turacos in western Kenya, to an average of 10 acres (4 ha) per pair for Schalow's on the Nyika Plateau in Malawi, and 37 acres (15 ha) per pair for the yellow-billed turaco in Gabon.

All turacos are highly vocal, and the raucous calling of each of the 15 species of green turacos (Tauraco spp.) combined with the loud, resonant "kok-kok-kok-kok" calls of the great blue are among some of the most characteristic sounds of the African forests, just as the plaintive, nasal calls of the go-awaybirds are so typical of the African savannas. A day in the life of a turaco begins around dawn when an individual calls and others nearby respond immediately. Individuals and family groups soon begin feeding in fruiting trees, but as the day warms up, they spend long periods preening and basking in the morning sun. Where two or more species occur together, the calls of one will frequently initiate aggressive responses from others. Such "counter-singing" is commonly encountered between yellow-billed and green turacos in Gabon, Knysna, and purple-crested turacos in South Africa, Schalow's and purple-crested in Malawi, and black-billed and Ruwenzori turacos in Rwanda. As evening approaches most turacos move towards their favored roosting trees, and again periods of prolonged calling may be a feature of such journeys to the roosting site.

The harsh, barking calls of each of the 15 species of green turacos are extremely similar, differing only slightly in tempo and pitch. For most it is a loud, raucous barking, often preceded by a higher-pitched hoot, the function of which is simply territorial advertisement, only in the Ruwenzori turaco is there any major variation. The two *Musophaga* species (Ross's and violet turacos) engage in long choruses of deep, rolling,

gargling "cou-cou-cou-cou-cou" notes which tend to run together producing a continuous, pulsating, almost monkey-like chorus, and which is even more pronounced when two or more individuals call in unison. The three go-away-birds utter a series of plaintive, nasal call notes, some of which are described by many as if saying "g'way, g'way." The two plantain-eaters call in a series of high-pitched laughing or cackling "cow-cow-cow" or "how-how-how" notes.

Feeding ecology and diet

Turacos consume large quantities of both wild and cultivated fruits and are important agents in the dispersal of seeds of indigenous trees throughout sub-Saharan Africa. Several species also eat flowers and leaves, caterpillars, moths, beetles, snails, slugs, and termites, particularly during the breeding season. Although the English name of plantain-eater is used for two species, and was formerly given to the family as a whole, neither plantains nor cultivated bananas form any part of the diet of any turaco in the wild.

Throughout the equatorial forests of West and Central Africa, fruits of the parasol (Musanga) and waterberry (Syzygium) trees are particularly favored, and in areas where Polyalthia, Cissus, and Ficus species have regular heavy fruitings, these also provide the staple foods of most forest turacos. Leaves and flowers seem to be particularly important to the great blue, constituting on average more than 25% of their overall diet. Elsewhere, in the acacia savannas of Africa, the go-away-birds and plantain-eaters have a far more varied diet consisting not only of fruit, but also large quantities of leaves, flowers, seed pods, and emerging termite alates. Water is a major requirement, and in southern Africa groups of 20-30 gray go-away-birds (Corythaixoides concolor) have been recorded at favored water sources. A gray go-away-bird has been observed carrying water to a nearby fledged young. Gray go-away-birds have also eaten clay, the only recorded example of geophagy among turacos.

Reproductive biology

The onset of the rainy season stimulates courtship activity among all turacos, resulting in much calling and the chasing of one another from tree to tree, mutual feeding, opening and closing of the bill, raising and lowering of crests, bowing and flirting of the tail, and in the green forest species, much wing- spreading to display the bright crimson primaries. All breed solitarily, and while most species are probably monogamous, some go-away-birds have assistants to help feed the young and defend the territory. Such "helpers" are likely offspring from a previous brood.

All species build a flat and often flimsy nest of sticks, very similar to those of pigeons and doves (Columbidae). Nests of the forest turacos are placed in thick foliage of trees or shrubs 16–66 ft (5–20 m) above ground, while those of go-away-birds and plantain-eaters are often in acacias, at times unconcealed. Clutch size of savanna species is two or three eggs; all other turacos normally lay two eggs. The rounded eggs vary in color from white or grayish-white to cream, glossy bluish-white, or pale ivory-green. Incubation is by both sexes, and varies from



A gray go-away-bird (*Corythaixoides concolor*) at its nest. (Photo by W. Tarboton/VIREO. Reproduced by permission.)

22–23 days in the smaller green turacos, to 27–28 days in the plantain-eaters and go-away-birds, and 29–31 days in the great blue. The hatchlings are at a relatively advanced stage of development with a thick coat of black, brownish, or gray down, and in some species a well-developed wing claw. All nestlings are fed by regurgitation, and in most species the parents swallow the chick's feces as soon as discharged. Young become extremely active between two and three weeks, and commonly leave the nest to climb about in nearby branches long before they can fly. Most make their first attempts at flight at 28–35 days, but remain dependent upon their parents for some time longer, with young great blue turacos being fed for up to three months after leaving the nest.

Conservation status

As of 2000, only three species of turacos are listed by the IUCN as facing some degree of threat. However, with the rate of habitat loss in Africa accelerating all too quickly, species with restricted ranges have become the most highly vulnerable and require constant monitoring. The indiscriminate trapping and export of thousands of turacos annually has had its effect on several species. While a number of turacos have been listed under CITES (Convention on International Trade in Endangered Species), it is debatable whether existing legislation has had any beneficial effects on the birds. Under IUCN criteria (in 2001) for assigning threatened status, Bannerman's turaco is listed as Endangered, Prince Ruspoli's is Vulnerable, and Fischer's is Near Threatened.

The last turaco species to be described, Bannerman's turaco, is restricted to small, fragmented forest patches in the Bamenda highlands of western Cameroon, and is one of the most threatened birds in Africa. Between 1965 and 1985 indiscriminate forest clearance reduced its habitat by half, and today its survival is only possible if the existing forests on Mts. Oku and Ijim are guaranteed lasting protection. While it is

estimated that fewer than 2,000 individuals remain in the Bamenda highlands, prospects for its long-term survival are bleak. The people living in and around its forested habitats walk through these forest patches daily to eke out a subsistence that will ultimately result in more forest being cleared. The population, numbered at 250,000 in the 1990s, will grow to half a million or more by 2025, and the numbers of Bannerman's turaco will be further reduced. In southern Ethiopia, Prince Ruspoli's turaco has an equally restricted range in the mixed broad-leaf and acacia woodlands that in some areas are becoming seriously degraded by continuing human encroachment and demands for wood fuel. Equally alarming is the impact of human encroachment on the remaining coastal forests in East Africa. Fischer's turaco has an extremely restricted and diminishing range in southern Somalia, coastal Kenya, and northeastern Tanzania. On the island of Zanzibar an endemic subspecies is facing habitat loss of unprecedented proportions.

Significance to humans

Turacos have long been exploited by humans for food and their feathers. For centuries turaco feathers have adorned ceremonial headdresses of African royalty and elders. In Kenya, feathers from Schalow's, Ross's, and Hartlaub's turacos have been regularly seen in ceremonial headdresses of the Masai tribe, while in Cameroon a red flight feather from Bannerman's turaco in an elder's black hat indicates his position as a "chindoh" or traditional council member. Elsewhere, particularly in parts of southern Africa, the gray go-away-bird is considered something of a pest, being highly destructive to the soft-skinned fruits and vegetables grown on large commercial plantations.

The demand from the cage-bird trade around the world has resulted in large scale trapping and export of turacos, most notably from Guinea, Sierra Leone, Liberia, Ghana, Togo, and Tanzania. Loopholes in legislation are ruthlessly exploited, so that for every 10 turacos that survive the journey from Africa to a captive environment, 50, maybe hundreds, may perish in the process, due largely to the often cruel and appalling methods of capture and the resulting stress of confinement. In an effort to halt such exports, several responsible zoos and aviaries around the world are establishing captive breeding programs involving several species of turacos. Turaco husbandry has made great advances in recent years, and it is hoped that in the near future, legislation will be in place to ensure that only birds bred in captivity will be available to other zoos, aviaries, and turaco breeders.



1. Purple-crested turaco (*Gallirex porphyreolophus*); 2. Gray go-away-bird (*Corythaixoides concolor*); 3. Western gray plantain-eater (*Crinifer piscator*); 4. Hartlaub's turaco (*Tauraco hartlaubi*); 5. Ross's turaco (*Musophaga rossae*); 6. Great blue turaco (*Corythaeola cristata*); 7. White-bellied go-away-bird (*Criniferoides leucogaster*); 8. Ruwenzori turaco (*Ruwenzorornis johnstoni*). (Illustration by Joseph E. Trumpey)

Species accounts

Great blue turaco

Corythaeola cristata

SUBFAMILY

Corythaeolinae

TAXONOMY

Musophaga cristata, Vieillot, 1816, Sierra Leone. Monotypic.

OTHER COMMON NAMES

English: Blue plantain-eater; French: Touraco geant; German: Riesenturako; Spanish: Turaco Gigante.

PHYSICAL CHARACTERISTICS

28–30 in (70–76 cm); male 1.9–2.1 lb (857–949 g), female 1.8–2.7 lb (822–1,231 g). The giant of the family, readily identified by its overall greenish blue and yellow plumage, blue-black crest, bright yellow bill, tipped red, long wide tail, and chestnut posterior underparts. Juveniles similar but duller and with much smaller crest.

DISTRIBUTION

Equatorial Africa from Guinea Bissau, Liberia and Ivory Coast east through Nigeria, Cameroon, Gabon, and Congo to Uganda, Rwanda, Burundi, northwest Tanzania, and western Kenya.

HABITAT

Lowland and montane forest from sea-level to over 7,000 ft (2,400 m).



BEHAVIOR

Generally found in pairs or family groups, feeding in tall forest trees. Highly territorial and vocal, with their loud guttural "cow-cow-cow-cow" calls and deep, resonant purring notes a feature of the African rainforests.

FEEDING ECOLOGY AND DIET

Primarily a fruit eater, but also consumes large quantities of leaves and flowers when certain fruits become scarce. Recorded eating algae.

REPRODUCTIVE BIOLOGY

A solitary breeder, generally laying two pale blue-green eggs in a nest that is nothing more than a platform of sticks with a shallow rim, but well hidden in a tall, leafy forest tree. Both sexes incubate for approximately one month, and nestlings climb outside of the nest a month later. The young fledge at around five to six weeks, but remain dependent on the adults for up to three months.

CONSERVATION STATUS

The most widespread of all turacos. Although not globally threatened, continuing forest destruction, hunting, and trapping for export will result in a decline in numbers in many parts of West Africa, most notably in Guinea, Liberia, Sierra Leone, Ivory Coast, Nigeria, and Togo.

SIGNIFICANCE TO HUMANS

Widely considered a delicacy over much of West Africa, as well as being a highly sought after species in the traditional fetish markets of Nigeria. ◆

Ross's turaco

Musophaga rossae

SUBFAMILY

Musophaginae

TAXONOMY

Musophaga rossae, Gould, 1851, West Coast of Africa (precise locality unknown). Monotypic.

OTHER COMMON NAMES

English: Lady Ross's violet plantain-eater; French: Touraco de Lady Ross; German: Rossturako; Spanish: Turaco de Ross.

PHYSICAL CHARACTERISTICS

20–21 in (50–53 cm); male 13.8–15.7 oz (390–444 g), female 13.9–14.0 oz (395–398 g). A striking large, glossy violet-blue turaco, with conspicuous crimson crest, yellow bill and frontal shield, while in flight, the brilliant red primaries contrast sharply with the dark violet-blue body and tail. Juveniles lack frontal shield; crown of head is black with small red patch in the center.

DISTRIBUTION

Widely distributed in central and eastern Africa from the Dem. Rep. Congo, Uganda and western Kenya south to eastern Angola and northern Zambia. Extralimital populations occur in the northern Central African Republic, Cameroon, northeast-



ern Gabon, and at scattered localities along the Caprivi Strip and in the Okavango Delta region of northwestern Botswana.

HABITAT

Typically a bird of the gallery forests and riverine woods from around sea level to over 5,000 ft (1,750 m), but reaching 8,200 ft (2,500 m) in montane forests along the southern Sudan/northeastern Uganda border.

BEHAVIOR

Generally found in pairs or family groups, with much calling between individuals and nearby groups. Some seasonal movement into deciduous thickets and Brachystegia woodlands at onset of the rains in Zambia and Botswana, presumably related to the emergence of fruiting trees. Highly territorial and aggressive towards other turacos when breeding.

FEEDING ECOLOGY AND DIET

Largely frugivorous, but diet frequently supplemented with flowers, shoots, and flying termites. Will also feed on cultivated fruits such as guavas and loquats where available.

REPRODUCTIVE BIOLOGY

One or two almost cylindrical creamy white eggs are laid in a rather flimsy, pigeon-like platform of twigs, generally well hidden in dense tree foliage, mistletoe, or creepers. Incubation shared by both sexes for 24–26 days. On hatching the young are covered in dark brown down. Nestlings begin to climb out of the nest into nearby branches after 24 days, and generally leave the nest tree after a month, but remain with the adults for several weeks.

CONSERVATION STATUS

Although not considered a threatened species, as all African forests and woodlands continue to shrink and give way to subsistence agriculture, it is the gallery and riverine forests that are being destroyed most rapidly. Formerly traded in some

numbers from East and Central Africa, but trade appears to have declined in recent years. Habitat loss is the most serious threat facing this species.

SIGNIFICANCE TO HUMANS

Feathers, particularly from the red primaries, are used to decorate ceremonial Masai headdresses in southwestern Kenya. ◆

Ruwenzori turaco

Ruwenzorornis johnstoni

SUBFAMILY

Musophaginae

TAXONOMY

Gallirex johnstoni Sharpe, 1901, Ruwenzori Mountains, Uganda. Two subspecies.

OTHER COMMON NAMES

English: Johnston's mountain turaco; French: Touraco du Ruwenzori; German: Kammschnabelturako; Spanish: Turaco del Ruwenzori.

PHYSICAL CHARACTERISTICS

17–18 in (43–46 cm); 8.2–8.7 oz (232–247 g). A brilliant green and violet blue turaco with red primaries conspicuous in flight. Short glossy green or purplish blue crest on hindcrown; nape dull crimson, chin and throat blue black. Distinctive peachyred patch on an otherwise green breast; wings and tail deep violet blue. Shape of bill highly distinctive with a rounded culmen rising to a narrow bony ridge between the eyes. Eyelids scarlet surrounded by highly variable loral areas; these being emerald green and fully feathered in *kivuensis*, but simply bare yellowish skin with some pinkish red below and behind the eyes in nominate birds.



DISTRIBUTION

R. j. johnstoni: Ruwenzori mountains and at Mount Kabobo (Dem. Rep. Congo), where originally described as T. j. bredoi. R. j. kivuensis: Montane forests of the Itombwe and Kivu Highlands (Dem. Rep. Congo), Virunga volcanoes, Nyungwe Forest (Rwanda/Burundi), and southwest Uganda.

HABITAT

Endemic to high mountain forest between 6,500 and 11,000 ft (2,000–3,400 m) on either side of the Albertine Rift.

BEHAVIOR

Occurs in pairs or small family groups, with many individuals remaining paired and aggressively defending territories throughout the year. Particularly favors the bamboo zones and areas dominated with epiphytes and lianas.

FEEDING ECOLOGY AND DIET

Eats primarily fruits and berries, but large quantities of leaves and flowers are also consumed. Where sympatric with the great blue and black-billed turacos, all three species can frequently be found feeding alongside each other in the same fruiting tree.

REPRODUCTIVE BIOLOGY

One or two dull grayish-white eggs are laid in a nest that is little more than a small platform of sticks, generally 10–15 ft (3–5 m) above ground in a bamboo thicket. Incubation and fledging periods for this species remain unknown.

CONSERVATION STATUS

Not globally threatened, but with continuing habitat degradation as a result of prolonged civil unrest throughout its restricted range, it remains a species in need of constant monitoring.

SIGNIFICANCE TO HUMANS

Although no trade reported in this species, it has long been hunted for food in the Democratic Republic of Congo. ◆

Purple-crested turaco

Gallirex porphyreolophus

SUBFAMILY

Musophaginae

TAXONOMY

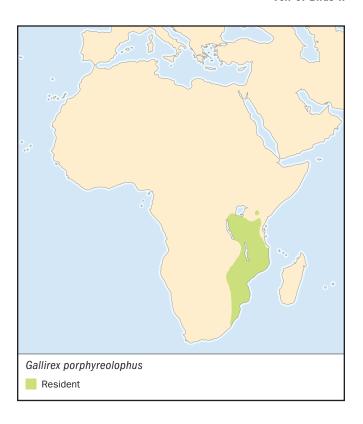
Corythaix porphyreolophus Vigors, 1831, Durban, South Africa. Two subspecies.

OTHER COMMON NAMES

English: Purple-crested lourie; French: Touraco a huppe splendide; German: Glanzhaubenturako; Spanish: Turaco Crestimorado.

PHYSICAL CHARACTERISTICS

16–18 in (40–46 cm); 7.7–11.6 oz (218–328 g). A striking iridescent green-and-violet turaco with a dark violet purple crest and conspicuous red flight feathers. Upper back and breast green washed with rose pink in nominate birds, but lacking any wash in *chlorochlamys*. Lower back and wings grayish blue, tail glossy violet blue. Posterior underparts pale bluish slate in nominate birds, but dull greenish gray in *chlorochlamys*. Juveniles similar to adults but red primaries duller and less extensive.



DISTRIBUTION

G. p. porphreolophus: South Africa from Natal and eastern Transvaal north to Mozambique and Zimbabwe, intergrading with chlorochlamys in the Zambezi Valley. G. p. chlorochlamys: Zambia east to Malawi and northern Mozambique, and north to Tanzania, southeastern and central Kenya, Burundi, and Rwanda.

HABITAT

Typically in moist woodlands, but locally in miombo and well-timbered suburban parks and gardens. Generally below 5,000 ft (1,500 m), but reaches 6,000 ft (1,800 m) in central Kenya.

BEHAVIOR

Generally in pairs or small family groups, but flocks of up to 20 birds have been observed at favored fruiting trees or watering points. At onset of the rains in Zimbabwe, there is a marked dispersal away from riverine woods into the surrounding miombo woodlands.

FEEDING ECOLOGY AND DIET

Mainly fruits and berries, while in many parts of southern Africa will readily feed at suburban bird feeders.

REPRODUCTIVE BIOLOGY

Two or three rounded, glossy white eggs are laid in a flimsy, unlined platform of sticks 10–30 ft (3–10 m) above ground, well concealed among matted tree creepers or dense parasitic growth. Both sexes incubate for 22–23 days; hatchlings are covered with a thick grayish brown down. The young become active at about three weeks, when they begin to move out of the nest and into the surrounding branches, and make their first flight at around 38 days.

CONSERVATION STATUS

Locally common in many parts of southern Africa, but in eastern Africa the population is declining due to continuing loss of habitat and in some areas indiscriminate trapping.

SIGNIFICANCE TO HUMANS

During the early part of the twentieth century this species was hunted by Zulu warriors in southern Africa for their red flight feathers, which were used as adornments when going into battle. Today the same red primary feathers can be seen in the headdresses of African royalty and elders in Swaziland. •

Hartlaub's turaco

Tauraco hartlauhi

SUBFAMILY

Musophaginae

TAXONOMY

Corythaix hartlaubi Fischer and Reichenow, 1884, Mt. Meru, northern Tanzania. Monotypic.

OTHER COMMON NAMES

English: Blue-crested plantain-eater, black-crested turaco; French: Touraco de Hartlaub; German: Seidenturako; Spanish: Turaco de Hartlaub.

PHYSICAL CHARACTERISTICS

16–17 in (40–44 cm); 6.9–9.7 oz (195–275 g). A dark iridescent green turaco with brilliant red primaries conspicuous in flight. Rounded bushy crest and nape glossy blue-black; chin, cheeks, neck, mantle, throat, and breast dark green; lower back, folded wings, and tail deep violet blue; thighs and belly dull blackish washed with green. Prominent white patch in front of the eye separated from a white line extending from gape to ear coverts by a black loral patch and narrow black line immediately below the eye. Orbital ring and bare skin behind the eye red. Juveniles similar to adults but duller and with less red in primaries.



DISTRIBUTION

An East African endemic centered around the Kenyan Highlands, extending into north Tanzania at Loliondo, Longido, mounts Meru and Kilimanjaro, the Pares and West Usambara mountains. It reaches east Uganda at mounts Elgon, Moroto, and Morongole.

HABITAT

Evergreen montane forests between 4,550 and 10,500 ft (1,400–3,250 m), as well as in well-timbered suburban parks and gardens around Nairobi and other central Kenyan towns.

BEHAVIOR

Typically in pairs or family groups, congregating in groups of up to 20 individuals at favored fruiting trees. In many areas pairs defend a core territory year round, and each day work a well-defined feeding route within territorial boundaries. Flight appears weak and labored with much flapping and gliding, and generally for only short distances. Courtship displays by the male are noisy and involve much fanning and jerking of the tail, raising and lowering of the crest, and half opening of the wings to display crimson flight feathers. Once the pair bond is established, the pair engages in frequent bill rubbing, and the male offers food to the female at frequent intervals.

FEEDING ECOLOGY AND DIET

Primarily eats fruits and berries, but will also consume flowers, caterpillars, moths, and beetles. Appears particularly attracted to black or dark red fruits, and captive birds readily devour black grapes.

REPRODUCTIVE BIOLOGY

Two rounded dull white eggs are laid in a shallow platform of loosely interlaced twigs, some 7–25 ft (2.5–8 m) above ground, and generally among thick tree foliage. Incubation is by both sexes for 22–23 days. Newly hatched chicks are covered in black down, and for the first few days are fed on regurgitated caterpillars and fruit pulp. At 17–18 days the nestlings are able to climb all over the nest tree, rarely being in the nest itself, and are able to make their first flight at around 28 days.

CONSERVATION STATUS

Although fairly common in Kenya, the northern Tanzanian population has been seriously impacted by years of indiscriminate trapping and export, resulting in high mortality and diminishing populations in several areas. Tanzania has been the sole exporter of wild-caught birds, and despite annual quotas of 200 birds, this has been disregarded for many years.

SIGNIFICANCE TO HUMANS

A popular cage bird with large numbers in zoos and aviaries in the United Kingdom, Europe, North America, Mexico, and the Far East, with considerable breeding success, thus reducing the need for the continued importation of wild birds from Tanzania.

Gray go-away-bird

Corythaixoides concolor

SUBFAMILY

Criniferinae

TAXONOMY

Corythaix concolor Smith, 1833, inland of Port Natal (Durban), South Africa. Four subspecies.

OTHER COMMON NAMES

English: Gray lourie; French: Touraco concolore; German: Graularmvogel; Spanish: Turaco Unicolor.

PHYSICAL CHARACTERISTICS

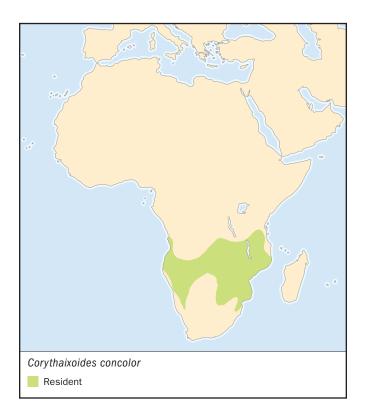
18–20 in (46–51 cm); 7.1–12.0 oz (202–340 g). Adult has entire head and body warm smoky gray, being palest around the eyes, and darkest on the chin, throat, tail, and primary coverts. In most forms there is a suffusion of olive green on the breast, though this is hardly noticeable in the field. Crown feathers are long and partly decomposed, forming a slightly shaggy crest that varies in length, and which can be raised or depressed at will, but when flattened, projects well beyond the back of the head. Juveniles similar to adults but with shorter crest and a buffy tinge to the overall appearance.

DISTRIBUTION

Locally common throughout the northern parts of South Africa from Zululand and the eastern Transvaal north to Mozambique, Zimbabwe, Zambia, Malawi, and southeastern Tanzania, and west to Botswana, Namibia, Angola, and southern Dem. Rep. Congo. Up to four races have been recognized, though racial variation is difficult to interpret. The presence of darker birds in the east and paler ones in dry western areas may to be attributed to a cline with differing characteristics among birds due to changes in the environment.

HABITAT

Typically a bird of the drier, open woodlands and savannas of southern Africa, with a marked preference for those areas dominated by acacias. While principally a species adapted to dry woodlands, it is very much dependent on water, a factor that accounts for its absence from otherwise suitable habitat such as the dry central and southwest Kalahari. In recent decades has readily adapted to suburban parks and gardens around Johannesburg.



BEHAVIOR

Generally found in pairs, small family groups, or parties of three to 20 birds, hopping, climbing, and bounding about in trees and bushes with much dexterity. Alert and inquisitive, it will often perch on the topmost branches of trees with a marked upright posture, raising and depressing its crest, and jerking its tail as it calls. Flight is strong and direct with alternating gliding and flapping. Movements of up to 40–60 individuals or more have been observed on several occasions, possibly in response to fluctuating food or water supplies. At all times will react aggressively toward other turacos, chasing them away from fruiting trees, bird feeders, and water, yet readily sharing such resources with other birds such as pigeons, parrots, barbets, orioles, and starlings.

FEEDING ECOLOGY AND DIET

Feeds primarily on fruits, but will also consume large quantities of flowers, foliage, and termites. In many areas considered a pest by gardeners and commercial horticulturalists due to its destructive consumption of cabbages, lettuce, legumes, and soft-skinned fruits.

REPRODUCTIVE BIOLOGY

One to four, but usually three white or pale grayish-blue eggs are laid in a flimsy, pigeon-like platform of sticks some 15–20 ft (3–6 m) above ground, generally in an acacia tree. Both sexes incubate for 26–28 days. Newly hatched young are covered in dense brown or grayish brown down. They become active at 14–18 days, clambering around the branches of the nest tree, taking their first short flights at about 23 days, and finally becoming fully fledged at around four weeks. On several occasions three to six birds have been recorded attending to and feeding young in the nest. Such "helpers" are probably young birds from an earlier brood.

CONSERVATION STATUS

A wide-ranging and generally common species throughout its range. Currently no known threats to either its habitat or overall population.

SIGNIFICANCE TO HUMANS

Long considered a bird of ill repute among the Kalahari bushmen, who complain bitterly that it deliberately warns wild animals of their approach. ◆

White-bellied go-away-bird

Criniferoides leucogaster

SUBFAMILY

Criniferinae

TAXONOMY

Chizaerhis leucogaster Ruppell, 1842, southern Ethiopia. Monotypic.

OTHER COMMON NAMES

English: White-bellied plantain-eater; French: Touraco a ventre blanc; German: Weissbauch-Larmvogel; Spanish: Turaco Ventriblanco.

PHYSICAL CHARACTERISTICS

19–21 in (48–53 cm); 6.0–8.8 oz (170–250 g). A large grayand-white turaco with a stiff and pointed brownish gray crest rising from the forehead. Upperparts, sides of head, chin, and entire neck and breast gray, rest of underparts white. Black



flight feathers with white bases form a conspicuous white speculum in flight; tail black with a broad white median band. Bill blackish in male, pea green in the female (sometimes yellowish when breeding). Juveniles similar to adult but browner.

DISTRIBUTION

Widely distributed in the arid and semi-arid savannas of eastern and northeastern Africa from Somalia, Ethiopia, and southern Sudan south through northern Uganda, northern and eastern Kenya to central Tanzania.

HABITAT

Typically in hot, low acacia savannas from sea level to 4,550 ft (1,400 m), but reaching 6,500 ft (2,000 m) on the Laikipia Plateau in central Kenya.

BEHAVIOR

A common and often conspicuous bird, occurring singly, in pairs, or family groups. Flies somewhat slowly with rather rapid wingbeats and much gliding. Like all turacos becomes extremely agile once landed. A noisy bird with a variety of sheep-like bleating calls.

FEEDING ECOLOGY AND DIET

Flowers, leaf shoots, and young acacia seed pods form an important aspect of their diet, as do the fleshy ripe fruits of *Balanites* trees and bushes. Will also readily eat exotic fruits as *Carica* (papaya) and *Psidium* (guava) if offered at bird feeders. Flowers and foliage of many dry country plants are consumed in vast quantities, as are their fruits whenever available.

REPRODUCTIVE BIOLOGY

Two or three glossy pale bluish green eggs are laid in a rather small, flat structure of twigs some 10–40 ft (3–12 m) above ground, generally in an acacia or *Balanites* tree. Incubation is by both sexes for 27–28 days. On hatching the young are covered in dark grayish brown down with a patch of bare skin

around the eyes. They are fed a regurgitated pulp by both parents, and on a few occasions other birds have been observed "helping" at the nest. Fledging period remains unrecorded.

CONSERVATION STATUS

Not globally threatened, and with no major threats to either its habitat or populations. With some trapping and export reported from Tanzania, it is recommended that it be listed in Appendix 3 of the CITES legislation.

SIGNIFICANCE TO HUMANS

None known. ◆

Western gray plantain-eater

Crinifer piscator

SUBFAMILY

Criniferinae

TAXONOMY

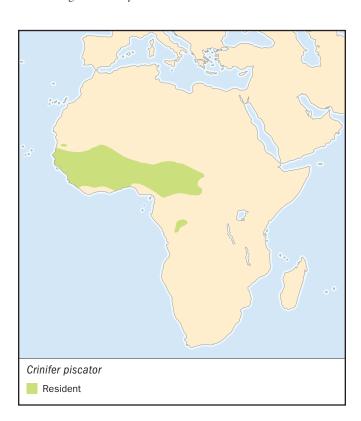
Falco piscator Boddaert, 1783, Senegal. Monotypic.

OTHER COMMON NAMES

English: Gray plantain-eater; French: Touraco gris; German: Schwarzschwanz-Larmvogel; Spanish: Turaco Gris Occidental.

PHYSICAL CHARACTERISTICS

19–20 in (48–51 cm); 11.6–12.3 oz (330–350 g). A predominantly gray-and-white turaco with a large lemon-yellow bill. Adults have forehead, crown, lores, cheeks, chin, and throat dark brown. A shaggy dark brown nape crest with whitish edges is unique among turacos. Upperparts silvery gray with dark brown spots; the lower breast, belly, flanks, thighs, and under tail coverts are white with heavy brown streaking, particularly on the thighs. Primary feathers black with a central third of the



inner webs white, forming a conspicuous white wing patch in flight; tail largely blackish brown. Juveniles less silvery gray on upperparts and lack any crest on an otherwise all dark head.

DISTRIBUTION

Widespread throughout the sub-Saharan acacia steppe, wooded savannas, and cultivation from southern Mauritania, Senegambia, Guinea, and Sierra Leone east to Nigeria, Cameroon, Lake Chad, and the Central African Republic. Also disjunctly along the Congo River south of Stanley Pool.

HABITAT

Typically from sea level to 4,225 ft (1,300 m) in open wooded savannas and thorn scrub with scattered tall trees, while in the more semi-arid areas it keeps mainly to the thicker stands of vegetation and riparian woods. In many areas has adapted to cultivation and the neighborhood of villages, particularly where favored fruiting trees are available. Has readily adapted to parks and gardens in many countries.

BEHAVIOR

A gregarious species, occurring generally in pairs or small groups. Always a noisy bird, with one seldom perching or joining its mate without a great deal of commotion. Pair bonding is exceptionally strong, with much calling, bowing, tail fanning, and food exchanges taking place during all greeting displays. Courtship display flights are always noisy and impressive. Less agile in running along branches than other turacos, as a result tends to fly more, albeit for short distances with much gliding

alternating with rapid wingbeats. Frequently comes to ground to drink.

FEEDING ECOLOGY AND DIET

A wide variety of wild and cultivated fruits are eaten, together with flowers, seed pods, and invertebrates, while the name plantain-eater is erroneous. Flowers constitute a major part of the diet, possibly as high as 50% in some individuals. Favored fruits include figs, mangos, and guavas, also the wild date (*Phoenix reclinata*), oil palm fruits (*Elaeis guineensis*), and the widely introduced neem (*Azadirachta indica*).

REPRODUCTIVE BIOLOGY

Generally two grayish white or pale bluish white eggs, oval and slightly glossy, are laid in a fairly substantial platform of dry sticks some 12–50 ft (4–15 m) above ground in a leafy tree. Incubation is by both sexes for 27–28 days, and on hatching the young are covered in grayish-brown down. Fledging period for this species unrecorded.

CONSERVATION STATUS

Not globally threatened, being widespread and locally abundant over much of the West African savannas, reaching a density of one bird per 2.5 acres (per hectare) in some areas of *Acacia scorpioides* woodland in Senegal. Commonly hunted and trapped for export in several countries, most notably Guinea.

SIGNIFICANCE TO HUMANS

A highly sought after species in the traditional fetish markets of Nigeria. lack lack

Resources

Books

del Hoyo, J., A. Elliott, and J. Sargatal, eds. *Handbook of the Birds of the World.* Vol.4, *Sandgrouse to Cuckoos.* Barcelona: Lynx Edicions, 1997.

Fry, C.H., S. Keith, and E.K. Urban. *The Birds of Africa*. Vol. 3. New York: Academic Press, 1988.

Periodicals

Moreau, R.E. "Some Aspects of the Musophagidae." *Ibis* 100 (1958): 67–112; 238–270.

Veron, G., and B.J. Winney. "Phylogenetic Relationships Within the Turacos (Musophagidae)." *Ibis* 142 (2000): 446–456.

Organizations

International Touraco Society. Brackenhurst, Grange Wood, Netherseal, Nr Swadlincote, Derbyshire DE12 8BE United Kingdom. Phone: +44 (0)1283 760541. E-mail: agaperki@dircon.co.uk

Donald Arthur Turner

Cuculiformes Cuckoos, anis, and roadrunners

(Cuculidae)

Class Aves
Order Cuculiformes
Suborder Cuculi
Family Cuculidae
Number of families 1

Thumbnail description

Small to medium-sized landbirds, with slightly curved and narrow bills, zygodactyl feet and long tails, and usually inconspicuous colors, generally light gray or light brown to black

Size

6.3-27.6 in (16-70 cm); 0.03-1.11 lb (17-550 g)

Number of genera, species

38 genera; 129 species

Habitat

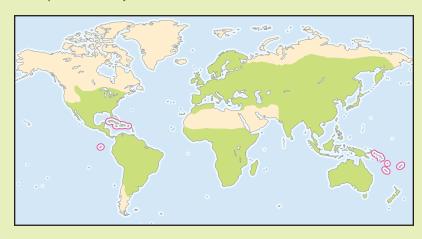
Mainly forest and woodland, although some species live in open countries and semi-arid regions

Conservation status

Critically Endangered: 2 species; Endangered: 1

species; Vulnerable: 6 species; Near

Threatened: 9 species; Extinct (since 1600): 1



Distribution

Present on all continents except Antarctica

Evolution and systematics

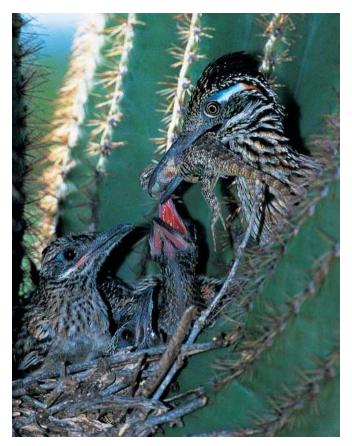
Cuckoos owe their popularity to their fascinating reproductive strategy, the so-called brood parasitism. Brood parasites are those bird species that lay their eggs in the nests of other birds, or hosts, who then raise the parasitic young. The family Cuculidae belongs to the order Cuculiformes and includes 38 genera and 129 species within six subfamilies: Cuculinae (Old World cuckoos), Phaenicophaeinae (malkohas and couas), Centropodinae (coucals), Coccyzinae (American cuckoos), Crotophaginae (anis), and Neomorphinae (New World ground cuckoos, roadrunners). Of these, only Cuculinae and Neomorphinae present the existing 50 obligate brood parasitic species. Molecular phylogenetics indicate that cuckoos are not closely related to any other family of birds, despite their morphologic similarity to the turacos, doves, and some parrots.

Old World cuckoos are most closely related to the malkohas, which are similar to the coucals; American cuckoos are most closely related to the anis, which, in turn, are most closely related to the New World ground cuckoos. Studies based on single or a few traits, such as skeletal characters, arrive at different relationships within the family, although most studies support the existence of the above named six subfamilies. A phylogeny based on 28 behavioral and ecological characters suggests that Neomorphinae and Phaenicophaeinae are polyphyletic groups, placing the obligate parasite *Tapera* (Neomorphinae) and the facultative parasite

Coccyzus (Phaenicophaeinae) within the Cuculinae. This would imply that brood parasitism arose only once in the evolutionary history of cuckoos. However, a molecular phylogeny supports the monophyly of three main clades: Cuculinae, Phaenicophaeinae, and Neomorphinae-Crotophaginae, with parasitic species within the three of them, thus postulating that brood parasitism had a polyphyletic origin. Clamator, traditionally situated within the Cuculinae, is grouped in this phylogeny with the Phaenicophaeinae.

Physical characteristics

Cuckoos and their relatives are terrestrial, all capable of flight. They present zygotactyl feet, with inner and outer toes directed backwards and the other two toes facing forwards. The bill curves downward slightly with a protruding hook at the tip of the upper mandible. Cuckoos usually have inconspicuous colors, such as light gray or light brown to deep red-brown and black. The plumage is usually shiny or shimmering. The basic color is often overshadowed by light or dark transverse bands and less often by longitudinal striping, particularly below, on the wings, and the tail. White areas also occur. The feather shafts may be shiny and stand out as white. Aside from the large yellow and green areas of some Chrysoccocyx species, the only vivid colors in cuckoos are the frequently colored bills, the red eyes (mostly in older birds), and the colored or sometimes black, naked areas about the eyes. The



Greater roadrunner (*Geococcyx californianus*) adult feeding a nestling in a saguaro cactus in Tucson, Arizona. (Photo by C.K. Lorenz. Photo Researchers, Inc. Reproduced by permission.)

plumage is cryptically colored in many brood-parasitic species, and may be adaptive to ecological problems of recognition and social association with their hosts. The juvenal plumage of common koels (*Eudynamys scolopacea*) somewhat resembles that of their host species, differing between geographical areas where they parasitize different hosts. Sexual dimorphism in plumage occurs in very few species, among them some malkohas, the African and Asian glossy cuckoos, and the common koel. Males and females are the same in size for most species, although they occasionally differ.

Distribution

The Cuculidae occur throughout America, Eurasia, Australia, and Africa. In America, they are absent from the most southern areas as well as a wide region in the north. In Africa there is a gap in their distribution in the northern third of the continent, coinciding with the Sahara Desert, and this gap extends to Arabia and nearby deserts. Finally, there are no cuckoos in the cold areas situated to the very north of Asia. Species differ widely in the extension of their distribution areas. Some of them present vast geographic distributions, such as the common cuckoo (*Cuculus canorus*), which occurs from the Iberian Peninsula to Japan and Siberia to India, with individuals wintering in South Africa. The darkbilled cuckoo (*Coccyzus melacoryphus*), the greater ani

(Crotophaga major), and the American striped cuckoo (Tapera naevia) are present in most of South Africa. However, it is more common for cuckoo species to have a more limited distribution. For example, some Cuculus are characteristic of a few islands in the Philippines, Borneo, and Sumatra; Cercococcyx spp. occurs in small areas of Africa; couas (Coua spp.) are endemic of Madagascar, and the green-billed coucal (Centropus chlororhynchus) occurs only in Sri Lanka.

Habitat

Most cuckoo species are arboreal and live in trees, many of them in the tropics and subtropics. The forests inhabited by most species are unspoiled primary rainforests, which are the only habitat for several species in Asia. Other cuckoos appear in different kind of forests, mangroves, and marshes, as well as human-made habitats such as plantations, city parks, and gardens. Several cuckoos live in open country and semiarid, hot areas in Australia, Mexico, and Central America. Brood parasites occur in virtually any possible place where potential hosts can be found. The best example is the common cuckoo, whose list of potential hosts exceeds 125, and as a consequence can be found nearly anywhere. The altitudinal range occupied by cuckoos is also wide, but the majority of species live in low lands, with few going above 6,600 ft (2,000 m). In fact, most examples of cuckoos at high altitudes are birds on passage, in places such as the Himalayas or Andes.

Behavior

Social organization

Cuckoos are mainly solitary birds, living on their own, or in pairs, during the breeding season, but a number of species are colonial, living in groups all year. Anis (*Crotophaga* spp.) and the Guira cuckoo (*Guira guira*) live in social groups in which several pairs or females share a nest. These four species can be considered cooperative breeders.

Social behavior and communication

Most species possess very characteristic calls that are easy to identify. These calls vary from whistles in some *Cuculus*, to screams in great spotted cuckoos (*Clamator glandarius*), rattles in the roadrunner, and guttural sounds in the ground cuckoos. Songs and calls of cuckoos are remarkably similar throughout their range. Calls are used to announce territories and attract mates, and thus most variations in calls are given by males during the breeding season, when males may call all day. Females generally do not call, or they may utter a shorter version of the male call. Communication in social contexts usually involves calls, chatters, and a variety of displays.

Territoriality

Not much is known about the territorial behavior of cuckoos in the nonbreeding season. During the breeding season most cuckoos are territorial, with cooperative breeders and monogamous species defending territories around their nests. Less clear is what happens to brood parasites. In some species females seem to use a discrete, exclusive area for laying, whereas in others, such as in the case of the great spotted cuckoo, the laying areas widely overlap.

Feeding ecology and diet

Cuckoos are basically insectivorous, specializing in caterpillars, including many hairy, noxious species avoided by other birds. The common cuckoo and the great spotted cuckoo, for example, eat the hairy caterpillars of the processionary moth. Cuckoos are also generalized predators that take grasshoppers, cicadas, spiders, and other insects. Some species take tree frogs, snails, lizards, and even other birds. It is well-known that some parasitic species not only lay in a host's nest but also prey upon its eggs and chicks. A few species such as some koels and the channel-billed cuckoo, are vegetarians, feeding mainly, but not exclusively, on fruit.

Reproductive biology

Mating system

Most cuckoo species are monogamous and, in fact, even within the groups of cooperative anises, there seems to exist distinctive pairs of male and female. At least a few species (Coccyzus pumilus and Centropus grillii, for example) show polyandrous mating arrangements, where a female copulates with several males. The mating system of the common cuckoo in Japan has been characterized as polygamous, with substantial numbers of both males and females having multiple partners. Great spotted cuckoos in southern Spain also show polygamous mating arrangements, although most individuals seem to be genetically monogamous.

Brood parasitism

One of the most striking reproductive strategies of the animal kingdom is brood parasitism, a term intimately associated with cuckoos, although at least 78 cuckoo species take care of their young themselves. Fifty cuckoo species are obligate brood parasites, laying their eggs in the nests of other species, the hosts, who then carry out all parental duties. A few more species are facultative brood parasites, and besides building their own nest, they sometimes lay eggs in the nests of other species. Most of our information on cuckoo brood parasitism comes from the common cuckoo and the great spotted cuckoo. Other reasonably well-studied brood parasites are some of the *Chrysococcyx* species, the common koel, and the American striped cuckoo.

Host bird species

The majority of hosts chosen as "foster parents" by parasitic cuckoos are passerines. Most hosts are insectivorous, although parasitic cuckoos do not exclude blossom-visitors, nor those of mixed diet, nor even seed eaters, such as buntings. The host birds may either nest openly or in hollows of any kind. Among them are birds smaller than the wren, yet ravens are also included. Birds weighing from as little as 0.2 oz (7 g) and up to about 2 lb (1,000 g) will rear foster young who will weigh about 0.05–2 lb (25–1,000 g) by the time they are ready to feed for themselves.

The number of known hosts of the various cuckoo species ranges from only a few to the more than 125 recorded for the common cuckoo. There exists a distinction between "generalists" and "specialists" parasites. The first, such as the com-



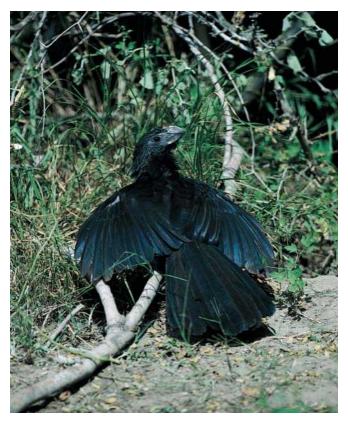
Male and female roadrunner (*Geococcyx californianus*) mating. The male holds an insect in his bill. (Photo by Wyman Meinzer/Okapia. Photo Researchers, Inc. Reproduced by permission.)

mon cuckoo, uses many hosts regularly whereas specialists show preferences for one or a few species. For example, the main host of great spotted cuckoos in Europe is the magpie (*Pica pica*), although they can be found in the nests of other passerines as well. This distinction between generalists and specialists is a controversial one, since even in the extreme case of common cuckoos each female seems to parasitize only one host, thus deserving the term specialist rather than generalist. Cuckoos of the genera *Chrysoccocyx* and *Cuculus* are specific to a discrete group of primary hosts, although there may be considerable overlap between species in the use of secondary hosts. Some authors suggest that most cuckoos are host specific, at least group-specific, as a consequence of competition between various cuckoo species within one territory; that is, competition is avoided by choosing different hosts.

The main hosts of cuckoos vary depending on the distribution of the parasitic cuckoo. The common cuckoo has some 15 main hosts over Europe, and more if one considers its entire area of distribution. Wagtails and reed warblers are main hosts, or at least preferred hosts, almost everywhere. However, in some places other species are preferentially parasitized: in Japan one of the main hosts of common cuckoos is the azurewinged magpie. Great spotted cuckoos, on the other hand, show a clear preference towards magpies in Europe, whereas they parasitize mainly crows and starlings in Africa.

Coevolutionary interactions between hosts and parasites

Brood parasitism strongly reduces host reproductive success. This takes place in three manners. Firstly, females of some species (*Cuculus*, for example) remove one or more host eggs at laying. Secondly, parasitism often reduces hatching success of the remaining host eggs; great spotted cuckoos, for example, crack or peck some eggs in the magpie clutches they parasitize. Finally, cuckoo nestlings inflict severe host losses in two ways: either the newly hatched cuckoo chick evicts all the eggs or young in the nest, or cuckoo chicks drive their foster siblings to starvation by monopolizing parental care. Thus natural selection strongly favors any kind of behavior or trait that counters the negative effect of parasitism. These



A groove-billed ani (*Crotophaga sulcirostris*) sunning in south Texas. (Photo by Larry Ditto. Bruce Coleman Inc. Reproduced by permission.)

adaptations against parasitism put pressures on the parasitic species to develop counteradaptations against host defenses. Hosts and parasites are then engaged in a so-called "evolutionary arms-race" in which adaptations on one side produce the evolution of counteradaptations on the other.

Biological cuckoo races

One of the most studied adaptations of parasites to egg rejection by hosts is the development of egg mimicry. Frequently the eggs of parasitic cuckoos are very similar to the eggs of their host species. The eggs of the lesser cuckoo in Japan are chocolate-colored and laid beside those of Blyth's reed warbler, whose eggs are the same color but much smaller. Great spotted cuckoos lay eggs that are very similar in color and size to magpie eggs, being only slightly different in shape. However, the best example is again the common cuckoo: although this species is able to lay about 15-20 different types of eggs, each female lays a single type (presumably throughout her life) that in most cases is a nearly perfect copy of a particular host's eggs. Among them are egg types that closely resemble the eggs of warblers, shrikes, pipits, or redstarts. Then there are mixed types, such as the ones resembling those of the robin and the ones resembling those of the red-backed shrike. As females only lay one kind of egg, it has been long argued that the common cuckoo is divided into "gentes" or host races, lineages of females that parasitize a main host and whose eggs resemble the eggs of this host. The mimicry is a

counteradaptation to the ability of hosts to discriminate and reject cuckoo eggs. Detailed molecular studies support this idea, proving that individual females only lay one kind of egg and preferentially in a single host, although mistakes are possible. These studies support the hypothesis that gentes are restricted to female lineages, with cross-mating by males to maintain the cuckoo genetically as a species. They are also consistent with the idea that genes affecting egg type are located in the female-specific W sex chromosome, and that the female cuckoo places her eggs in the nests of the bird species that has raised her. In so doing the cuckoo submits her eggs to rejection by the same species and, thus, subjects them to a continuing process of natural selection.

Nest and nest building

Brood parasitic species do not build any nest. However, the remaining species do so in a variety of forms. Malkohas and relatives (Phaenicophaeinae) build shallow nests in trees. Coucals build domed nests of grass and leaves. The Coccyzinae build saucer-shaped nests in trees. Cooperative breeders use a flat or shallow bowl in a tree. Roadrunners build nests with a platform of sticks that may be in the ground or on top of a bush or tree.

Cuckoo eggs

The appearance of cuckoo eggs varies extraordinarily. The eggs of the common cuckoo can be a solid white, blue or a loam-yellow, or they may have markings, closely resembling the eggs of the host birds. The eggs of many cuckoo species always have the same monotones: white, blue, shades ranging from blue-green to yellow-green, or red-brown to chocolate-brown. In others the monotone background is overlaid with a thick, white, chalky layer. Spotted eggs almost always represent adaptation to host eggs by natural selection. Non-parasitic cuckoos always lay solid-color eggs without the chalky overlay, or at most a thin one. Presumably the original eggs of the entire cuckoo phylum looked like these.

The size of the eggs varies between 2% and 25% of the weight of the female; relatively speaking, the smallest eggs are those of the channel-billed cuckoo and the largest are those of the greater ani. Parasites who prey upon small songbirds usually lay relatively small eggs; those who parasitize crows as host birds lay correspondingly larger ones. The weight of the common cuckoo's egg averages 0.1 oz (0.08–0.16 oz; 2.3–4.5 g); the eggs are almost always a little larger than the host's eggs and differ from them in their broad oval shape.

Parasitic cuckoo eggs usually have a harder and thicker shell than those of the hosts and are thus especially protected against breakage. The egg of a warbler, for example, cannot support a load greater than 20.9 lb (9.5 kg), while a cuckoo egg will break only under a load greater than 30.2 lb (13.7 kg).

Clutch size

Nonparasitic species have a clutch size that varies, comprising only a few eggs. Parasitic species are characterized by larger clutch sizes, although it is difficult to determine their average. Molecular studies have assigned between four and 12 eggs to great spotted cuckoo females. Common cuckoos always lay just one egg in a nest, and it seems clear that this is

because a second egg would have no success, being evicted by the first chick after hatching. If a nest contains two or even three cuckoo eggs, they are most likely from different females. Some other cuckoo species more frequently lay several eggs in the same nest. As many as 16 eggs from the koel have been found in one nest and 13 from the great spotted cuckoo in Africa; it is in these species (koels and *Clamator* cuckoos) that several chicks may be raised since they do not kill their foster siblings. In this case we assume that several females may lay in a single host nest. In great spotted cuckoos molecular parentage analyses confirmed that multiple parasitized magpie nests are the product of both a female laying several eggs in a single nest and several females (up to three) laying one or more eggs in the same nest.

Duration of incubation, young cuckoos

As far as we know parasitic cuckoos require only a short incubation period; the information we have on this indicates 10 or 11 to 15 days. It would be logical to assume that self-brooding cuckoos, too, originally had a short brooding period. But this cannot be reconciled with the long brooding period of the self-brooding roadrunner, which lasts 18 days.

Most cuckoo chicks grow rapidly, even those of non-parasitic species; some of them may leave the nest in as early as 10 days, while the larger species can take up to 20 days. In fact nestlings of parasitic species tend to stay longer in the nests, as much as twice the nestling period of non-parasitic species of the same size: 18–26 days.

Common cuckoos leave the nest at an age of 16–24 days. After they have flown out, young cuckoos will still beg insistently and get food not only from their foster parents, but also from other birds. Songbirds often sway in the air before the giant baby, or perch on its back, or insert their heads deeply into its throat. In about 21 days after it has left the nest the young cuckoo is independent. Most parasitic species monopolize parental care of their foster parents for several weeks after fledging.



Guira cuckoos (*Guira guira*) drying and warming in the sun in Mbaracayu, Paraguay. (Photo by Terry Whittaker. Photo Researchers, Inc. Reproduced by permission.)

Conservation status

Although the real conservation status of most cuckoos is not well-known, they are assumed to be fairly common and under no immediate threat. The only species at risk of declining are those of tropical forests and those on islands with small populations. Among the species considered at risk are *Centropus steerii*, confined to Mindoro, *Phaenicophaeus pyrrhocephalus*, *Carpococcyx viridis*, *Centropus nigrorufus*, and a few more species living on islands.

Significance to humans

Cuckoos are of no special significance to humans, although they are particularly popular due to their breeding habits. The term cuckold is used in several languages to refer to a man cheated by his wife. They also are called rainbirds in many places because they seem to anticipate rain with their calls early in the rainy season. Nestling coucals are eaten for medicinal purposes in Borneo.



1. Great spotted cuckoo (*Clamator glandarius*); 2. Long-tailed koel (*Urodynamis taitensis*); 3. Drongo cuckoo (*Surniculus lugubris*); 4. Banded-bay cuckoo (*Penthoceryx sonneratii*); 5. Greater ani (*Crotophaga major*); 6. American striped cuckoo (*Tapera naevia*); 7. Thick-billed cuckoo (*Pachycoccyx audeberti*); 8. Common cuckoo (*Cuculus canorus*); 9. Common koel (*Eudynamys scolopacea*); 10. Channel-billed cuckoo (*Scythrops novaehollandiae*). (Illustration by Brian Cressman)



1. Green-billed malkoha (*Rhopodytes tristis*); 2. Dideric cuckoo (*Chrysococcyx caprius*); 3. Horsfield's bronze-cuckoo (*Chalcites basalisx*); 4. Blue coua (*Coua caerulea*); 5. Greater coucal (*Centropus sinensis*); 6. Pheasant cuckoo (*Dromococcyx phasianellus*); 7. Common hawk-cuckoo (*Cuculus varius*); 8. Yellow-billed cuckoo (*Coccyzus americanus*); 9. Greater roadrunner (*Geococcyx californiana*). (Illustration by Brian Cressman)

Species accounts

Great spotted cuckoo

Clamator glandarius

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus glandarius Linnaeus, 1758, northern Africa and Gibraltar. A smaller race, choragium, described from South Africa.

OTHER COMMON NAMES

French: Coucou geai; German: Häherkuckuck; Spanish: Críalo Europeo.

PHYSICAL CHARACTERISTICS

13.8–15.4 in (35–39 cm); 0.25 lb (124 g). Thirteen cervical vertebrae and a feather crest. Dusky brown, flight feathers graybrown, tail tipped white, crown gray and face black, eye ring gray to red, bill black. Juveniles have crown and face black, and flight feathers rufous.

DISTRIBUTION

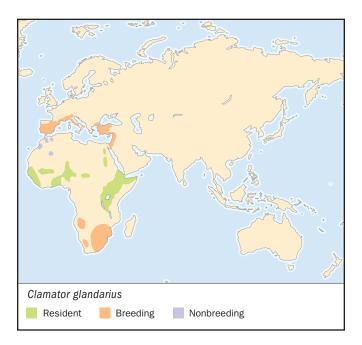
Iberian Peninsula, South France, Turkey and Cyprus, Iran and Iraq, Middle East to Egypt. Sub-Saharan Africa from Senegal to Ethiopia. North Somalia, Kenya, Tanzania, Angola, and South Africa. All populations winter in Africa.

HABITAT

Semi-arid open woodland, scrubs, and cultivation; in Europe open areas; oak and pine forests, also olive and almond groves. Below 6,600 ft (2,000 m).

BEHAVIOR

Harsh guttural voice: "gah, gah, gah...gak, gak, gak... ko, ko, ko," falling in pitch and increasing in tempo. Easy to see in pairs at the beginning of the breeding season; male feeds cater-



pillars to the female. Evidence for absence of territorial behavior during breeding season in southern Spain. Adults breeding in the Iberian Peninsula winter in southern Africa. Birds in West Africa are local migrants, although there are some residents

FEEDING ECOLOGY AND DIET

Insects, mainly caterpillars, also termites, grasshoppers, and moths. Feeds on trees, sometimes on the ground.

REPRODUCTIVE BIOLOGY

Mainly monogamous, although polygamous mating arrangements occur. Brood parasitic; the magpie is its main host in the Mediterranean, also crows are used, and starlings in Africa. There is no ejection of host eggs by nestlings. They lay a large number of eggs (maybe up to 25, 12 for sure), distributed over many nests of hosts. Over extensive regions there is only one egg type. Incubation 12–15 days, shorter than hosts. There may be more than one chick per magpie nest successfully fledging. It fledges as soon as 16 days, fed by foster parents for one to two more months. Young form social groups attended by magpies.

CONSERVATION STATUS

Not globally threatened. Generally uncommon throughout most of its range, expanding in South Europe and Middle East.

SIGNIFICANCE TO HUMANS

None known. ◆

Thick-billed cuckoo

Pachycoccyx audeberti

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus audeberti Schlegel, 1879, Madagascar. Three subspecies recognized.

OTHER COMMON NAMES

French: Coucou d'Audebert; German: Dickschnabelkuckuck; Spanish: Crialo Piquigrueso.

PHYSICAL CHARACTERISTICS

14.2 in (36 cm), 0.23 lb (115 g). Adult gray above, lores white, wings blackish, tail barred brown and black; white below; eye ring yellow, iris brown. Bill blackish or yellow. Its appearance and call, "Ooy-yes-yes," are reminiscent of a hawk.

DISTRIBUTION

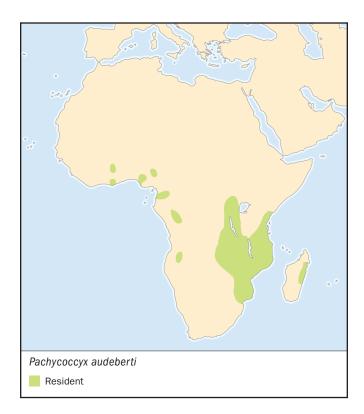
Sierra Leone through Ghana, Nigeria, and Cameroon to Congo and Zaire, Kenya and Tanzania, Zambia, Zimbabwe, and Mozambique. *P. a. audeberti* confined to Madagascar.

HARITAT

Miombo woodlands, lowlands, and riverine forests.

BEHAVIOR

Non-migratory, or with local movements.



FEEDING ECOLOGY AND DIET

Insects, mainly hairy caterpillars.

REPRODUCTIVE BIOLOGY

Brood parasitic; hosts are African shrikes (*Prionops*). Incubation 13 days, nestlings evict host eggs and chicks. Fledges in 28 days.

CONSERVATION STATUS

Not globally threatened, uncommon to rare.

SIGNIFICANCE TO HUMANS

None known. ◆

Common hawk-cuckoo

Cuculus varius

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus varius Vahl, 1797, Tranquebar, India. Two subspecies recognized.

OTHER COMMON NAMES

English: Ceylon hawk cuckoo, brain-fever bird; French: Coucou shikra; German: Wechselkuckuck; Spanish: Cuco Chikra.

PHYSICAL CHARACTERISTICS

13 in (33 cm); 3.6 oz (104 g). Tails are banded, with bars on the abdomen and flanks.

DISTRIBUTION

Nepal, India, Bangladesh, Myanmar, and Sri Lanka.



HABITAT

Montane forests, deciduous and evergreen wooded areas; also pine forests, gardens, groves, and bamboo thickets.

BEHAVIOR

Loud, shrieking call, often heard singing at night with a bright moon.

FEEDING ECOLOGY AND DIET

Insects, including caterpillars, termites, grasshoppers, beetles; they also eat fruits and berries. Arboreal and secretive foragers.

REPRODUCTIVE BIOLOGY

Brood parasitic; breeding March-July in India, and January-April in Sri Lanka.

CONSERVATION STATUS

Not globally threatened, fairly common within most of their distribution area, but rare in Sri Lanka.

SIGNIFICANCE TO HUMANS

None known. ◆

Common cuckoo

Cuculus canorus

SUBFAMILY

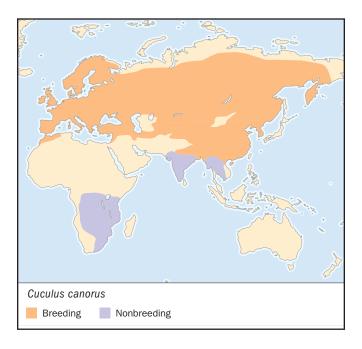
Cuculinae

TAXONOMY

Cuculus canorus Linnaeus, 1758, Sweden. Four subspecies recognized.

OTHER COMMON NAMES

French: Coucou gris; German: Kuckuck; Spanish: Cuco Común.



PHYSICAL CHARACTERISTICS

12.6–13 in (32–33 cm), 0.23 lb (115 g). Males dark gray above, tail blackish brown, spotted and tipped with white, unevenly barred black. Gray to white underparts, eye ring yellow, iris brown to orange, bill black. Females similar, although rufous on upper breast; females of *canorus* subspecies occur in a rufous (hepatic) morph.

DISTRIBUTION

Europe and Asia, from Iberian Peninsula and North Africa to Siberia, Kamchatka, and Japan. Winters in southern Africa and southern Asia.

HABITAT

Forests and woodlands, open wooded areas, steppes, meadows, and reedbeds.

BEHAVIOR

Males sing a loud "cuck-oo" in spring, silent in winter. Migratory in northern part of the distribution range.

FEEDING ECOLOGY AND DIET

Mainly caterpillars, and other insects such as dragonflies, crickets, beetles. Prey on eggs and nestlings of songbirds.

REPRODUCTIVE BIOLOGY

Solitary most of the time, both females and males have multiple partners, but no clear social relationships. Brood parasitic; over 120 hosts, eggs are polymorphic, resembling the eggs of the different hosts. Incubation 12 days, nestlings evict host eggs and chicks; nestling period around 18 days. Fledgling fed by foster parents for two or three weeks after leaving the nest.

CONSERVATION STATUS

Not globally threatened. Common and vocally conspicuous (but difficult to see) throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Dideric cuckoo

Chrysococcyx caprius

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus caprius Boddaert, 1783, Cape of Good Hope. Monotypic.

OTHER COMMON NAMES

English: Diederik cuckoo, didric cuckoo; French: Coucou didric; German: Goldkuckuck; Spanish: Cuclillo Didric.

PHYSICAL CHARACTERISTICS

7.5 in (19 cm), 1.1 oz (32 g). Bronze-green above, white below with barred green flanks.

DISTRIBUTION

Sub-Saharan Africa and South Arabia.

HABITAT

Open woodlands, acacia savanna, and in gardens of towns.

BEHAVIOR

Species has both sedentary and migratory populations.

FEEDING ECOLOGY AND DIET

Insects, mainly caterpillars; seeds.

REPRODUCTIVE BIOLOGY

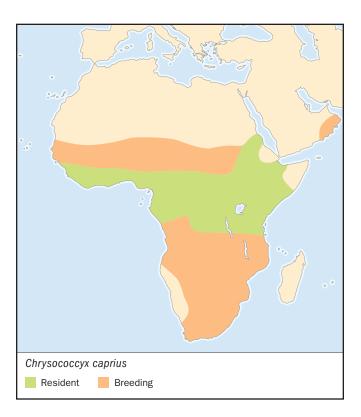
Breeds with rains. Brood parasitic; two-day-old chick evicts host offspring.

CONSERVATION STATUS

Not globally threatened.

SIGNIFICANCE TO HUMANS

None known. ◆



Horsfield's bronze-cuckoo

Chalcites basalis

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus basalis Horsfield, 1821, Java. Monotypic.

OTHER COMMON NAMES

English: Australian bronze-cuckoo, narrow-billed bronze-cuckoo, rufous-tailed bronze-cuckoo; French: Coucou de Horsfield; German: Rotschwanzkuckuck; Spanish: Cuclillo de Horsfield.

PHYSICAL CHARACTERISTICS

6.7 in (17 cm), 0.77 oz (22 g). Brownish bronze above, streaked throat with barred flanks and sides of breast. Black, slender bill.

DISTRIBUTION

Australia and Tasmania; winters north.

HABITAT

Open woodlands, scrubs.

BEHAVIOR

Resident and seasonally migratory.

FEEDING ECOLOGY AND DIET

Insects, mainly caterpillars.

REPRODUCTIVE BIOLOGY

All brood parasitic; chicks evict host offspring.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆



Banded bay cuckoo

Penthoceryx sonneratii

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus sonneratii Latham, 1790, India. Sometimes placed in the genus Cacomantis. Five subspecies.

OTHER COMMON NAMES

French: Coucou de Sonnerat; German: Sonneratkuckuck; Spanish: Cuco Bayo.

PHYSICAL CHARACTERISTICS

8.7 in (22 cm), 1.3 oz (37 g). Bright rufous or bay above, barred with brown, white line under eye, tail with black band and white tip, iris yellow to brown, bill black.

DISTRIBUTION

Sri Lanka, India, Nepal, Bangladesh, and Myanmar to southwest China, Thailand and Indochina, Malaysia, Sumatra, Borneo, Palawan, Java.

HABITAT

Forests, deciduous and evergreen, secondary scrub.

BEHAVIOR

Resident in most of its area, although partially migratory in areas.

FEEDING ECOLOGY AND DIET

Caterpillars and bugs.

REPRODUCTIVE BIOLOGY

Brood parasitic; nestlings evict host eggs and chicks.

CONSERVATION STATUS

Not threatened, fairly common in much of its range.

SIGNIFICANCE TO HUMANS

None known. ◆



Asian drongo-cuckoo

Surniculus lugubris

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus lugubris Horsfield, 1821, Java. Four subspecies.

OTHER COMMON NAMES

French: Coucou surnicou d'Asie; German: Drongokuckuck; Spanish: Cuclillo-drongo Asiático.

PHYSICAL CHARACTERISTICS

9.8 in (25 cm), 1.2 oz (35 g). Glossy black, tail square, white bands on undertail coverts and underwing, iris brown, bill black.

DISTRIBUTION

Punjab and lower Himalayas east through Nepal to Assam, from South Central China to Indochina, South India, Sri Lanka, Java, Bali, Malaysia, Sumatra, Borneo, Sulawesi, and North Moluccas.

HABITAT

Open forests and scrubs, bamboo jungle; occasionally gardens and mangroves.

BEHAVIOR

Resident, seasonally migratory and nomadic. The northern subspecies winters on Malaysia.

FEEDING ECOLOGY AND DIET

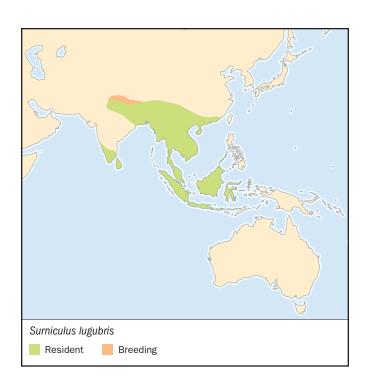
Caterpillars and other soft insects, sometimes figs.

REPRODUCTIVE BIOLOGY

Brood parasitic; hosts are mainly babblers; nestlings evict the eggs and chicks of hosts.

CONSERVATION STATUS

Not globally threatened. Unevenly distributed within its range.



SIGNIFICANCE TO HUMANS

None known. ◆

Common koel

Eudynamys scolopacea

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus scolopaceus Linnaeus, 1758, Malabar. Seventeen subspecies recognized.

OTHER COMMON NAMES

English: Asian koel, black billed koel, Australian/blue headed koel; French: Coucou koël; German: Indischer koel; Spanish: Koel Común.

PHYSICAL CHARACTERISTICS

15.4–18.1 in (39–46 cm), 0.43–0.65 lb (215–327 g). Subspecies vary quite a lot, mostly in the plumage of females; males are glossy black, iris red, bill light green.

DISTRIBUTION

Nepal, Pakistan to India, Sri Lanka, South China and Indochina, Thailand, Malaysia, Philippines, Sulawesi, Moluccas, New Guinea, Bismarck Archipelago, North and East Australia.

HABITAT

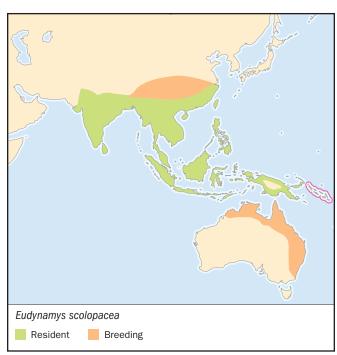
Forests, edge and scrub, plantations, and orchards.

BEHAVIOR

Different voices similar to a loud "ko-el" and "kow-kow." Resident or makes irregular movements.

FEEDING ECOLOGY AND DIET

Feeds in tree canopy; fruits such as figs, berries, papayas, and tamarinds consumed. Also a few insects and snails.



REPRODUCTIVE BIOLOGY

Brood parasitic; hosts include crows, drongos, orioles, and honeyeaters. May lay more than one egg per nest; chicks do not always evict host offspring, but still decrease their success. Females sometimes feed juveniles.

CONSERVATION STATUS

Not threatened. Common throughout much of its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Long-tailed koel

Urodynamis taitensis

SUBFAMILY

Cuculinae

TAXONOMY

Cuculus taitensis Sparrman, 1787, Tahiti. Currently situated also in the genus Eudynamys. Monotypic.

OTHER COMMON NAMES

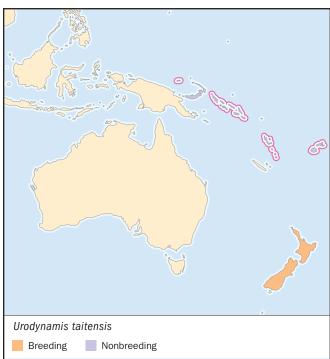
French: Coucou de Nouvelle-Zélande; German: Langschwanzkoel; Spanish: Koel Colilargo.

PHYSICAL CHARACTERISTICS

15–16.5 in (38–42 cm), 0.24 lb (120 g). Male, long-tailed, rufous-barred brown above, head blackish; below, white to rufous, iris yellow, bill yellow-horn, nostril slit-like. Females more rufous.

DISTRIBUTION

New Zealand and many islands in Oceania: Carolines, Fiji, Tonga, Samoa, Norfolk, Bismarck Archipelago.



HABITAT

Forest and scrub.

BEHAVIOR

Sometimes several males call in a social group, similar to a lek. Long-distance migrant, breeding in New Zealand and wintering in Melanesia, Micronesia, and Polynesia. Migrates at night. Immatures remain in the wintering areas until they are two years old.

FEEDING ECOLOGY AND DIET

Insects, crabs, lizards, eggs, nestlings.

REPRODUCTIVE BIOLOGY

Brood parasitic; hosts are songbirds. Nestling evicts host offspring; nestling period is around 21 days.

CONSERVATION STATUS

Not globally threatened, although some populations are declining because of habitat loss.

SIGNIFICANCE TO HUMANS

None known. ◆

Channel-billed cuckoo

Scythrops novaehollandiae

SUBFAMILY

Cuculinae

TAXONOMY

Scythrops novaehollandiae Latham, 1790, New South Wales. Monotypic.

OTHER COMMON NAMES

French: Coucou présageur; German: Fratzenkuckuck; Spanish: Cuco Tucán.





PHYSICAL CHARACTERISTICS

23.6 in (60 cm), 1.24 lb (623 g). Gray with black spots above, tail with subterminal black band and white tip, light gray below, huge bill, dark and pale gray. Bare skin around eye red, iris red.

DISTRIBUTION

Sulawesi, Buru, Flores, north and east Australia. Winters in Moluccas, Lesser Sundas, Aru, New Guinea, and Bismarck Archipelago

HABITAT

Edge of forests or along rivers, mangroves, and lowlands.

BEHAVIOR

Migratory and seasonal in Australia. The voice is a loud "gaak" rapidly repeated. Males feed females before copulating.

FEEDING ECOLOGY AND DIET

Fruit and insects.

REPRODUCTIVE BIOLOGY

Brood parasitic; crows and other corvids as hosts, also Australian magpies and magpie larks. Unknown if eviction occurs, but host chicks sometimes disappear from the nest.

CONSERVATION STATUS

Not globally threatened, uncommon in much of its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Green-billed malkoha

Rhopodytes tristis

SUBFAMILY

Phaenicophaeinae

TAXONOMY

Melias tristis Lesson, 1830, Sumatra; error=Bengal. Six subspecies.

OTHER COMMON NAMES

English: Greater or large green-billed malkoha; French: Malcoha sombre; German: Großer grünschnabelkuckuck; Spanish: Malcoha Sombrío.

PHYSICAL CHARACTERISTICS

19.7 in (50 cm), 4.0 oz (115 g). Body gray with glossy green above; long tail with broad white tips; bare red skin around eye; pale green bill.

DISTRIBUTION

Thailand, Myanmar, Malaysia, Sumatra, India, Indochina, Kangean Is., South China.

HABITAT

Forests, bamboo, scrub, plantations.

BEHAVIOR

Resident.

FEEDING ECOLOGY AND DIET

Mainly insects, also lizards and frogs.

REPRODUCTIVE BIOLOGY

Nest is a flat platform of sticks. Eggs: 2-4. Monogamous.



CONSERVATION STATUS

Not globally threatened; has adapted to a number of humanmodified habitats.

SIGNIFICANCE TO HUMANS

None known. ◆

Blue coua

Coua caerulea

SUBFAMILY

Phaenicophaeinae

TAXONOMY

Cuculus caeruleus Linnaeus, 1776, Madagascar. Monotypic.

OTHER COMMON NAMES

English: Blue Madagascar coucal; French: Coua bleu; German: Blau-Seidenkuckuck; Spanish: Cúa Azul.

PHYSICAL CHARACTERISTICS

18.9–19.7 in (48–50 cm), 8.2 oz (235 g). Dark blue above and below; bare blue skin around eye; black bill.

DISTRIBUTION

Madagascar.

HABITAT

Forest and mangroves.

BEHAVIOR

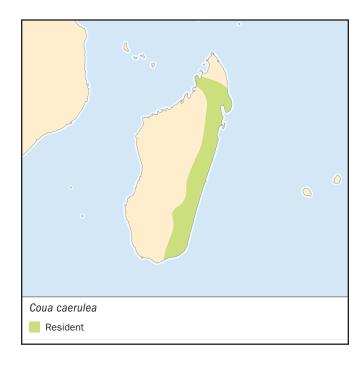
Resident.

FEEDING ECOLOGY AND DIET

Insects, small reptiles, and fruits.

REPRODUCTIVE BIOLOGY

Nests are bowls of twigs, on trees or bushes. One egg.





Not globally threatened.

SIGNIFICANCE TO HUMANS

Subject to trapping and hunting. ◆

Greater coucal

Centropus sinensis

SUBFAMILY

Centropodinae

TAXONOMY

Polophilus sinensis Stephens, 1815, Ning Po, China. Six subspecies.

OTHER COMMON NAMES

English: Common or large coucal, common crow-pheasant, lark-heeled cuckoo; French: Grand coucal; German: Heckenkuckuck; Spanish: Cucal Chino.

PHYSICAL CHARACTERISTICS

18.5–20.5 in (47–52 cm); 8.3–9.4 oz (236–268 g). Black, with chestnut back and wings. Long and broad black tail; black bill.

DISTRIBUTION

Pakistan, India, Sri Lanka, Bangladesh, Myanmar, China, Thailand, Indochina, Sumatra, Borneo, Philippines, Java, Bali, Kangean Is.

HABITAT

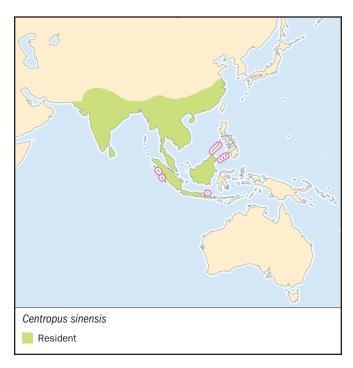
Forest, grassland, mangroves, scrub, cultivations, marshes, reedbeds, gardens.

BEHAVIOR

Resident and locally migratory.

FEEDING ECOLOGY AND DIET

Large insects, small vertebrates, snails, fruits, and seeds.



REPRODUCTIVE BIOLOGY

Breeds in rains. Nest is large globular ball of twigs and leaves or grass. Eggs 2-4. Monogamous.

CONSERVATION STATUS

Common throughout its range. Not globally threatened.

SIGNIFICANCE TO HUMANS

Nestlings are captured for medicinal purposes in Borneo. ◆

Greater ani

Crotophaga major

SUBFAMILY

Crotophaginae

TAXONOMY

Crotophaga major J. F. Gmelin, 1788, Cayenne. Monotypic.

OTHER COMMON NAMES

French: Ani des palètuviers; German: Riesenani, Spanish: Garrapatero Mayor.

PHYSICAL CHARACTERISTICS

18.1 in (46 cm); male 5.7 oz (162 g), female 5.1 oz (145 g). Glossy blue-black, long tails, bill arched and laterally compressed.

DISTRIBUTION

Central and South America.

HABITAT

Tropical evergreen forest, pastures, marshes, mangroves.

BEHAVIOR

Resident with local movements. Group-living, defend territories.

FEEDING ECOLOGY AND DIET

Mainly insects, also lizards, seeds, fruits, and berries.



REPRODUCTIVE BIOLOGY

Cooperative breeders, nesting in loose colonies. Socially monogamous. Nests are a bulky platform of sticks. Lay 2–5 eggs.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Yellow-billed cuckoo

Coccyzus americanus

SUBFAMILY

Coccyzinae

TAXONOMY

Cuculus americanus Linnaeus, 1758, South Carolina. Monotypic.

OTHER COMMON NAMES

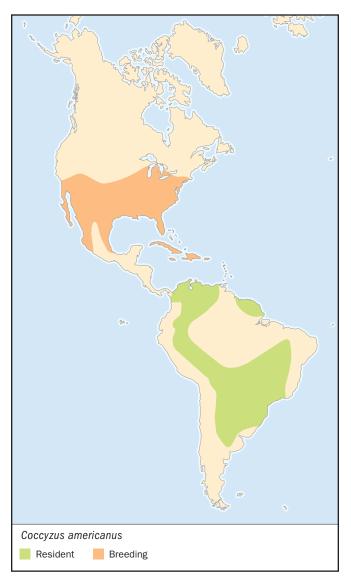
French: Coulicou à bec jaune; German: Gelbschnabelcuckuck; Spanish: Cuclillo Piquigualdo.

PHYSICAL CHARACTERISTICS

11.8 in (30 cm); male 2.0 oz (58 g), female 2.4 oz (68 g). All brownish to gray above, and white, rufous, or a combination of gray and rufous below. Tails long, gray with white tips below. Large bill is black above, yellow below.

DISTRIBUTION

North and South America.



HABITAT

From tropical forest to open woodland and scrub.

BEHAVIOR

Migratory; migrates at night.

FEEDING ECOLOGY AND DIET

Large insects, caterpillars, lizards, berries, and fruit.

REPRODUCTIVE BIOLOGY

Monogamous, nest is a flat platform of sticks. 2-5 eggs.

CONSERVATION STATUS

Not globally threatened. Has disappeared in areas of western United States because of loss of riparian woodland habitat.

SIGNIFICANCE TO HUMANS

None known. ◆

Greater roadrunner

Geococcyx californiana

SUBFAMILY

Neomorphinae

TAXONOMY

Saurothera californiana Lesson, 1829, California. Monotypic

OTHER COMMON NAMES

French: Grand géocoucou; German: Wegecuckuck; Spanish: Correcaminos Grande.

PHYSICAL CHARACTERISTICS

22.1 in (56 cm); male 0.64 lb (320 g), female 0.58 lb (290 g). Slender, long tails and legs; streaked brown above; crested; tail with white tips; bare skin behind eye; black bill.

DISTRIBUTION

Southwest United States and Mexico.

HABITAT

Arid lowland scrub.

BEHAVIOR

Resident, pairs in territory all year. They can fly, but usually run on bare ground.

FEEDING ECOLOGY AND DIET

Opportunistic; insects, spiders, lizards, snakes, birds, rabbits.

REPRODUCTIVE BIOLOGY

Monogamous; nest in an open platform of sticks. 2–6 eggs. Males incubate at night. Hatching is asynchronous (eggs may hatch up to seven days apart).



CONSERVATION STATUS

Not threatened. However, local populations' range is decreasing in urban areas.

SIGNIFICANCE TO HUMANS

None known. ◆

American striped cuckoo

Tapera naevia

SUBFAMILY

Neomorphinae

TAXONOMY

Cuculus naevius Linnaeus, 1766, Cayenne. Two subspecies recognized.

OTHER COMMON NAMES

French: Géocoucou tacheté; German: Streinfenkuckuck; Spanish: Cuclillo Crespín.

PHYSICAL CHARACTERISTICS

10.2–11.4 in (26–29 cm), 0.10 lb (52 g). Brown above, head with striped black and rufous crest, prominent black alula, white below with black streaks in throat and chest. Bare skin around eye yellow, iris brown to green, bill brown.

DISTRIBUTION

Southern Mexico to Panama, Colombia, Ecuador, North Peru, Brazil, Bolivia, Paraguay, and Argentina.



HABITAT

Scrub, grassland, open country with scattered trees and bushes.

REHAVIOR

Shy and solitary; song with 3–5 whistled notes, "pee, pee, pee, pee, peedee,"; conspicuous when singing from a post or wire. Resident, except in Argentina, seasonal.

FEEDING ECOLOGY AND DIET

Forages on vegetation and on the ground; insects, especially grasshoppers and caterpillars.

REPRODUCTIVE BIOLOGY

Brood parasitic; hosts with covered nests, such as wrens, fly-catchers, and sparrows. Nestlings use their sharp bill to kill host chicks; fledge in 18 days.

CONSERVATION STATUS

Not threatened, common to uncommon, expanding in Central America and Brazil.

SIGNIFICANCE TO HUMANS

None known. ◆

Pheasant cuckoo

Dromococcyx phasianellus

SUBFAMILY

Neomorphinae

TAXONOMY

Macropus phasianellus Spix, 1824, Tonantins, northwest Brazil. Monotypic.

OTHER COMMON NAMES

French: Gèocoucou faisan; German: Fasanenkuckuck; Spanish: Cuclillo Faisán.

PHYSICAL CHARACTERISTICS

5.1 in (13 cm), 0.63 oz (18 g). Dark brown above, short rufous crest, long tail with white tips, white below.

DISTRIBUTION

Central and South America.

HABITAT

Tropical evergreen forest.



BEHAVIOR

Secretive and solitary.

FEEDING ECOLOGY AND DIET

Insects, lizards.

REPRODUCTIVE BIOLOGY

Brood parasitic; hosts include flycatchers. Host offspring disappear after cuckoo hatches.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

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Monotypic order: Cuculiformes Vol. 9: Birds II

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Juan Gabriel Martínez, PhD

Strigiformes (Owls)

Class Aves Order Strigiformes Number of families 2

Number of genera, species 27 genera;

206-215 species

Photo: Screech owl (*Otus asio*) owlets share a branch. (Photo by Joe McDonald. Bruce Coleman Inc. Reproduced by permission.)



Evolution and systematics

Barn owls (Tytonidae) and typical owls (Strigidae) constitute a distinctive order (Strigiformes) of nocturnal predators. With the possible exception of owlet-nightjars (Aegothelidae), they are unlikely to be confused with any other group of birds. Like diurnal birds of prey (Falconiformes), they have a strongly hooked beak and sharp talons that they use to capture live animals. This convergence in morphology and behavior led early taxonomists to classify hawks and owls in the same order, the Raptores. However, morphological and genetic data clearly indicate that nightjars (Caprimulgiformes), rather than hawks, are the closest living relatives of owls.

The oldest known fossil owl, *Ogygoptynx wetmorei*, was found in 58-million-year-old Paleocene deposits from Colorado. Fossil owls from the Tytonidae and three extinct families are known from roughly 50-million-year-old Eocene deposits in North America and France. *Bubo poirrieri* and *Strix brevis* from the Lower Miocene of France and the United States, respectively, at 22–24 million years old, are the oldest fossils attributed to the Strigidae. Thus, tytonids likely arose before strigids in the evolutionary history of owls.

Determining the number of living species of owls has proven to be difficult because many congeneric species are similar in appearance. The discovery that vocalizations provide important clues to owl taxonomy has radically altered the view of how many species exist. Studies based on vocalizations, often supplemented with DNA evidence, have resulted in a much larger species list than was envisioned in the 1990s. In their 1991 book, *Owls of the World*, Rob Hume and Trevor Boyer recognized 151 species. By 2000, however, the leading references treated more than 200 species. Depending on which authority is followed, the grand tally rests

between 207 and 215 species: 16–18 in the Tytonidae (two genera) and 189–197 in the Strigidae (25 genera).

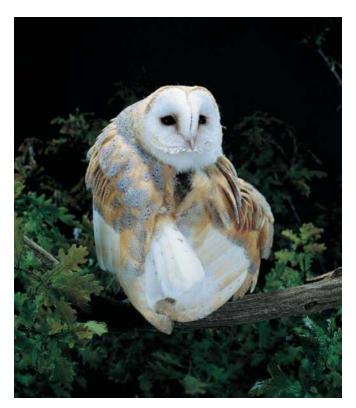
Physical characteristics

Owls vary in size from the diminutive elf owl (*Micrathene whitneyi*) at 1.41 oz (40 g) to the massive Eurasian eagle-owl (*Bubo bubo*) at 9.25 lb (4.2 kg). Few other avian orders exhibit such a large range in body size. Most species have a large head, a short neck, a facial disc that surrounds forward-pointing eyes, and cryptic plumage. Strigids differ from tytonids in having a rounded rather than a heart-shaped facial disc, four rather than two notches in the sternum, a rounder skull with relatively larger eye openings, and a naked uropygial (oil) gland. In addition, the talon on the third toe has a smooth edge in strigids versus a serrated edge in tytonids.

Plumage colors are dominated by browns and grays distributed in complex patterns that help provide camouflage for roosting owls. Some tytonids have nearly solid white underparts, although their upperparts are cryptically marked. All tytonids have dark brown eyes. In contrast, many strigids have bright yellow irides (plural of iris), and the two species of white-faced owls (*Ptilopsis*) have striking orange-red irides. The sexes are virtually identical in appearance in most species; when differences exist, females tend to be darker and more heavily marked than males, especially on the underparts.

About half of the strigids have a distinctive plumage feature that is somewhat of a misnomer, the so-called ear tufts. Prominent ear tufts are restricted to nocturnal forest species and may function to provide camouflage during daytime by breaking up the outline of an owl that is perched in vegetation. Ear tufts have nothing to do with hearing. They are absent in tytonids except for the oriental bay owl (*Phodilus*)

Order: Strigiformes Vol. 9: Birds II



Juvenile male barn owl (*Tyto alba*) preening. (Photo by Jane Burton. Bruce Coleman Inc. Reproduced by permission.)

badius), which has two short tufts formed by extensions of the upper edge of its facial disc.

Owls rely heavily on their keen sense of hearing to locate and capture prey at night. They can perceive a wide range of sound frequencies, and they use differences in arrival time and intensity of sounds at each ear to obtain precise information on the horizontal and vertical location of a sound source. The ability of owls to localize a sound source in this manner is enhanced by extremely large ear openings that are positioned asymmetrically on the sides of their head.

Owls have large eyes with large pupils, and unlike most birds, their retinas contain a preponderance of rod cells that are sensitive to low light. Despite their night-adapted vision, owls do not see well when it is extremely dark. On average, the minimum amount of light needed to see an object is two times lower in tawny owls (*Strix aluco*) than in humans, but variation in performance is such that the light-gathering ability of the most sensitive human eyes is similar to that of the least sensitive owl eyes. An owl's vision is sufficient for it to avoid obstacles in low light but does not allow it to see all objects below the forest canopy on the darkest nights. Thus, forest owls probably rely on spatial memory to avoid obstructions, or else they restrict their activity to the crepuscular hours when there is more light.

Distribution

Owls inhabit every continent but Antarctica. About 80% of the species occur in the tropics: 25% in Central and South

America, 25% in Asia, 20% in Africa, and 10% in Australasia. The barn owl (*Tyto alba*) is nearly cosmopolitan, occurring throughout the tropics and in much of the United States and Europe. Six owl species are Holarctic, one of which, the short-eared owl (*Asio flammeus*), also has colonized the remote islands of Hawaii and the Galápagos. At the other extreme, 15 species of *Otus* have minuscule ranges on tropical islands in the Pacific and Indian oceans. Some mainland species also have restricted ranges. The Itombwe owl (*Tyto prigoginei*) is known from only two locations in the Congo, and the longwhiskered owlet (*Xenoglaux loweryi*) is confined to a small area in the Peruvian Andes.

Habitat

Owls occupy all major terrestrial habitats, from moist tropical jungles and temperate coniferous forests to grasslands and deserts, but approximately 95% of all species live in some sort of forested habitat. They also use human-altered landscapes such as farmlands, pastures, and suburban woodlots. Some Otus, Bubo, Glaucidium, and Ninox coexist with humans in wooded neighborhoods in many parts of the world. Fish-owls (Ketupa) of Asia and fishing-owls (Scotopelia) of Africa specialize on aquatic prey and are closely tied to streamside forests and mangroves, but no owls are strictly aquatic. In general, owls are absent from extremely high elevations and from the harshest deserts.

Behavior

Owls are well known for being nocturnal, but many species are active in daylight, including snowy owls (*Nyctea scandiaca*), short-eared owls, and most species of *Glaucidium*. By day, nocturnal species perch quietly in a concealed site, using their cryptic plumage to help blend into their surroundings. Owls often are considered fearless because they allow close approach by humans before taking flight. However, this "tameness" is part of their behavioral repertoire to avoid detection by predators.

Given that many species are nocturnal, it should come as no surprise that vocal displays are important in the lives of owls. An owl's hoot is its song, which typically is used to attract mates or to repel conspecific intruders. In *Ninox*, *Aegolius*, and *Asio*, songs are emitted exclusively by males and function mostly to attract mates. Once a male becomes paired, he stops singing and generally restricts his vocalizing to brief calls during food deliveries. In many other owls, both pair members emit similar songs for territory advertisement and courtship, although males are more vocal than females.

Adult owls typically exhibit little movement outside of their territories. Fewer than 20 species are truly migratory, and in only half of these is migration undertaken by a large segment of the population. Species that feed on cyclic rodents like voles and lemmings tend to be nomadic, moving large distances to new areas when prey populations dwindle at their previous breeding sites.

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Feeding ecology and diet

Owls consume a wide variety of prey types, and although a few species occasionally eat carrion, all owls catch and eat live animals. Many species eat invertebrates. Seventy-five percent of the 40 species of *Otus* for which diet information is available appear to specialize on insects. Amphibians are not major prey item of any owl species, but fish-owls and fishingowls often eat frogs. Some *Otus* and *Glaucidium* incorporate snakes and lizards into their diet.

Birds seldom account for a large number of prey items in owl diets, although some *Glaucidium* seem to specialize on them. Small mammals such as shrews and rodents are major prey items for many medium and large-sized owls, especially in northern latitudes, and the larger eagle-owls (*Bubo*) often feed on medium-sized mammals such as hares, rabbits, skunks, and even monkeys.

Reproductive biology

Most owls defend exclusive breeding territories and are non-social while nesting. Burrowing owls (*Athene cunicularia*) and long-eared owls (*Asio otus*) do not defend territories and may nest as close as 50 ft (15 m) from conspecifics. Mating systems tend toward monogamy, with one male and one female maintaining an exclusive pair bond while caring for their young. DNA fingerprinting has been used in studies of genetic parentage in four species of strigids, and in each case the birds proved to be genetically monogamous. Extra-pair copulations have been observed in burrowing owls and flammulated owls (*Otus flammeolus*). Several species of *Asio* regularly form communal roosts of 10–30 or more birds during the nonbreeding season.

Most owls breed only once per year. Barn owls are striking exceptions, regularly breeding twice per year in temperate latitudes and virtually year-round in the tropics. Mammal-eating species often nest in late winter or early spring, whereas insectivorous species generally nest in late spring or early summer. To attract a mate, males begin vocalizing about a month before nesting begins. Breeding displays often involve courtship feeding in which males bring prey items to females. Copulations are seldom observed because they take place at night.

Owls have a decided penchant against nest building. Many of the medium-sized and large species use old stick nests built by other birds, niches in broken-top snags, or cavities in cliffs. Still others nest on the ground, including snowy owls, shorteared owls, and marsh owls (*Asio capensis*). The burrowing owl is unique in nesting below ground in burrows constructed by badgers, prairie dogs, and ground squirrels or in natural or man-made holes. The smallest species nest in tree cavities excavated by woodpeckers.

Owls lay white eggs that are roundish in shape. Small insectivorous species lay small clutches (two to four eggs), as do large carnivorous and piscivorous species. On average, the small-rodent specialists lay larger clutches (five to eight eggs), especially when prey are abundant. Eggs are usually laid at two-day intervals, and incubation typically begins with the



Multiflash photography shows a little owl (*Athene noctua*) in flight. (Photo by Stephen Dalton. Photo Researchers, Inc. Reproduced by permission.)

first egg, resulting in nestlings of very different ages within a single nest.

Females perform all of the incubation and brood-rearing duties, whereas males provide most of the food for the female and young. Incubation periods range from 22 days in the smallest species to 32 days in the larger ones. Upon leaving the nest, young of the cavity-nesting species are fairly well developed and somewhat adept at flying, whereas young of the open-nesting species leave the nest two to three weeks before they can fly, hopping or walking along tree branches to distance themselves from the nest. These "branchers" have high survival, and their early departure from the nest probably reduces their vulnerability to predation.

Conservation status

According to BirdLife International's Threatened Birds of the World, 27 owls are at risk of extinction, and another 20 species are considered Near Threatened. Fourteen of the 27 high-risk species are endemic to small islands, which are especially vulnerable to human disturbance and invasion by exotic predators, and 12 occur in tropical areas that have been devastated by timber harvest. Only one, Blakiston's eagleowl Bubo blakistoni, occurs outside the tropics. It, too, is threatened by habitat destruction as well as by indiscriminate shooting. Two species of owls receive protection under the Endangered Species Act of the United States government. The ferruginous pygmy-owl Glaucidium brasilianum is listed as Endangered, and the spotted owl Strix occidentalis is considered Threatened. Populations of both species have declined due to destruction of critical habitat in the United States.

Order: Strigiformes Vol. 9: Birds II

Habitat loss is the biggest problem faced by owls. Forest fragmentation disrupts the functioning of communities, and because owls are at the top of the food chain, they are highly susceptible to the negative effects of these changes. Moreover, some owls do not tolerate disturbance, so human encroachment can make an area unsuitable even under moderate levels of habitat alteration. Other threats that may be important on a local scale include collisions with automobiles and fences, electrocution, illegal shooting, and pesticides.

Significance to humans

Regarded as symbols of wisdom by the ancient Greeks and serving as a source of delight and wonderment into the twenty-first century, humans have been captivated by owls for millennia. Owls have been depicted on coins, currency, and in numerous forms of art, and they also have been the subjects of poetry and prose. Yet, they frequently elicit fear and superstition and have been considered bad omens throughout the world. In many cultures, owls were believed to fore-

tell illness or death to people who encountered them. In Africa, it is still widely believed that owls are messengers of death, and to hear one is a sure sign of impending misfortune. In parts of China and Southeast Asia, legend says that owls relish the blood of newborn babies, and several Native American groups have stories of children being spirited away and eaten by owls.

Whether real or perceived, some owls have become a problem at airports because they are attracted to open areas surrounding runways that offer excellent habitat for small rodents. Hunting owls sometimes collide with aircraft, causing serious damage to both parties, but thus far no crashes.

On the positive side, educational efforts by scientists and conservationists have enabled many people to appreciate the potential for owls and other predators to help control rodent numbers. As a result, farmers and ranchers have installed specially designed boxes in the eaves of barns or placed them in forests to encourage owls to nest. Owls are also highly sought after by birdwatchers, who make special efforts to observe them throughout the world.

Resources

Books

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Periodicals

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Jeffrey S. Marks, PhD

Barn owls

(Tytonidae)

Class Aves
Order Strigiformes
Suborder Strigi
Family Tytonidae

Thumbnail description

Medium-sized owls with large head, dark eyes, heart-shaped facial disc, and with finely patterned plumage much like the wings of some moths

Size

9-22 in (23-57 cm)

Number of genera, species

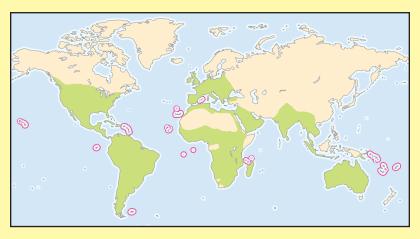
2 genera; 17 species

Habitat

Most terrains, from forest to desert to urban areas, in cool temperate to tropical zones

Conservation status

Endangered: 3 species; Vulnerable: 1 species



DistributionAlmost worldwide

Evolution and systematics

Barn owls are represented in the fossil record back to the Paleocene (65 million years ago), along with at least four now-extinct owl families. The Tytonidae was most diverse through the Eocene, Oligocene, and Lower Miocene, with nine species in five genera, including two now-extinct subfamilies that shared characters of the extant genera *Tyto* and *Phodilus*. The highly diverse hawk owls (family Strigidae) arose by the Lower Miocene, and superseded the Tytonidae. The rise and diversification of owls have been linked to the tertiary radiation of small mammals.

Tyto owls appeared by the middle Miocene, and diversified through the Pliocene and Pleistocene. The now-extinct species were larger than modern Tyto, with some gigantic forms on islands. Some of these forms persisted until recent times (the Holocene Epoch). The common barn owl (Tyto alba) is known from the Pleistocene. The present center of diversity in the Australian region, with relict species in Africa, Madagascar, and Southeast Asia, suggests that the family originated in Gondwanaland.

Owls were formerly thought to be related to the diurnal birds of prey, order Falconiformes, but DNA comparisons have shown that they are instead related to the nightjars (Caprimulgiformes). Studies of anatomy, behavior, biochemistry, and genetics have shown that the barn owls, although closely related to the hawk owls (Strigidae), are distinct at the family level.

Barn owls, genus *Tyto*, and bay owls, genus *Phodilus*, are sufficiently different for separation into the subfamilies Tytoninae and Phodilinae. As of 2001, science recognizes 16 species in the genus *Tyto*, and one species in *Phodilus*, with a total of about 65 subspecies. Almost half of these are sub-

species of the widespread common barn owl, which has many isolated populations on islands.

Physical characteristics

As noted by Iain Taylor in his book Barn Owls, published in 1994, these owls "when hunting over a meadow ... have an ethereal quality that can be matched by no other bird." Barn owls are large-headed, short-tailed owls with a pale bill, and dark, frontally-set eyes in a flat, heart-shaped, prominently-rimmed facial disc. They range in size from 9-22 in (23-57 cm) and 0.4-2.8 lb (187-1,260 g). They are colored in browns and grays, often with a pale underside, and the dorsal plumage is intricately patterned in moth-like marbling, mottling, and flecking. The plumage is soft and fluffy, with flexible flight feathers in the large wings. Barn owls have a comb-like serration on the inner edge of the middle claw, absent in the Strigidae, but present in the nightjars. A nestling barn owl is characterized by its "long" face and bill, and emerging facial disc, and it develops extensive down that hides growing feathers. Other characteristics of barn owls which separate them from hawk owls include a tufted preen gland, primary feathers that are not narrowed at the tips or emarginated, an inner toe as long as the middle toe, and ear openings that are long slits covered by a flap of skin.

Distribution

Barn owls occur almost worldwide, being absent only from polar regions, the coldest parts of Eurasia and North America, and the driest Saharan and Middle Eastern deserts. The common barn owl is one of the most widely distributed land birds, being found on all continents except Antarctica as well Family: Barn owls Vol. 9: Birds II



A 40-day-old barn owl (*Tyto alba*). (Photo by Jane Burton. Bruce Coleman Inc. Reproduced by permission.)

as on many islands, although only vagrants have reached New Zealand. One species occurs in Europe, the Mediterranean, the Middle East, North America, and South America; three occur in Africa; two in Madagascar and the Caribbean; four in Southeast Asia; and 11 in Australasia. There are two endemic species in Africa, one each in Madagascar and the Caribbean, two in Southeast Asia, and nine in Australasia. Their current range is little changed from their historical range, except that the common barn owl has disappeared from southern Scandinavia, Malta, and Aldabra, and the eastern grass owl (*Tyto longimembris*) may be extinct in Fiji. The Australian masked owl (*Tyto novaehollandiae*) has become locally extinct in some agricultural parts of southern Australia.

Habitat

Barn owls inhabit forested, wooded, and open habitats from the tropics to the cool temperate zones. They reach their greatest diversity in the tropics and subtropics, where several species coexist by partitioning the habitat. In Australia the sooty owl (*Tyto tenebricosa*) and lesser sooty owl (*T. multi-*

punctata) inhabit rainforest or moist hardwood forest with a rainforest understory, and take prey in trees and shrubs as well as on the ground. The Australian masked owl inhabits drier, more open and grassy forest or woodland, or limestone cave systems in treeless areas, and takes mainly terrestrial prey. The common barn owl inhabits open woodland, grassland, and urban areas, and takes small terrestrial prey. The eastern grass owl specializes in aerial foraging for terrestrial prev in rank grassland. In Southeast Asia the Oriental bay owl (Phodilus badius) inhabits rainforest. Similarly, the Itombwe owl (Tyto prigoginei) and the Madagascar red owl (T. soumagnei) inhabit rainforest, alongside the common barn owl and African grass owl (*T. capensis*) of open habitats. Barn owls roost in cavities such as tree hollows and caves, or in dense foliage, and nest in hollows or in caves, except for the grass owls which roost and nest on the ground in thick cover.

Behavior

Barn owls occur singly, in pairs, or in family groups consisting of the pair and recently fledged, dependent young. In times of abundant prey, the smaller species of open habitats may hunt and roost in loose aggregations. Barn owls roost alone, except during the courtship phase of the breeding cycle, when the male may roost with the female in a cavity that becomes the nest. On rousing at dusk, and through the night, they advertise or maintain contact with screeching, screaming, or whistling calls, unlike the hooting of hawk owls. At close range, they communicate with quieter trilling or chattering calls.

If cornered by a perceived enemy, barn owls bluff in a threat display of puffed-up plumage, outspread wings, swaying on their perch, loud snapping of the bill, and hissing or screeching. If pressed, they lunge with the bill, strike with a foot, or eject malodorous feces. The larger barn owls of forest and woodland, such as the sooty owl, are strongly territorial and defend large, exclusive home ranges. The smaller species, such as the common barn owl, are less territorial and defend only a small area immediately about the nest. Most territorial defense is vocal, but defenders will approach an intruder with the threat display, or even chase, grapple, and fight.

Barn owls usually sleep during the day, upright on one leg with the facial disc pinched into a triangular shape, and the closed wings hunched forward to hide most of the pale underside. They hunt through the night, often from a series of perches, but smaller species also hunt on the wing. During times of food shortage, the small species of open country will hunt on dull afternoons. They return to their roosts at dawn, sometimes calling from or near the roost.

Breeding adult barn owls behave as sedentary pairs occupying permanent home ranges. Newly independent juveniles disperse, moving in search of food or vacancies in the breeding population. After prolific breeding in good times, dispersing individuals of the smaller, open-country species are irruptive, occupying marginal habitats in numbers while conditions are favorable, and even breeding there. There may be mass starvation and death when conditions deteriorate, followed eventually by a new boom-and-bust cycle. Most juveniles disperse to within 30–60 mi (50–100 km) of their birth

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place, although some common barn owls and grass owls disperse hundreds of miles (kilometers).

Feeding ecology and diet

Barn owls prey on a variety of vertebrates and invertebrates, mainly small mammals supplemented by birds, reptiles, amphibians, and large insects. They specialize on rodents and rodent-like mammals such as shrews or small marsupials. They forage by watching and listening from a series of perches or, in the smaller species of open country, by aerial searching and hovering. They swoop to seize prey in the claws and kill it with a bite to the neck before plucking and dismembering it or, if the prey is small, swallowing it whole. Later, at the roost, they disgorge pellets of fur or feathers that contain the skulls and other bones of their prey. When fresh, the dried pellets of barn owls have a characteristically dark, "glazed" mucous coating.

Barn owls are highly specialized for detecting prey by sound, enabling them to make captures in total darkness even when they cannot see their targets. Acute directional hearing enables them to pinpoint the sounds of mammals rustling and squeaking, to within 1–2° in the horizontal and vertical planes. The facial disc acts as a parabolic dish for focusing and amplifying sounds, and channeling them to the asymmetrical ear

openings that locate the source of sounds by parallaxis. Muscles behind the ears move the facial ruff, as if the intently listening owl is cupping its ears. Owls also have frayed edges to the flight feathers for silent flight, thus avoiding detection by their prey.

Reproductive biology

Courtship among barn owls is vocal and sometimes aerial. Male and female sooty owls engage in prolonged duets of trilling calls. Male Australian masked owls and eastern grass owls perform a prolonged circling and chattering or trilling flight, respectively. Male common barn owls screech incessantly and perform a hovering flight near the nest, and pursue the female about the site with chattering calls. Males of the well-known species also bring food to the female, which begs like a juvenile. Mating, preceded by twittering calls, courtship feeding, and mutual preening, takes place at or near the nest, and culminates with a squealing call. In the better-known species, the mating system is permanent monogamy for the life of either partner.

Barn owl eggs are white and rounded oval, and take around five weeks to hatch. The clutch size is from one or two in the sooty owls to seven or eight in the common barn owl and



A barn owl (*Tyto alba*) flies through a barn window with its prey in Germany. (Photo by Wolfgang Buchhorn/Okapia. Photo Researchers, Inc. Reproduced by permission.)

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Common barn owl (*Tyto alba*) pellets, which may contain the undigested fur, feathers, and bones of their prey. (Photo by W. Greene/VIREO. Reproduced by permission.)

grass owls in good seasons. For most species the nest site is a natural or artificial cavity, such as a tree hole, but for the grass owls it is a tunnel and chamber within rank vegetation on the ground. Chicks hatch in sparse, pale down which is soon replaced by a thicker down. The growing feathers eventually show through as the down is shed, so that when fully fledged at around two months of age the owlets still have tufts of down on the head and thighs. By the time they leave the nest and fly, owlets are adult-sized but have shorter wings and tails because their flight feathers have not yet fully emerged from sheaths.

Incubation and brooding are undertaken solely by the female, which is fed on the nest by the male. The clutch is laid at two-day intervals and incubated from the start, so that eggs hatch sequentially and in a brood there is a range of ages. In times of food shortage, the youngest chicks may starve and be cannibalized. When the chicks are half-grown, feathering, and able to keep themselves warm, the female joins in providing for the family. Prey is at first dismembered and fed piecemeal to the chicks, but growing owlets are soon able to swallow whole surprisingly large items, such as rats. Fledged barn owls remain dependent on their parents for several weeks in small species to several months in large forest species, and can breed at one year of age.

In temperate regions barn owls lay in spring, and rarely manage more than one brood in a season. In warmer regions the laying season extends from autumn to spring, the onset of laying determined by food supply. In good years the smaller species of open habitats may raise two or three broods in succession, or even breed continuously during plagues of rodents.

Conservation status

Although barn owls are cryptic and under-recorded, several species such as the common barn owl, grass owls, sooty

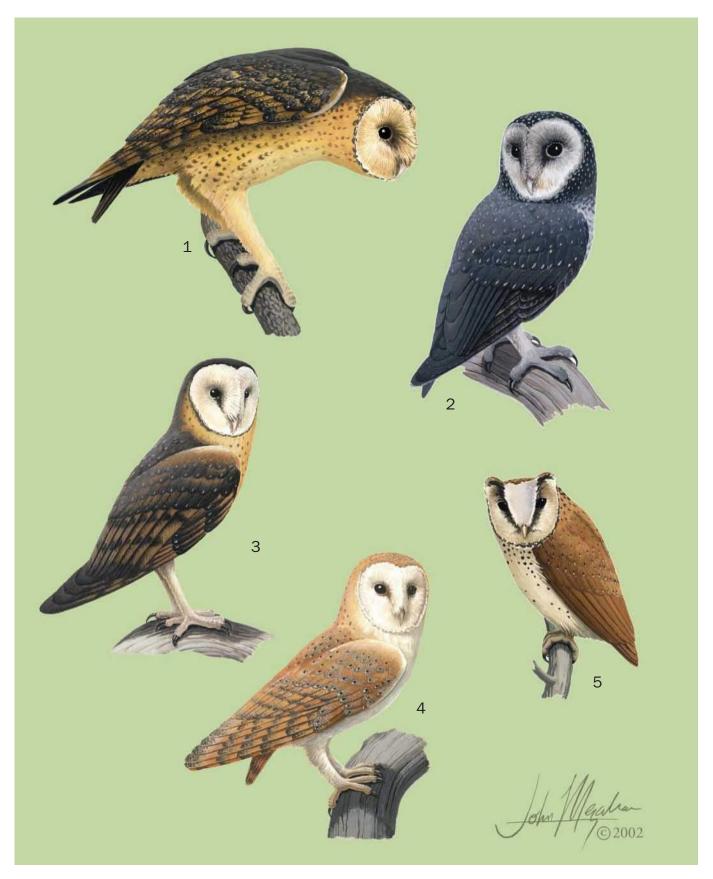
owl, and Australian masked owl are widespread and uncommon to locally common, or are common in a limited area (lesser sooty owl). Most are rarely encountered, endemic species with restricted ranges on small, tropical forested islands, particularly in Indonesia and Melanesia. Several are on the IUCN Red List. The Minahasa masked-owl (T. inexspectata) is listed as Vulnerable. The Madagascar red owl, the African bay owl (P. prigoginei), and the Taliabu masked owl (T. nigrobrunnea) are listed as Endangered. The lesser masked owl (T. sororcula) of the Moluccas, Sulawesi barn owl (T. rosenbergii), Andaman barn owl (T. deroepstorffi), and the ashy-faced owl (T. glaucops) of Caribbean islands, are also endemic species with highly restricted ranges. Two subspecies of the Australian masked owl were listed as Vulnerable on the Australian Environment Protection and Biodiversity Conservation Act 1999, but this situation was revised in 2000 to two subspecies classified as Near Threatened and two as Endangered.

Many members of the barn owl family have suffered population declines. The main reason is habitat loss: deforestation and logging in Australia and the tropics; conversion of natural grasslands to cultivation in the tropics and subtropics; and intensified agriculture in Western countries, with loss of foraging habitat and nest or roost sites. Rodenticides can also cause owl deaths. As of 2000, populations were estimated at 10,000 breeding individuals for the Australian subspecies of the sooty owl, a total of 21,300 for the Australian masked owl (all subspecies combined), and 10,000 for Australian populations of the eastern grass owl. In 1999, the European population of the common barn owl was estimated at 110,000–230,000 breeding pairs, meaning that its global population could be up to ten times that figure.

Significance to humans

Barn owls, by virtue of their nocturnal habits, ghostly appearance, eerie calls, and association with cemeteries and desolate places, have been featured in the mythology, literature, and art of all cultures since ancient times. As noted by Murray Bruce in Vol. 5 of the *Handbook of the Birds of the World*, "Few birds have accumulated such a wealth of varying and contradictory beliefs about them . . . [they are] feared or venerated, despised or admired, considered lucky or unlucky, and wise or foolish." They feature in superstitions concerning magic and witchcraft, prophecy, weather, birth, death, and other phenomena, and in potions, medicines, recipes, motifs, and the mummified contents of tombs. Common barn owls occasionally acquire a luminescent property to their plumage, which may contribute to the origin of legends concerning the "Will o' the wisp," "Jack o'lantern," and similar phenomena.

In modern times, barn owls have become popular as destroyers of rodent pests, and welcomed with the assistance of nest boxes in farm or town buildings. Common barn owls were introduced to some islands, with disastrous consequences for the endemic fauna. Barn owls are usually not dangerous to humans, although some individuals may defend owlets against human intruders at the nest by swooping and striking with their claws. The large species in Australia have become prominent in the debate over logging of old-growth forests.



1. Australian masked-owl (*Tyto novaehollandiae*); 2. Sooty owl (*Tyto tenebricosa*); 3. Eastern grass-owl (*Tyto longimembris*); 4. Common barn owl (*Tyto alba*); 5. Oriental bay-owl (*Phodilus badius*). (Illustration by John Megahan)

Family: Barn owls Vol. 9: Birds II

Species accounts

Sooty owl

Tyto tenebricosa

SUBFAMILY

Tytoninae

TAXONOMY

Strix tenebricosus John Gould, 1845, New South Wales. Two subspecies recognized (*Tyto t. tenebricosa* and *Tyto t. arfaki*). Lesser sooty owl (*T. multipunctata*), smaller, more spotted, and paler ventrally, is sometimes regarded as conspecific, or belonging to the same species.

OTHER COMMON NAMES

English: Greater sooty or black owl, dusky barn owl; French: Effraie ombrée; German: Rußeule; Spanish: Lechuza Tenebrosa.

PHYSICAL CHARACTERISTICS

Male 15–17 in (37–43 cm), 1.1–1.5 lb (500–700 g); female 17–20 in (44–51 cm), 1.9–2.5 lb (875–1150 g). Large, dark owl with large eyes set in rounded facial disc, massive feet. Sooty gray with fine white spots, pale belly. Female larger. Juvenile darker, with downy head and thighs when first fledged.

DISTRIBUTION

T. t. tenebricosa: coastal southeast Australia; T. t. arfaki: New Guinea

HABITAT

Tall, dense, moist forest including rainforest and eucalypt forest with a dense shrub layer of rainforest species. In montane



New Guinea extends above the tree line, into boulder fields in alpine grassland.

BEHAVIOR

Nocturnal, solitary, secretive. Roosts in tree hollows, dense foliage, ravines, or caves. Sedentary and strongly territorial, advertising with a long, descending scream or wail. Defends home range of 1.5–3.9 mi² (4–10 km²).

FEEDING ECOLOGY AND DIET

Preys mostly on arboreal and terrestrial mammals such as rodents and possums, which it detects by watching and listening from perches.

REPRODUCTIVE BIOLOGY

Monogamous. Laying recorded in most months, but usually autumn to spring. Nests in tree hollow or ledge in cave. Clutch one or two eggs, incubated for five or six weeks. Fledge at about three months.

CONSERVATION STATUS

Not threatened. Widespread, but uncommon. Listed on Appendix II of CITES.

SIGNIFICANCE TO HUMANS

Prominent in the old-growth forest debate in Australia in the 1990s, as an indicator species for sustainable logging practices. ◆

Australian masked owl

Tyto novaehollandiae

SUBFAMILY

Tytoninae

TAXONOMY

St[rix]? Novae Hollandiae Stephens, 1826, New South Wales. Five or six subspecies recognized; doubtfully valid T. n. galei usually merged with kimberli, and Tasmanian castanops sometimes regarded as full species. Forms species complex with other masked owls in Melanesia and east Indonesia: golden masked owl (T. aurantia) in Bismarck Archipelago, Manus masked owl (T. manusi) in Admiralty Island, lesser masked owl (T. sororcula) in southern Moluccan and Tanimbar islands, Taliabu masked owl (T. nigrobrunnea) in Sula Islands, and Minahasa masked owl (T. inexspectata) in northern Sulawesi.

OTHER COMMON NAMES

English: Masked/tasmanian masked/chestnut-faced/cave owl; French: Effraie masquée; German: Neuhollandeule; Spanish: Lechuza Australiana.

PHYSICAL CHARACTERISTICS

Male 13–17 in (33–42 cm), 0.9–1.8 lb (420–800 g); female 15–22 in (38–57 cm), 1.2–2.8 lb (545–1260 g). Large, pale or dark owl with large eyes set in rounded facial disc, large feet. Mottled brown and rufous (orange-brown to reddish brown) dorsally with rufous underside, or mottled gray and buff dorsally with white underside. Wings barred, underside finely spotted. Female larger. Juvenile has downy head and thighs when first fledged.

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DISTRIBUTION

Two or three subspecies peripheral in continental north, northeast and south Australia; one subspecies in Tasmania; one subspecies on islands off northern Australia; and one subspecies in southern New Guinea.

HABITAT

Tall, grassy forest and woodland, often near open country, extending into treeless areas where there are caves.

BEHAVIOR

Nocturnal, solitary, secretive. Roosts in tree hollows, dense foliage in gullies, or in caves. Sedentary. Territorial when breeding, advertising with a loud, harsh screech. Defends home range of 1.5–4.2 mi² (4–11 km²).

FEEDING ECOLOGY AND DIET

Preys mostly on terrestrial mammals, especially rodents, which it detects by watching and listening from perches.

REPRODUCTIVE BIOLOGY

Monogamous. Laying recorded in most months, but usually autumn to spring. Nests in tree hollow. Clutch 1–4 eggs, usually two or three, incubated for 33–35 days. Fledge at two months.

CONSERVATION STATUS

Widespread, but uncommon to rare. Listed on Appendix II of CITES. Two continental Australian subspecies are classified as Near Threatened and two island subspecies (Tasmania and Northern Territory) are Endangered under the Australian Environment Protection and Biodiversity Conservation Act.

SIGNIFICANCE TO HUMANS

Prominent in the old-growth forest debate in Australia in the 1990s, as an indicator species for sustainable logging practices. ◆

Common barn owl

Tyto alba

SUBFAMILY

Tytoninae

TAXONOMY

Strix alba Scopoli, 1769, Italy. Twenty-seven to 30 subspecies recognized. Species complex includes ashy-faced owl (*T. glaucops*) of Caribbean islands, and Sulawesi barn owl (*T. rosenbergii*). In 1999, form on Andaman Islands elevated to full species rank as Andaman barn owl *T. deroepstorffi*. Some other dark, well-marked subspecies on tropical islands may also be full species.

OTHER COMMON NAMES

English: Barn/cave/screech/white/ghost owl; French: Effraie des clochers; German: Schleiereule; Spanish: Lechuza Común.

PHYSICAL CHARACTERISTICS

11–17 in (29–44 cm), 0.4–1.5 lb (187–700 g). Small, usually pale owl with small eyes set in heart-shaped facial disc, small feet. North American subspecies larger. Mottled gray and buff dorsally, with white to buff underside finely spotted. Some island forms darker, browner dorsally and rufous ventrally. Female similar. Juvenile has downy head and thighs when first fledged.

DISTRIBUTION

Five subspecies from Europe and Mediterranean to Middle East; one subspecies in sub-Saharan Africa and Madagascar; four subspecies on islands around Africa; one subspecies in India and Sri Lanka to Indochina and southern China; two subspecies from Malay Peninsula to eastern Indonesia; three



Family: Barn owls Vol. 9: Birds II

subspecies in Melanesia; one subspecies in Australia; one subspecies from North America to Caribbean; four subspecies on Caribbean islands; one subspecies on Galápagos; and four subspecies in Central and South America. Some disagreement on the number of subspecies, particularly in the Caribbean and South America, with some authorities also recognizing subspecies in Madagascar and Polynesia. Some disagreement over whether Caribbean forms *insularis* and *nigrescens* belong with *T. alba* or *T. glaucops*. Introduced to Seychelles and Hawaii.

HARITAT

Wide variety of open wooded or treeless, grassy or brushy habitats, extending to rocky areas, caves, wetland verges, and urban areas.

BEHAVIOR

Nocturnal, crepuscular, and sometimes diurnal. Solitary, or in loose aggregations where prey is abundant. Roosts solitarily or communally in natural or artificial cavities or other shelter, from tree hollows, caves and dense foliage to buildings. Often resident, but also dispersive and irruptive. Breeding pairs are sedentary, occupying home ranges of 1.1–3.7 mi² (2.9–9.5 km²), but defend an area of only a few yards around the nest. Call is a falsetto screech, sometimes likened to a woman screaming.

FEEDING ECOLOGY AND DIET

Preys on a wide variety of invertebrates and small vertebrates, but mostly on rodents, detected by watching and listening from perches or low quartering flight.

REPRODUCTIVE BIOLOGY

Monogamous. Can lay in all months, and may have two or three broods in a year when prey is abundant, but at high latitudes lays in spring. Nests in a variety of natural and artificial cavities. Clutch usually 4–7 eggs; exceptionally up to 16 may involve two females laying in one nest. Incubation 29–34 days, fledging 7–10 weeks.

CONSERVATION STATUS

Not globally threatened. Very widespread, and uncommon to locally common or even abundant during plagues of prey species. Some local declines in intensively farmed Western countries, and the status of some subspecies restricted to small islands is uncertain. Listed on Appendix II of CITES.

SIGNIFICANCE TO HUMANS

Has a long history of folklore in Europe, the Mediterranean, and among tribal peoples. Luminescing barn owls may have contributed to the origin of mythology concerning the Will o'the wisp, Jack o'lantern and similar phenomena. Has achieved popularity as a destroyer of rodents. ◆

Eastern grass owl

Tyto longimembris

SUBFAMILY

Tytoninae

TAXONOMY

Strix longimembris Jerdon, 1839, India. Five or six subspecies recognized. Forms a species complex with the similar African grass owl (*T. capensis*), with which sometimes regarded as conspecific.



OTHER COMMON NAMES

English: Grass owl; French: Effraie de prairie; German: Graseule; Spanish: Lechuza Patilarga.

PHYSICAL CHARACTERISTICS

Male 13–14 in (32–36 cm), 0.6–0.8 lb (265–375 g); female 14–15 in (35–38 cm), 0.7–1.3 lb (320–582 g). Small, pale or dark owl with small eyes set in rather long, square facial disc, long bare legs. Mottled brown and buff dorsally, underside white or buff, finely spotted. Female larger and darker. Juvenile darker, with downy head and thighs when first fledged.

DISTRIBUTION

One subspecies from India through Indonesia to Australia; one subspecies in Indochina and eastern China; one subspecies in Taiwan; one subspecies in the Philippines; and one or two subspecies in New Guinea.

HABITAT

Rank grassland, heath, crops, and wetland verges of rushes and reeds.

BEHAVIOR

Nocturnal and crepuscular, rarely diurnal. Solitary, or in loose aggregations when prey is abundant. Roosts, solitarily or communally, in dense ground cover. Resident, but also dispersive and irruptive. Territorial when breeding, defending the nesting area with trilling calls and soft screeches. Up to 40 pairs of grass owls may nest in 0.2 mi² (0.4 km², with as little as 55 yards (50 m) between neighboring nests.

FEEDING ECOLOGY AND DIET

Preys mostly on rodents, detected by watching and listening from low searching flight.

REPRODUCTIVE BIOLOGY

Monogamous. Lays in autumn and winter. Nest is a scrape or pad on the ground, under covering vegetation. Clutch is 3–8

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eggs, incubated for 31 days. Can run and leave the nest at 4–5 weeks, fully fledged and fly at two months.

CONSERVATION STATUS

Not globally threatened. Widespread and uncommon to rare, although locally common in coastal eastern Australia during times of abundant prey. Listed on Appendix II of CITES.

SIGNIFICANCE TO HUMANS

In Australia has become a flagship species, as a destroyer of rodents in sugar cane. ◆

Oriental bay owl

Phodilus badius

SUBFAMILY

Phodilinae

TAXONOMY

Strix badia Horsfield, 1821, Java. Six subspecies recognized. Formerly regarded as closely related to Itombwe owl or Congo bay owl (*P. prigoginei*), but the latter species more resembles *Tyto* and as of 1999 has been placed in that genus.

OTHER COMMON NAMES

English: Bay owl, Asian bay owl; French: Phodile calong; German: Maskeneule; Spanish: Lechuza Cornuda.

PHYSICAL CHARACTERISTICS

9–13 in (23–33 cm), 0.6–0.7 lb (255–308 g). Small chestnut owl with facial disc like barn owl, though squarer, divided down forehead and interrupted at throat, and peaked at corners (like small "ear" tufts). Barred and spotted dorsally, paler and spotted ventrally. Female and juvenile similar.

DISTRIBUTION

One subspecies in southwestern India; one subspecies in Sri Lanka; one subspecies from northeastern India through Indochina to southeastern China; and three subspecies in Malaysia and Indonesia. Subspecies uncertain for single record in Philippines.

HABITAT

Forest, and groves and plantations in farmland near forest.

BEHAVIOR

Nocturnal and elusive, solitary. Roosts in tree hollows and dense foliage. Calls with a variety of mainly whistling and screeching notes.



FEEDING ECOLOGY AND DIET

Preys on small vertebrates and insects, detected by watching and listening from perches.

REPRODUCTIVE BIOLOGY

Presumed monogamous. Lays in spring at higher latitudes, autumn-winter dry season in tropics. Nests in tree hollows, in crowns of palms, or occasionally in nest boxes. Clutch 3–5 eggs.

CONSERVATION STATUS

Considered uncommon to rare, but probably under-recorded. Listed on Appendix II of CITES.

SIGNIFICANCE TO HUMANS

Owls are regarded as evil spirits by some tribal peoples in Southeast Asia. ◆

Resources

Books

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Organizations

- Australasian Raptor Association. 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: htm>
- World Working Group on Birds of Prey and Owls. P.O. Box 52, Towcester, NN12 7ZW United Kingdom. Phone: +44 1 604 862 331. Fax: +44 1 604 862 331. E-mail: WWGBP@aol.com Web site: http://www.Raptors-International.de

Stephen Debus, MSc

Owls (Strigidae)

Class Aves
Order Strigiformes
Family Strigidae

Thumbnail description

Typical owls have large, rounded heads, forwardfacing eyes, facial discs of feathers, and strong, hooked beaks; solid, stocky bodies with dense feathering; moderately short tails; strong feet with talons; subtle coloration makes these birds well camouflaged

Size

4.7–29.5 in (12–75 cm); 1.4–148 oz (40– 4,200 g)

Number of genera, species

25 genera; 189 species

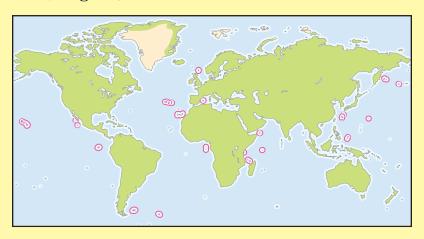
Habitat

Forest, woodlands, tundra, desert, savanna, parkland, urban, coastal, wetlands, mangroves

Conservation status

Critically Endangered: 3 species; Endangered: 4 species; Threatened: 2 species; Vulnerable: 12

species



Distribution

All continents except Antarctica

Evolution and systematics

The oldest known record of an owl, the fossil *Ogygoptynx wetmorei* from about 58 million years ago (mya), was discovered in Colorado, USA. The available fossil record suggests a major radiation of owls about 50 million years ago, although exactly when the Strigidae appeared is not clear. It seems that the original owls were large in comparison to modern owls. The Tytonidae preceded the Strigidae in the fossil record. *Bubo poirrieti*, found in France 24–22 mya, and *Strix brevis*, from western North America, are the earliest records of Strigid owls yet discovered.

Linnaeus put the hawks (Falconiformes) and the owls (Strigiformes) in the same group because of their physical characteristics and carnivorous habits. They retained this classification for 130 years until M. Furbringer, H. von Gadow, and others pointed out the similarities of the owls to the Caprimulgiformes (nightjars, frogmouths, and oilbirds). Most modern taxonomists still consider the Caprimulgiformes to be the closest relatives of the owls, a relationship supported by DNA-DNA hybridization data.

Historically, there have been huge arguments about the number of species and particularly subspecies among the owls. Some disputes have been resolved through the use of DNA to discover who is related to whom; however, at this point, no two books give exactly the same answers. Considering the popularity of owls and the number of species, there are surprisingly few books on owls of the world. The owls of

the Northern Hemisphere are covered reasonably well, but those in the Southern Hemisphere are covered rather less well. *Handbook of the Birds of the World*, volume 5, divides the Strigidae into three subfamilies (Striginae, Surniinae, and Asioninae), six tribes (Otini, Bubonini, Strigini, Surniini, Aegoliini, and Ninoxini), 25 genera, 189 species, and 548 subspecies.

Physical characteristics

The Strigidae, sometimes known as the typical owls, is an enormous and varied family, yet it is very distinct—there is no doubt an owl is an owl. The largest of these owls are the eagle-owls, genus Bubo. The northern race of the Eurasian eagle-owl (*Bubo bubo*) is a huge bird weighing as much as 9.2 lb (4,200 grams) with a length 23.6–29.5 in (60–75cm). A close runner-up is Blakiston's eagle-owl (Bubo blakistoni), an extremely rare fishing owl found only in Japan, Siberia, and far northeast China, which is 23.6–28.3 in (60–72 cm) in length. On the other end of the scale are the ridiculously tiny pygmy owls of the genus Glaucidium. The least pygmy owl (Glaucidium minutissimum) lives up to its name, weighing only an average of 1.7 oz (47.8 g). This species is a massive 20% heavier than the elf owl (Micrathene whitneyi), the most delicate of all the owls at 1.4 oz (40.2 g) and only 5.3–6.1 in (13.5–15.5 cm) in length.

Between these two extremes of size are nearly 200 other owl species of every size and color. The males tend to be Family: Owls Vol. 9: Birds II



An elf owl (*Micrathene whitneyi*) nests in a saguaro cactus (*Carnegiea gigantea*) in Arizona. (Photo by Craig K. Lorenz. Photo Researchers, Inc. Reproduced by permission.)

smaller than the females, although this is often most noticeable in the owls that feed on vertebrates rather than invertebrates. There are exceptions—male burrowing owls (*Athene cunicularia*) are slightly larger than the females, as are the males of some of the *Ninox* species. All the owls have a large, domed, rounded head with forward-facing eyes. Probably the most striking feature of the owls is the facial disc of feathers. This, along with the forward-facing eyes and the bill often almost hidden by feathers, makes them appear to have a "face." The disc, which is more pronounced in the barn owls (Tytonidae), works like a parabolic reflector, focusing sound towards the owl's ears.

Owls have remarkably subtle plumage, with beautiful muted colors including browns, golds, grays, black, creams, and white. There is tremendous variation among the different species, but in all species the plumage has evolved to blend in with various backgrounds and habitats. Camouflage is essential to an owl during daylight hours. As predators, owls are hated and feared by most other birds and, if spotted in the daytime, they are mobbed furiously by many different genera of birds. Even tiny passerines try to drive them away. The

mobbing of owls is such a powerful instinct in other birds that even dead, stuffed owls are attacked, with some birds going so far as to physically strike the owls. Consequently the coloration of an owl is crucial as camouflage. Some are so well camouflaged that they become almost invisible when seen against the bark of a tree.

Owls are nocturnal birds, although many can and do hunt in half light and daylight. Their modified hearing and highly specialized feathers allow them to hunt successfully after sunset. Owls use sound as a directional aid to assist in locating prey at night. Their ears are set asymmetrically in their skulls, with one set slightly higher than the other, and one sometimes of larger size. This allows the owl to pinpoint sound very accurately while in flight. In addition to this adaptation, owl feathers have evolved to facilitate silent flight. The surface of most of the feathers is not smooth, but covered in a very fine down. The trailing edge of the flight feathers (primaries and secondaries) is much softer and less defined than that of diurnal birds of prey, and only the outer edge of the leading primary is serrated like a comb. All these adaptations contribute to silent flight, which in turn aids hunting in the dark. Most owls have feathers growing to a greater or lesser extent right down to their talons. These feathered feet give the owls extra protection from biting rodents, and in many species, provide extra insulation against cold temperatures. The exceptions are the fishing owls—they have bare feet more suited for getting wet regularly.

Distribution

With the exception of Antarctica, owls are found throughout the world. Snowy owls (*Nyctea scandiaca*) inhabit the frozen tundra of the north, living above the tree line during summer months and breeding as far north as 82°50′. A few species, including the snowy owl, circumnavigate the globe and are distributed in both the New World and the Old World. The northern hawk owl (*Surnia ulula*) and the great gray owl (*Strix nebulosa*) are also found just south of the tree line all around the top of the world.

The scops-owls (genus Otus) are the largest genus in the Strigidae with 63 species. They could almost be described as island specialists, since 30 of the species are found on large or small islands. Many of them are found on tiny "islands" of habitat. For example, the Madagascar scops-owl (Otus rutilus) is found, as its name implies, throughout Madagascar. The Puerto Rican screech owl (Otus nudipes) is found in Puerto Rico, is thought to be extinct on the Island of Vieques, and may be found on Culebra Island and the Virgin Islands. (Indeed, this is a classic case of how little is really known about many species of owls, particularly the scops-owls.) The island species have the highest number of endangered species some, like the Seychelles scops-owl (Otus insularis), which is Critically Endangered, are limited to only a single island. Twenty-seven of the 63 species are located in Southeast Asia and 13 species are found in South America. Fifty-five species are found between the tropic of Cancer and the tropic of Capricorn, since these tiny owls generally do not survive well in colder weather.

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Among the eagle-owls, the great horned owl (*Bubo virginianus*) has the greatest range, extending from Alaska to Argentina. The Eurasian eagle-owl is similarly widespread in the Old World, ranging from Spain and Norway to eastern China, Russia, and northern Hokkaido in Japan. As with any species covering such a wide range there are many subspecies, 14 within the Eurasian eagle-owl and 12 in the great horned owl.

Of the seven species of fishing owls, three occur in southeastern Asia and three in Africa. The northern most and also most endangered is Blakiston's eagle-owl, which inhabits southeastern Siberia, Manchuria, Sakhalin Island, Hokkaido, and the southern Kuril Islands.

The wood-owls (genus *Strix*) are spread quite evenly throughout the world, although, as their name implies, they are mainly found in the world's forests. The tribe Ninoxini, genus *Ninox*, is all found through Southeast Asia and Australia with one species found in New Zealand. There are two exceptions in this distribution—the brown hawk-owl (*Ninox scutulata*), which ranges from India north to Siberia and Japan, and the white-browed hawk-owl (*Ninox superciliaris*), which occurs only in Madagascar and is also the only *Ninox* with brown eyes instead of yellow. (Its relationship to *Ninox* requires further research.) The most widespread of the typical owls is the short-eared owl (*Asio flammeus*), occurring in North and South America, Europe, Asia, and some parts of Africa, but not in Australasia.

Habitat

Owls have evolved to inhabit just about every remaining forest on Earth. With a few exceptions, the bulk of the typical owl species prefer to inhabit forests or woodlands. The richer the forest the higher the number of owl species that inhabit it, so both lowland and, less commonly, high-altitude tropical forests are home to many species. Because of the natural inaccessibility of the high-altitude forests, far less is known about the species that live there. The lowland tropical forests are relatively accessible to humans and have been extensively exploited and so the species living there are more likely to be threatened. All but a few of the scops-owls inhabit either rainforest or other forested and wooded areas, as do most of the eagle-owls. One exception is Savigny's eagle-owl (Bubo ascalaphus), also known as the desert eagle-owl, its glorious buff and sandy coloration making it an obvious desert dweller. Another species whose coloration is well adapted to the desert environment is Hume's owl (Strix butleri), which inhabits rocky gorges, desert wadis, and palm groves.

The fishing owls of the genera *Ketupa* and *Scotopelia* are more specialized and are found along the lakes, rivers, or swamps that are home to the fish upon which they prey.

The more northern species of pygmy-owls, such as the Eurasian pygmy-owl (*Glaucidium passerinum*) or the northern pygmy-owl (*Glaucidium californicum*), prefer either coniferous or deciduous forests and forest edges. A few, such as the pearl-spotted owlet (*Glaucidium perlatum*), occur in more open scrub land. The more southern species inhabit a wider variety of forests from the sparse open forests, scrub land, coastal and



The shape of an owl's skull, its facial disk, helps to funnel sound to its ears. (Illustration by Patricia Ferrer)

thorn scrub, which the ferruginous pygmy-owl (*Glaucidium brasilianum*) inhabits, to the dense primary forests that are preferred by the red-chested owlet (*Glaucidium tephronotum*).

One of the best known of the open habitat owls is the burrowing owl. This active and marvelous little owl inhabits the arid desert plains, grasslands, and prairies through North and South America, sometimes living close to human habitation. Unlike many owls, they are very obvious in their habits and thus are noticed more than many other species.

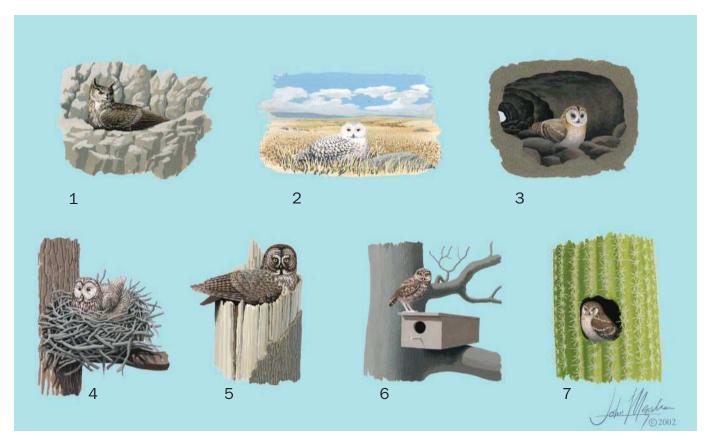
Apart from the white-browed hawk-owl of Madagascar, which occurs in varied terrain from open scrubland through forests to rocky coastal ravines, all the other *Ninox* species inhabit forests of some type depending on their range.

The last grouping of owls, the *Asio* species, all tend to inhabit various forests with the exception of the widely distributed short-eared owl and the marsh owl (*Asio capensis*). The latter inhabits open marshland and the short-eared owl encompasses a huge range that includes moorland, tundra, grasslands, marshlands, and montane forests.

Although not the most widespread, the great horned owl probably inhabits more varied habitats than any other owl species. Its adaptability has allowed it to survive in almost all habitats and its lack of fear of humans increases the numbers of habitats it can utilize.

The quality of the habitat dictates how well owls can survive there. If it is a rich, undisturbed habitat, owls will do well, but human disturbance generally reduces the numbers of owl species and limits their ability to utilize what is available. The long-term impact of habitat changes on owls is uncertain because so little is known about many of these species. Nest sites are crucial for good owl habitat, particularly as they rely on holes in trees, crevices, or other birds' nests. But even with good available nest sites, owls cannot flourish without a sufficient prey base. For example, owls that rely on the cyclical

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1. Eurasian eagle-owl (*Bubo bubo*) rock-nesting; 2. Snowy owl (*Nyctea scandiaca*) ground-nesting; 3. Hume's owl (*Strix butleri*) nesting in rock cavity; 4. Ural owl (*Stix uralensis*) in an old raptor's nest; 5. Great gray owl (*Strix nebulosa*) nesting on the stump of a broken tree; 6. Little owl (*Athene noctua*) with nesting box; 7. Elf owl (*Micrathene whitneyi*) in hole of a Gila woodpecker (*Melanerpes hypopolius*) in a saguaro cactus. (Illustration by John Megahan)

lemming population will produce a population explosion in a good lemming year. However, the habitat cannot sustain the increased numbers for long and there is usually a large die-off of owls when the prey base declines. Although some owls are coping with the effects of humans on habitat, many are not. Migrating owls can be affected by habitat changes at both wintering and breeding destinations on their migration and little is known about the migration of owls.

Behavior

Since they are nocturnal, owls generally do not do a great deal during the day, apart from hiding. This habit of keeping very still and thus allowing people to approach fairly closely gives the mistaken impression that owls are tame. They are, in fact, trying to avoid attention by not moving. Owls will pull their feathers tight to their bodies and lean close to the tree or rocks in which they are perching in order to blend into the background and avoid detection. Having said that, owls do enjoy sunshine occasionally, and after periods of dull weather will find a quiet place and sun themselves, sometimes lying down and spreading their wings and tail to catch the warmth. They also enjoy bathing.

Some of the owl species are more active during the day, and several populations have no choice in the matter. Owls

living in the far north, where daylight extends nearly 24 hours during summer months, have to hunt regularly during daylight. Other owls living where daylight hours are long during the summer also have no option but to hunt in daylight to feed growing young. Some species seem to choose to be active during the day—probably the most active are the burrowing owl and the little owl (*Athene noctua*), which is particularly dayactive during the summer. Many owls are crepuscular and will be seen hunting at dawn and dusk in the half light.

Most owls are solitary except during the breeding season. A few group together in the winter in roosts, such as the long-eared owl (*Asio otus*). This species normally has roosts of up to 20 individuals, but numbers as high as 100 have been reported. In addition, marsh owls and short-eared owls gather in winter roosts. Oddly, these three species and the burrowing owl are the only species that might be termed loose colony nesters.

Little is known about the social behavior of owls, since it is difficult to study bird behavior in the dark. It is known that much of their socializing is done vocally. Owls produce a huge variety of calls from the pig-like grunting of snowy owls to the classic twit twooooo hooting of the tawny owl and the deep hooting of the large eagle-owls. The little owl has a yelping call that is often heard during daylight hours in the summer. The southern boobook owl (*Ninox boobook*) is named after its call, which has a gentle cuckoo-like sound. Some species

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have been reclassified and re-identified by their differing calls. Many owls have a wide variety of calls, and the warning call of some of the eagle-owls sounds like a dog barking. Heard unexpectedly at night, these calls can be quite startling!

In addition to using their voices to contact potential mates, call to their young, warn off intruders, and mark territories, owls also convey messages by their physical stance. When vocalizing many owls lean forward and display a flash of white throat feathers that must be very visible at night. Different positions of the ear tufts are used to communicate as well. Owls also adopt an aggressive posture in defense by opening their wings, lifting and turning them so the backs of the wings face forward, and puffing up all their body feathers. This makes the owls appear to be more than double their actual size. When combined with loud clapping sounds that the owls produce with their beaks, this posture makes the owls appear formidable indeed.

Most owls are sedentary. Only a very few species from the more extreme climates (both far north and far south) are migratory, although little is known about their specific movements. Burrowing owls disperse and move south from their northern ranges in North America, but the more southern populations such as those in Florida are sedentary. Snowy owls move south for the winter months as do northern hawk-owls (*Surnia ulula*). Brown hawk-owls in the north of their range move south for overwintering as well.

Owls appear to defend only the territory directly surrounding their nesting area, rather than the whole of the range in which they regularly hunt. Territorial behavior occurs much more during the courtship and breeding season than in the winter. This behavior also is more prevalent in sedentary species, as opposed to migratory species, particularly those with fixed nests sites, such as cavities or caves.

As stated earlier, most owls are not active in the daytime, but quickly become active when dusk falls. Contrary to popular belief, owls cannot see well when it is extremely dark. Owls are able to see better in low light than humans are, but they cannot see in total blackness anymore than humans or other animals can. Owls' eyes have huge pupils that provide good vision in low levels of light and consequently the early and late parts of the night are generally preferred for hunting.

Feeding ecology and diet

Were is not for the humble voles, owls would be a less well-established family. Owls catch a variety of prey, but voles feature highly in many owl diets, and some owls are completely reliant on them.

Insects make up the bulk of the diet of most tiny owls, such as the *Scops* and *Glaucidium* species. These species also take small birds, reptiles, and amphibians. Small owls, such as the smaller members of the *Ninox* and *Strix* genera, have a similar diet, but also take slightly larger prey, such as birds and small mammals. Medium owls, such as Ural owls, take accordingly larger prey, adding mammals such as rats and young rabbits and other similarly sized creatures. Snakes are taken



A northern pygmy owl (*Glaucidium gnoma*) showing the "eyes" on the back of its head in Oregon. (Photo by Erwin & Peggy Bauer. Bruce Coleman Inc. Reproduced by permission.)

by owls as well, although they do not form a large part of owl diets, since snakes prefer to be out in the heat of the day and owls do not. The largest of the owls, the eagle-owls, take quite large prey, such as rabbits, pheasants, and even hares. Great horned owls are probably the most rapacious of the owls and have been known to kill red-tailed hawks (*Buteo jamaicencis*), but this relatively rare occurrence tends to happen over nest disputes. Some owls, such as the great gray owl, may appear large, but are, in fact, quite small under an impressive coat of feathers. They rely on voles and lemmings for the bulk of their diet. The size of an owl's feet is usually an indication of the size prey that it is capable of taking, although there are exceptions. The little owl is able to take baby rabbits that are as large if not larger than the owl itself.

Some owls specialize in particular kinds of prey. The fishing-owls (*Ketupa*), as their name implies, specialize in fish and the spectacled owl (*Pulsatrix perspicillata*) is known to prey upon crayfish and small crabs. Many owls will take bats if the chance arises.

As with diurnal birds of prey, owls use their well developed feet to catch their prey. They are, as far as is known, totally carnivorous. A very few of the diurnal birds of prey eat some plant matter, but owls are not generally known to do so. However, since they often swallow their prey whole, owls consume some vegetable matter secondhand.

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A northern pygmy owl (Glaucidium gnoma) brings a mouse to its nest in Montana. (Photo by Anthony Mercieca. Photo Researchers, Inc. Reproduced by permission.)

The hunting methods of owls are similar to those employed by many of the diurnal raptors with the exception of vultures and falcons. No owls swoop on their prey from a great height, nor do any owls specialize in feeding on carrion. As a general rule they do not soar either. Like many hunting birds, owls favor "still hunting." A number of favorite perches are regularly used in the home hunting range and the owls sit watching and listening for potential prey.

Hawk-owls, as their name implies, have a hawk-like shape and can use a hunting technique similar to that of the accipiters. The northern hawk-owl, in particular, is agile in the air and will take birds on the wing. Generally most owls prefer the perching method of hunting. They sit and wait for prey to appear and then drop or glide from their elevated perch to attack. Only owls with lighter wing loading, such as the long-eared owl and the short-eared owl do a great deal of aerial hunting. These species will quarter the ground, floating above rough grassland and reed beds or moorland to locate potential prey.

Most owls cache or hide excess food and come back to find and eat it later. All owls regurgitate a casting or pellet of indigestible food that is composed of the fur, feathers, and bones of their prey. Unlike many other aspects of owls' lives, a great deal is known about their diets because of this pellet, which contains much information about exactly what owls have been consuming.

Reproductive biology

Owls are generally monogamous, and some, such as the Ural owl (*Strix uralensis*) and some of the small scops-owls, form

pairs for life. Others pair up for one breeding season and may find a new mate the following season. Some owls are known to be polygamous; often mating behavior is species reliant on the fluctuations of vole and lemming populations. When there is a population explosion of prey species, the owls can afford to take two mates and try for two different broods of young. This has been documented in several northern species such as the snowy owl and the tawny owl (*Strix aluco*), but is best known among the boreal or Tengmalm's owl (*Aegolius funereus*).

Owls court their mates through calls and by providing food and nest sites. After calling females into their territory, males offer food to prove their suitability as a provider for young and often show females potential nest sites. Owls do not build nests of their own, but rather nest in shallow scrapes in the ground among tree roots, in shallow caves, in the cavity of a tree, or in old buildings, ruins, and wall cavities. A few owls, such as the burrowing owl, even nest underground. This owl often uses the burrows of other mammals, and its close relative, the little owl, has been known to nest in rabbit holes. Many larger owls use the nests of other birds, such as raptors and corvids. The owl's own regurgitated pellets often are used to line the nest.

All owls lay white, fairly rounded eggs. The number of eggs varies from species to species. The average clutch size is two to four eggs. Some eagle-owls and fishing-owls lay only one egg in a clutch. Burrowing owls can lay up to 10 eggs in a clutch, and snowy owls and northern hawk-owls increase their clutches up to 13 in good vole or lemming years. Incubation is done almost solely by the female, who stays with the hatched young until their secondary down has grown and they can thermoregulate.

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The male owl provides all the food for his mate during incubation and also provides all the food for the young for the first two weeks or so of their lives. He delivers vast amounts of prey to feed growing young. Once the young are large enough, the female will join him in hunting and providing food.

Young owls wander from the nest before they can fly. They climb using their beaks and talons to scramble up trees to return to the safety of the nest when necessary. Although owls fledge in approximately the same amount of time as similarly sized diurnal birds of prey, they do seem to develop more slowly and the last of the natal down can be visible for some time after young have fledged. Like diurnal birds of prey, young owls are reliant on parental care for some period after fledging, although generally little is known about the length of their dependency.

Conservation status

At least eight identifiable species of owls have become extinct in the last 300 years and the number is probably higher than that. Like many other species, owls have suffered from human disturbance. As noted by del Hoyo, Elliott, and Sargatal: "According to BirdLife International's 1994 appraisal of globally threatened birds, 21 (11%) of the 189 species of Strigids known to be alive today are in danger of extinction, and another 14 (7.4%) are classified as Near Threatened." Most of these are island species and most inhabit tropical forests. Even though we are sadly uninformed about the status and biology of many species of owls, it seems logical that if forests are removed, then those species reliant on them also will be lost.

As of 2000, seven species of owls are listed as Critically Endangered. The saddest example is probably the forest owlet (*Athene blewitti*) of India, rediscovered in 1997 after 113 years since the last verified record. Within six months of this exciting discovery, tree cutting had devastated the habitat of this illusive owl, dramatically reducing its chances of survival.

As with so many taxa, habitat destruction is the main cause for decline in most owl species; however, other factors also contribute. Blakiston's fish-owl—the second largest owl and supposedly highly revered in Japan—is one of the world's rarest owls, and is classified as Endangered. Habitat destruction, shooting, encroaching human populations, and destruction of the rivers where it fishes threaten the future survival of this owl.

Because owls are low and slow flyers, roads and motor vehicle traffic pose a significant danger to them, especially when roads cut through islands of habitat. Many owls are killed on the roads and this problem increases as traffic increases.

A great deal of research is needed to assess and understand the needs of owls worldwide. In addition, education to teach people the value of their natural resources and give a national sense of pride in their wildlife is crucial to the conservation of owls. As with all species, conservation of natural habitat is paramount to the survival of owls.

Significance to humans

Owls have a long history with humans. The relationship is probably not as close as that between humans and diurnal birds of prey, but, nevertheless, owls abound in myths, poems, paintings, and folklore. It is probably the owls' almost human "face" that makes them so popular with many people. However, owls are probably hated and feared in some cultures as much as they are liked and revered in others.

In Indian law and in Greek mythology owls represent wisdom. In many countries owls were believed to be a symbol of bad luck or death, while in others they were believed to guard the souls of women or ward off famine or plague. In a few places, owls have been eaten as food, but more often, particularly in Southeast Asia, owl body parts are used for medical purposes by traditional healers. In Africa, owls are not particularly popular and can be killed for many reasons.

Historically, in Europe, tame owls were tethered to attract corvids and other birds. When these birds came to mob the owl, they were shot by hunters and gamekeepers. Today owls are used in a similar way by scientists to attract falcons, harriers, or kites, so that they can be trapped for scientific research.

Owls have appeared on artifacts for thousands of years. Clay models and sculptures of owls or other artistic representations of owls can be found in many cultures. Today representations of owls are popular with collectors.

Because owls are active at a time when most humans are not, there generally is not a great deal of interaction between them. However, during the breeding season some owls become extremely defensive and may attack anything that comes within their nesting area. When people venture near a nest, either by mistake (as when walking a dog late at night) or on purpose, problems may arise. Owls are not generally aggressive, but can be potentially dangerous when defending their nesting areas from humans. The massive size difference between humans and owls makes owls perceive humans as potential predators.

In Europe, owls are very popular birds to keep in captivity among special interest groups. This led to some very successful captive breeding programs with over 50 species of owls bred so far. In the United Kingdom, barn owls (*Tyto alba*) have been bred and released under special license to increase dwindling numbers; in Canada and the United States, burrowing owls have been bred and released. It is important to remember, however, that the habitat has to be suitable and the cause for the birds' decline has to be mitigated before captive breeding and release programs can be successful.



1. Eastern screech-owl (*Otus asio*); 2. Southern white-faced owl (*Ptilopsis granti*); 3. Snowy owl (*Nyctea scandiaca*); 4. Seychelles scops-owl (*Otus insularis*); 5. Barred eagle-owl (*Bubo sumatranus*); 6. Eurasian scops-owl (*Otus scops*); 7. Blakiston's eagle-owl (*Bubo blakistoni*); 8. Great horned owl (*Bubo virginianus*); 9. Eurasian eagle-owl (*Bubo bubo*). (Illustration by Patricia Ferrer)



1. Tawny owl (*Strix aluco*); 2. Northern saw-whet owl (*Aegolius acadicus*); 3. Spectacled owl (*Pulsatrix perspicillata*); 4. Southern boobook owl (*Ninox boobook*); 5. Asian brown wood-owl (*Strix leptogrammica*); 6. Pearl-spotted owlet (*Glaucidium perlatum*); 7. Burrowing owl (*Athene cunicularia*); 8. Short-eared owl (*Asio flammeus*); 9. Northern hawk owl (*Surnia ulula*). (Illustration by Patricia Ferrer)

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Species accounts

Eurasian scops-owl

Otus scops

SUBFAMILY

Striginae, Tribe Otini

TAXONOMY

Strix scops Linnaeus, 1758 Italy. Six subspecies are recognized.

OTHER COMMON NAMES

English: European scops-owl, common scops-owl; French: Petit-duc scops; German: Zwergohreule; Spanish: Autillo Europeo.

PHYSICAL CHARACTERISTICS

6.3–7.9 in (16–20 cm); 2.1–4.8 oz (60–135 g). Both gray-brown and rufous-brown color phases occur. Head features a gray facial disc, darker around the yellow eyes, and small ear tufts. Upperparts are gray-brown to rufous-brown with dark streaks, bars, and lines. Underparts are lighter brown to buffish white with dark streaks, bars, and lines. Buffish white leg feathers and gray feet.

DISTRIBUTION

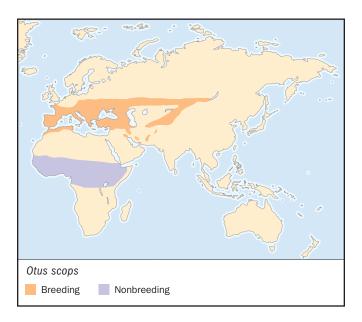
France, and all Mediterranean countries to northern Turkey; Volga River east and to Lower Baikal, Altai and Tien Shan; Iberia, Balearic Islands and North Africa; southern Asia Minor, Jordan and Israel and onto northwest Pakistan.

HABITAT

Prefers open, rather than dense, woodland, including woodland parks in towns, plantations, and scrubland.

BEHAVIOR

Northern birds are mostly migratory, while the southern birds are more sedentary. Migratory birds travel to Africa to winter. This owl is largely nocturnal, but occasionally is active during the day.



FEEDING ECOLOGY AND DIET

Mainly insectivorous; crickets and grasshoppers form much of its diet. Prey is taken by a short pounce from a perch or sometimes these owls will run after prey on the ground.

REPRODUCTIVE BIOLOGY

Nests in cavities, using tree cavities or holes in walls and old buildings. Lays two to six eggs. Incubation is generally 24–25 days. Young fledge at about 30 days and are cared for by their parents for about five weeks.

CONSERVATION STATUS

Not globally threatened, or considered rare. Locally common in parts of its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Seychelles scops-owl

Otus insularis

SUBFAMILY

Striginae, Tribe Otini

TAXONOM

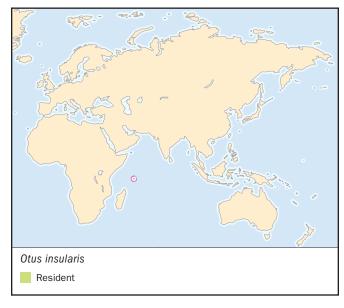
Gymnoscops insularis Tristam, 1880, Mahé Island, Seychelles. Monotypic.

OTHER COMMON NAMES

English: Bare-legged scops-owl; French: Petit-duc scieur; German: Seychelleneule; Spanish: Autillo de Seychelles.

PHYSICAL CHARACTERISTICS

7.9 in (20 cm). Weights not given. Overall color is yellowish brown or rufous. Head features minute ear tufts and the legs are bare.



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DISTRIBUTION

Mahé Island in Seychelles

HABITAT

Secondary forest on upper slopes and in valleys at elevations of 820–1,969 ft (250–600 m), usually close to water.

BEHAVIOR

Strictly nocturnal. Very little else is known.

FEEDING ECOLOGY AND DIET

Insects, tree frogs, and lizards.

REPRODUCTIVE BIOLOGY

Almost nothing known, but this owl is suspected of nesting in crevices and cavities in rocks on the ground. It may lay only one egg.

CONSERVATION STATUS

Critically Endangered. The extremely small population (estimated at 180–360 as of 2000) remains threatened by habitat destruction for housing development and forest clearance for agriculture and by introduced predators (e.g., rats, cats, etc.). Morne Seychellois National Park encompasses much of the highland forest where this species occurs.

SIGNIFICANCE TO HUMANS

None known.

Eastern screech-owl

Otus asio

SUBFAMILY

Striginae, Tribe Otini

TAXONOMY

Strix asio Linnaeus, 1758, South Carolina. Six subspecies are recognized.

OTHER COMMON NAMES

English: Common screech-owl; French: Petit-duc maculé; German: Ostkreischeule; Spanish: Autillo Yanqui.

PHYSICAL CHARACTERISTICS

6.3–9.8 in (16–25 cm). Female, 6.8 oz (194 g). Male, 5.9 oz (166 g). As with many scops-owls, there are two different color phases—a brown phase and a gray phase. Its erect ear tufts can be flattened to give the head a rounded appearance. This is probably the best known small owl in eastern North America.

DISTRIBUTION

Southern central and eastern Canada to Florida and northeastern Mexico.

HABITAT

Forest and woodlands.

BEHAVIOR

Sedentary. Hunts in open woodland probably to avoid detection by other predators. Mostly nocturnal, but also hunts at dawn and dusk and, occasionally, during the day.

FEEDING ECOLOGY AND DIET

Insects, worms, crayfish, small birds, and rodents. Makes straight perch-to-prey strikes and also hunts on the ground.



REPRODUCTIVE BIOLOGY

Cavity nester; prefers holes in trees. Clutch size is usually three to four, but may be as many as seven. Incubation is at least 26 days. Young fledge in 25–27 days, but remain dependent on the parents for eight to 10 weeks.

CONSERVATION STATUS

Not globally threatened; numbers decrease when forests are cleared.

SIGNIFICANCE TO HUMANS

None known.

Southern white-faced owl

Ptilopsis granti

SUBFAMILY

Striginae, Tribe Otini

TAXONOMY

Pisorbina leucotis granti Kollibay, 1910, Namibia. Until recently this bird was placed in the genus Otus. It is very closely related, but was shown to be different by molecular biology; it has larger eyes than Otus species. Monotypic.

OTHER COMMON NAMES

English: White-faced scops-owl, white-faced owl; French: Petit-duc de Grant; German: Südbüscheleule; Spanish: Autillo Cariblanco Sureño.

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PHYSICAL CHARACTERISTICS

8.7–9.4 in (22–24 cm). Female, 4.4–9.7 oz (125–275 g). Male, 6.5–7.8 oz (185–220 g). Head features long ear tufts, a whitish facial disc with a black rim, and orange-red to red eyes. Upperparts are darker gray with black markings. Underparts are lighter gray with thin dark streaks and lines.

DISTRIBUTION

Africa from equator on down.

HABITAT

Savanna, open woodlands, and forest edges.

BEHAVIOR

Sedentary, although it can be nomadic in drier parts of its range.

FEEDING ECOLOGY AND DIET

Large insects, small mammals, birds, and reptiles. Will hunt from perches including telegraph poles and even street lamps.

REPRODUCTIVE BIOLOGY

Uses old nests of other birds, such as pigeons, or nests in a cavity in a tree or branch. Lays two to three eggs. Incubation is 30–32 days. Young leave nest at four weeks.

CONSERVATION STATUS

Not globally threatened. Reasonably common in most of its range as of 2002.

SIGNIFICANCE TO HUMANS

None known. ◆

Great horned owl

Bubo virginianus

SUBFAMILY

Striginae, Tribe Bubonini

TAXONOMY

Strix virginiana J.F. Gmelin, 1788, Virginia. Twelve races are tentatively identified.

OTHER COMMON NAMES

French: Grand-duc d'Amérique; German: Virginiauhu; Spanish: Búho Americano.

PHYSICAL CHARACTERISTICS

20–23.6 in (51–60 cm). Female, 2.2–5.5 lb (1,000–2,500 g). Male, 1.5–3.2 lb (680–1,450 g). A large, powerful owl with a rust-colored facial disc, large, erect ear tufts, yellow eyes, and a white chin and throat. Upperparts are grayish to gray-brown,



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mottled and barred. Underparts are brownish with a reddish tinge, also mottled. The fully feathered legs and feet are buff to tawny.

DISTRIBUTION

Alaska to Hudson Bay through the United States, Mexico, and Central America; in South American from Colombia to the Guianas, Bolivia to northeastern Brazil and south to east-central Argentina.

HABITAT

Every type of woodland, farmland, desert with scrub, mountainous areas, mangroves, and urban areas.

BEHAVIOR

Mainly resident and territorial. Makes deep hooting calls to announce its presence. Hunts mostly at dusk or during the night, occasionally during the day.

FEEDING ECOLOGY AND DIET

Still hunts from a perch; makes shallow, gliding drops to its prey; very rapacious. Takes a huge variety of prey including birds as large geese, mammals (up to 90% of its diet), fish, snakes, insects, and even other owls.

REPRODUCTIVE BIOLOGY

Utilizes old nests of other large birds, or nests in hollows in trees and, sometimes, in caves or among tree roots. The breeding season varies from December to July because of this owl's wide range. It tends to breed earlier than other owls in the same locality. Lays one to three eggs. Incubation is 28–30 days. Young remain in the nest for 35–45 days and are cared for by their parents for up to five months.

CONSERVATION STATUS

Not globally threatened. It is a very common owl throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Eurasian eagle-owl

Bubo bubo

SUBFAMILY

Striginae, Tribe Bubonini

TAXONOMY

Strix bubo Linnaeus, 1758, Sweden. Fourteen subspecies are recognized.

OTHER COMMON NAMES

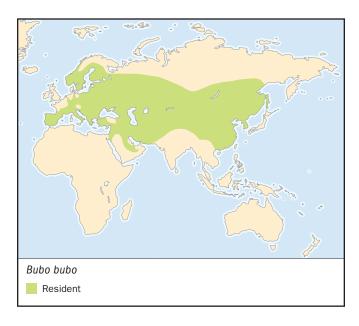
English: Common, great, or northern eagle-owl; French: Grand-duc d'Europe; German: Uhu; Spanish: Búho Real.

PHYSICAL CHARACTERISTICS

23.6–29.5 in (60–75 cm). Female, 2.2–5.5 lb (1,750–4,200 g). Male, 1.5–3.2 lb (1,500–2,800 g). The largest owl, it is almost barrel-shaped. It has prominent, erect ear tufts, golden to orange eyes, and a powerful, black beak. Legs and feet are fully feathered. The subspecies vary in size, overall color, and intensity of dark markings.

DISTRIBUTION

Europe from Spain to northern Norway and Finland on through Asia to Pacific, south to Iraq and Iran, Pakistan, and China.



HABITAT

The Eurasian eagle-owl is less able to cope with human habitation than its United States counterpart the great horned owl. It is found in more inaccessible areas—rocky terrains, wilderness, forests and woodlands, and rocky farmlands.

BEHAVIOR

This owl is territorial and mainly sedentary except in the very north of its range. It is primarily nocturnal, but is sometimes active at dawn and dusk as well. At the northern edge of its range, this owl is active during the day in summer.

FEEDING ECOLOGY AND DIET

Feeds mainly on mammals from voles to hares (hedgehogs are important in some areas), birds up to pheasant size, and occasionally diurnal birds of prey. It usually hunts from an open perch.

REPRODUCTIVE BIOLOGY

Often nests in rocky crevices and caves; will use old birds' nests, but seems to prefer the ground. Lays two to four eggs. Incubation is 34–36 days. Young fledge at 10 weeks. An average of 1.6 young are produced per successful nest.

CONSERVATION STATUS

Not globally threatened, but uncommon to rare throughout its range.

SIGNIFICANCE TO HUMANS

None known ◆

Barred eagle-owl

Bubo sumatranus

SUBFAMILY

Striginae, Tribe Bubonini

TAXONOMY

Strix sumatrana Raffles, 1822, Sumatra. Two subspecies are recognized.

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OTHER COMMON NAMES

English: Malay eagle-owl, Malaysian eagle-owl; French: Grand-duc bruyant; German: Malaienuhu; Spanish: Búho Malayo.

PHYSICAL CHARACTERISTICS

15.7–18.1 in (40–46 cm). This owl has a whitish face, dark brown, outward-directed ear tufts marked with white, and brown eyes. Upperparts are dark brown barred with rufous buff. Underparts are grayish white barred with brown. Beak and feet are yellow.

DISTRIBUTION

Southern Myanmar, peninsular Thailand, south to Sumatra and Bangka Island.

HABITAT

Evergreen and semi-evergreen forests, plantations, and even wooded gardens.

BEHAVIOR

Sedentary; territorial in nest area; nocturnal and crepuscular.

FEEDING ECOLOGY AND DIET

Large insects, small mammals, snakes, and small birds. Still hunter from a perch.

REPRODUCTIVE BIOLOGY

Usually lays one egg either in a large cavity or in and old hawk's nest. Incubation and fledging periods are not known.

CONSERVATION STATUS

Not globally threatened, this owl is reasonably common and adaptable.

SIGNIFICANCE TO HUMANS

None known. ◆

Blakiston's eagle-owl

Ruho hlakistoni

SUBFAMILY

Striginae, Tribe Bubonini

TAXONOMY

Bubo blakistoni Seebolm, 1884, Japan. Four subspecies are recognized.

OTHER COMMON NAMES

English: Blakiston's fish-owl; French: Grand-duc Blakiston; German: Riesenfischuhu; Spanish: Búho Manchú.

PHYSICAL CHARACTERISTICS

23.6–28.3 in (60–72 cm). One of the world's largest owls, it has a pale gray-brown facial disc, broad, horizontal ear tufts, yellow-orange eyes, and a white throat. Upperparts are buff-brown with darker streaks. Underparts are lighter buff-brown with thin, darker streaks. The legs are feathered almost to the base of the dark gray-brown toes.

DISTRIBUTION

Western Manchuria, eastern Siberia, far northeast China, Sakhalin Island, Hokkaido, and southern Kuril Islands.

HABITAT

Dense forests along rivers and sometimes on sea coast.

BEHAVIOR

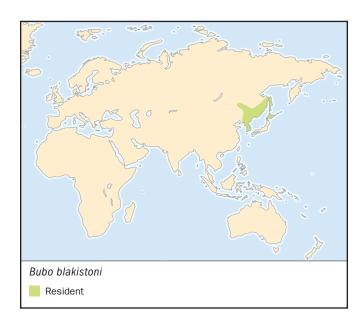
Sedentary. Highly territorial. Forages mainly at night or at dusk, but sometimes during the day.

FEEDING ECOLOGY AND DIET

Primarily fish, but also crustaceans, frogs, birds, and small mammals. Relies on areas of clear, slower moving water to hunt. Takes prey from a perched position or even wading in the water.

REPRODUCTIVE BIOLOGY

Nests in large holes in trees and broken branches, and also sometimes on the ground in tree roots or cavities. Normally lays two eggs. Incubation is 35–37 days. Young leave the nest



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at 35-40 days, but remain with their parents for several months.

CONSERVATION STATUS

Endangered. One of the world's rarest owls, its population has declined precipitously since the 1950s. Major threats include habitat destruction due to riverside development and deforestation. Depletion of the fish on which it depends for food (due to overfishing) also has a negative impact on the species. Attempts at captive breeding have been unsuccessful.

SIGNIFICANCE TO HUMANS

None known. ◆

Snowy owl

Nyctea scandiaca

SUBFAMILY

Striginae, Tribe Bubonini

TAXONOMY

Strix scandiaca Linnaeus, 1758, Lappland. Monotypic.

OTHER COMMON NAMES

English: Snow owl; French: Harfang des neiges; German Schnee-Eule; Spansih: Búho Nival.

PHYSICAL CHARACTERISTICS

21.7–27.6 in (55–70 cm). Female, 1.7–6.5 lb (780–2,950 g). Male, 1.5–5.5 lb (700–2,500 g). Heavy-bodied white owl with a large head, no ear tufts, yellow eyes, and a blackish beak nearly concealed by feathers. Males may have sparse gray or brown spots and bars. Females have more prominent dark barring, both above and below. Legs and feet are feathered.

DISTRIBUTION

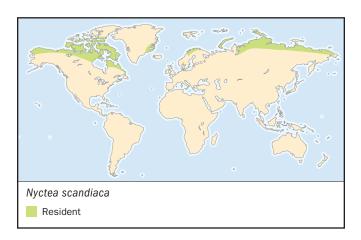
Arctic Circle.

HABITAT

Open, treeless tundra and moorlands.

BEHAVIOR

Migratory and nomadic; movements probably due to fluctuations in prey populations. It is most active at dawn and dusk; forages during the day in summer.



FEEDING ECOLOGY AND DIET

Lemmings and voles form the bulk of its diet, however, it also preys on birds (up to size of ptarmigan), mammals (up to the size of snowshoe hares), and fish. Hunts from a perch; usually captures prey on the ground after a low, gliding flight from the perch.

REPRODUCTIVE BIOLOGY

A ground nesting species that lays later in the year as spring comes later. Clutch size normally is three to five eggs, but up to 11 eggs may be laid in a year when vole or lemming populations are high. Incubation is 31–33 days. Young leave the nest at 20–28 days, but do not fly well until about 50 days.

CONSERVATION STATUS

Not globally threatened. Status of North American populations appears stable, but European populations may be declining.

SIGNIFICANCE TO HUMANS

None known. ◆

Asian brown wood-owl

Strix leptogrammica

SUBFAMILY

Striginae, Tribe Strigini

TAXONOMY

Strix leptogrammica Temminck, 1831, Borneo. Fourteen subspecies are recognized.

OTHER COMMON NAMES

English: Himalayan brown Owl, Himalayan wood-owl, Bartel's wood-owl, Malaysian wood-owl; French: Chouette leptogramme; German: Malaienkauz; Spanish: Cárabo Oriental.

PHYSICAL CHARACTERISTICS

15.7–21.7 in (40–55 cm). 17.6–24 oz (500–700 g). The owl has a whitish to light brown facial disc, brown eyes surrounded by a black band, a brown chin, and a white throat. Upperparts are



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lighter chestnut brown with some white or light bars on the shoulders, wings, and tail. Underparts are white to buff with fine brown bars (*leptogrammica* means finely barred stomach). Legs are feathered.

DISTRIBUTION

Forested areas on the west and east of India, Himalayas through to the coast of China, most of southeastern Asia including Sri Lanka, southern Thailand, Malay Peninsula, Borneo.

HABITAT

Thick, undisturbed forests both evergreen and deciduous.

BEHAVIOR

Sedentary; like most of the wood-owls it is very nocturnal and secretive.

FEEDING ECOLOGY AND DIET

Small mammals, birds (up to the size of pheasants), fruit bats, reptiles, and some insects. Still hunting from perch.

REPRODUCTIVE BIOLOGY

Nests in tree cavities, caves, and sometimes on cliff ledges. Lays two eggs. Incubation is 30–33 days.

CONSERVATION STATUS

Not globally threatened. Suffers from deforestation, but is secure in national parks and protected areas throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Tawny owl

Strix aluco

SUBFAMILY

Striginae, Tribe Strigini

TAXONOMY

Strix aluco Linnaeus, 1758, Sweden. Eleven subspecies are recognized.

OTHER COMMON NAMES

English: Eurasian tawny owl, Eurasian wood-owl, tawny wood-owl, brown owl; French: Chouette hulotte; German: Wald-kauz; Spanish: Cárabo Común.

PHYSICAL CHARACTERISTICS

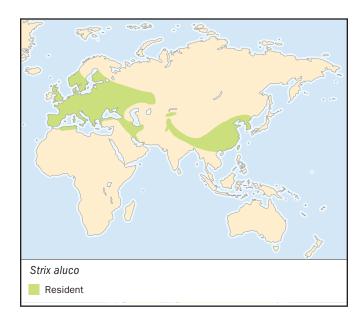
14.6–15.4 in (37–39 cm). Female, 19.5 oz (553 g). Male, 15.5 oz (440 g). Medium-sized, stocky owl with a large, round head and blackish brown eyes. Overall color varies from brown to rufous to gray with intermediates between these hues. Upperparts are mottled with darker streaks. Underparts are paler, also dark streaked with variable thin bars. Legs and most of the gray toes are feathered.

DISTRIBUTION

Great Britain except for Ireland, southern Scandinavia to North Africa through the Middle East to western Iran; Pakistan, northwest India, Nepal to southeast China and northern Indochina, Korea, and Taiwan.

HABITAT

Open forests and woodlands, farmland with woods, parks, urban areas with parks and gardens.



BEHAVIOR

Sedentary. This is a very vocal owl with wide range of calls. Chiefly nocturnal.

FEEDING ECOLOGY AND DIET

Wide variety of prey, including mammals (up to the size of squirrels and small rabbits), birds (up to the size of pigeons), amphibians, reptiles, insects, and occasionally fish. It has been known to take smaller owls. Still hunts from a perch; most prey is located by sound.

REPRODUCTIVE BIOLOGY

Generally nests in cavities, but will use old magpie nests. Mates for life. Usually lays three to five eggs, but has been known to lay up to nine. Incubation is 28–30 days. Normally two young are reared. Young fledge in 32–37 days and are independent about three months after fledging.

CONSERVATION STATUS

Not globally threatened. Common throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Spectacled owl

Pulsatrix perspicillata

SUBFAMILY

Striginae, Tribe Strigini

TAXONOMY

Strix perspicillata Latham, 1790, Cayenne. Six subspecies are recognized.

OTHER COMMON NAMES

French: Chouette à lunettes; German: Brillenkauz; Spanish: Lechuzón de Anteojos.

PHYSICAL CHARACTERISTICS

16.9-20.5 in (43-52 cm). 1.3-2.75 lb (590-1,250 g). A largish owl, it has a brown facial disc, white eyebrows and lores, and yel-

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low eyes. Head and neck are very dark blackish brown and the throat is white. The rest of the upperparts are dark brown with gray-brown bands on the flight feathers and tail. Underparts are buff with a brown breast band. Legs and toes are feathered.

DISTRIBUTION

Central America through to northeast Argentina; not found in high Andes.

HABITAT

Tropical and dry forests, scattered trees, coffee plantations, and forested streams.

BEHAVIOR

Sedentary. Nocturnal. Very vocal.

FEEDING ECOLOGY AND DIET

Mainly vertebrates, including mammals (up to the size of skunks), bats, birds, frogs, and lizards. Also takes crabs and crayfish. Hunts from a perch.

REPRODUCTIVE BIOLOGY

Cavity nester. Lays two eggs, but usually only one young survives. The chick leaves the nest in five to six weeks, but remains with the parents for up to a year after fledging. Juveniles take one to three years to develop adult plumage.

CONSERVATION STATUS

Not globally threatened. Fairly common where it is found.

SIGNIFICANCE TO HUMANS

None known.



Northern hawk-owl

Surnia ulula

SUBFAMILY

Surninae, Tribe Surniini

TAXONOMY

Strix ulula Linnaeus, 1758, Sweden. Three subspecies are recognized.

OTHER COMMON NAMES

English: Hawk owl; French: Chouette épervière; German: Sperbereule; Spanish: Cárabo Gavilán.

PHYSICAL CHARACTERISTICS

14.2–15.4 in (36–39 cm). Female, 11.3–12.2 oz (320–345 g). Male, 9.5–11.3 oz (270–320 g). This owl has a broad head, a whitish facial disc bordered with a broad black band, and yellow eyes. Upperparts are dark brownish black with white spotting. Underparts are whitish with heavy chocolate brown bars. The long tail is barred, and the legs and feet are covered with white feathers.

DISTRIBUTION

Alaska through Canada to Newfoundland; Scandinavia through to eastern China.

HABITAT

Northern forests up to the tree line, forest steppes, and some farmlands.

BEHAVIOR

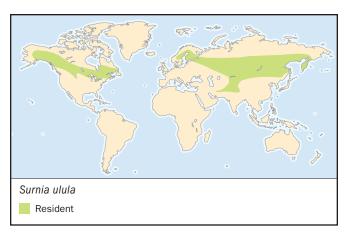
Nomadic; follows the abundance of prey species. Will winter in open land and use farm haystacks as hunting perches. Diurnal and nocturnal.

FEEDING ECOLOGY AND DIET

Prey consists of small mammals (including voles, lemmings, and even young hares), birds, insects, and amphibians. Hunts from a perch; will take birds from the air; hovers well; will take prey under snow, locating it by sound alone.

REPRODUCTIVE BIOLOGY

Nests in tree cavities or on the tops of broken stumps. Lays six to ten eggs, up to thirteen in good vole years. Incubation is 25–30 days. Young fledge at 25–35 days. Parents will try to distract predators by disabled display to draw attention away from young. Young become independent at about 75 days.



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CONSERVATION STATUS

Not globally threatened. As with many of the species reliant on fluctuations in prey numbers, this owl's numbers rise and fall accordingly.

SIGNIFICANCE TO HUMANS

None known. ◆

Pearl-spotted owlet

Glaucidium perlatum

SUBFAMILY

Surninae, Tribe Surniini

TAXONOMY

Strix perlatum Vieillot, 1817, Senegal. Two subspecies are recognized.

OTHER COMMON NAMES

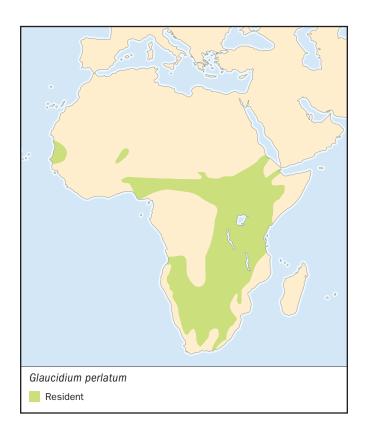
English: Pearl-spotted owl; French: Chevêchette perlée; German: Perlkauz; Spanish: Mochelo Perlado.

PHYSICAL CHARACTERISTICS

6.7–7.9 in (17–20 cm). Female, 2.2–5.2 oz (61–147 g). Male, 1.3–3 oz (36–86 g). A small owl with a cinnamon head, whitish facial disc, white eyebrows, and yellow eyes. Upperparts are cinnamon with white spots; flight feathers are dark brown with reddish bars. Underparts are white with broad brown streaks. The longish tail is brown with incomplete white bars.

DISTRIBUTION

Gambia to Sudan, Ethiopia, Uganda to north and east South Africa, Angola, and Namibia.



HABITAT

Bushveld, open and dense woodlands, and grasslands.

BEHAVIOR

Sedentary. Territorial throughout the year. An energetic hunter that takes prey considerably larger than itself at times. Hunts chiefly at night, but is the most diurnal African owl, especially in winter. False white "eye" patches on backs of wings may act as a deterrent to predators.

FEEDING ECOLOGY AND DIET

Many insects, arthropods, small mammals, birds (up to the size of doves), lizards, and bats. Hunts from perch and will chase birds in flight.

REPRODUCTIVE BIOLOGY

Cavity nester, especially using old nests of barbets or wood-peckers. Normally lays three eggs. Incubation is about 29 days. Usually rears one or two young. Young fledge in about 31 days.

CONSERVATION STATUS

Not globally threatened. Widespread and locally common.

SIGNIFICANCE TO HUMANS

None known. ◆

Burrowing owl

Athene cunicularia

SUBFAMILY

Surninae, Tribe Surniini

TAXONOMY

Strix cunicularia Molina, 1782, Chile. Nineteen subspecies are recognized.

OTHER COMMON NAMES

French: Chevêche des terriers; German: Kaninchenkauz; Spanish: Mochelo de Madriguera.

PHYSICAL CHARACTERISTICS

7.5–9.8 in (19–25 cm). Female, 4.2–8.8 oz (120–250 g). Male, 4.6–6.5 oz (130–185 g). This owl has a round head with an oval, buff to white facial ruff, yellow eyes, and a white chin and throat. Upperparts are brown with buff to white spots on the crown of the head, back, and shoulders. Underparts are buff to white with brown bars. The tail is short and the long legs are covered with white to buff feathers.

DISTRIBUTION

Southwest Canada to El Salvador, Florida, Bahamas, Cuba, and Isle of Pines; Venezuela, Colombia, Ecuador, Bolivia, southern Brazil to Tierra del Fuego.

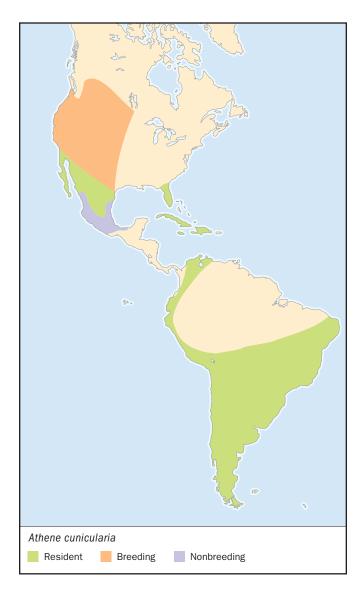
HABITAT

Arid, dry, open plains, deserts, savanna, farmlands, roadsides, and golf courses.

BEHAVIOR

Very active during the day. Lives in loose colonies. Sentries give alarm calls if predators are seen. Uses burrows for roosting and hiding as well as breeding. Northern races migrate south, southern races are sedentary.

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FEEDING ECOLOGY AND DIET

Mainly insects, also small mammals and small birds. Hunts on the ground, running and hopping after insects. Also will hover over tall grass cover and will take prey in flight on occasion.

REPRODUCTIVE BIOLOGY

Nests underground; will dig its own burrow or use the burrow of ground-dwelling mammals. Lays six to 11 eggs. Incubation is 28–30 days. Young fledge after about 44 days. First breeding at one year of age.

CONSERVATION STATUS

Not globally threatened, although listed as Endangered in some northern United States and some Canadian provinces. Declining over some parts of its range and expanding over others.

SIGNIFICANCE TO HUMANS

None known. ◆

Northern saw-whet owl

Aegolius acadicus

SUBFAMILY

Surniinae, Tribe Aegoliini

TAXONOMY

Strix acadica J.F. Gmelin, 1788, Nova Scotia. Two subspecies are recognized.

OTHER COMMON NAMES

English: Saw-whet owl, Queen Charlotte owl; French: Petite Nyctale; German: Sägekauz; Spanish: Mochuelo Cabezón.

PHYSICAL CHARACTERISTICS

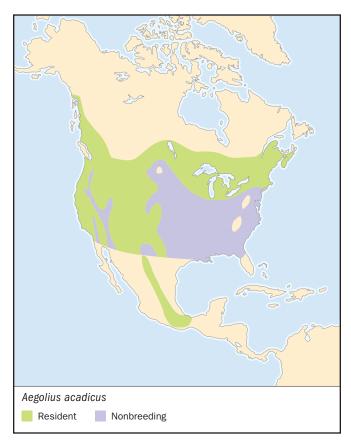
7.1–8.7 in (18–22 cm). Female, 3.5 oz (100 g). Male, 2.6 oz (75 g). One of the smallest owls, it has a large, round head with a buff to brownish facial disc, white eyebrows, and a white patch between the yellow to golden eyes. Forehead and crown of head are brown with white streaks. Upperparts are brown with white or buff spots on the nape of the neck, shoulders, and wing-coverts. Underparts are white tinged with buff and spotted or streaked with reddish brown. The short legs are heavily feathered to the talons.

DISTRIBUTION

Southern Alaska to southern United States through to eastern Canada down to northern Florida. Also a strip through the highlands of California and Mexico.

HABITAT

Forests; typically prefers coniferous forests.



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BEHAVIOR

Nocturnal, but occasionally may forage during the day. Migrates south to winter, although some birds are present in the breeding range all year round. The call of the male during mating season sounds like a saw being sharpened, giving the species its common name.

FEEDING ECOLOGY AND DIET

Mainly small mammals, especially mice and voles, some small birds, and insects. Hunts from a perch; locates prey using acute hearing and low-light vision.

REPRODUCTIVE BIOLOGY

Nests in cavities, such as old woodpecker holes. Lays five to seven eggs. Incubation is 27–29 days. There is some evidence of polyandry in good vole years.

CONSERVATION STATUS

Not globally threatened. Populations are stable, but vulnerable to reduction with loss of habitat.

SIGNIFICANCE TO HUMANS

None known. ◆

Southern boobook owl

Ninox boobook

SUBFAMILY

Surniinae, Tribe Ninoxini

TAXONOMY

Strix boobook Latham, 1801, Sydney area, New South Wales. Tentatively, ten subspecies are recognized.

OTHER COMMON NAMES

English: Boobook owl, streaked boobook, northern boobook, Australian boobook, red boobook, dark boobook owl; French: Ninoxe d'Australie; German: Boobookkauz; Spanish: Nînox Australiano.

PHYSICAL CHARACTERISTICS

9.8–14.2 in (25–36 cm). Female, 11.1 oz (315 g). Male, 8.8 oz (250 g). This owl takes its name for its most common call, a repeated double hoot that sounds like "boo-book." It has a round head with an indistinct facial disc, white eyebrows, and eyes that vary in color from yellow to hazel. Upperparts are dark brown with white spots. Underparts are whitish with reddish brown streaks and spots.

DISTRIBUTION

Australia, southern New Guinea, Roti, Timor, Alor, Let, Moa, Babar, and Kai Islands.

HABITAT

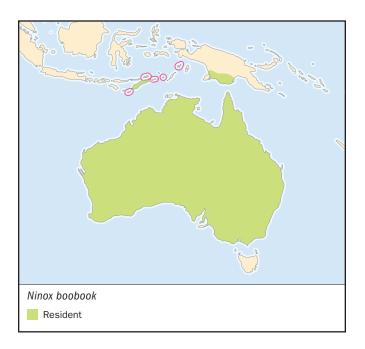
Very varied habitat, including dry and wet forests, semi-arid deserts, and farmlands.

BEHAVIOR

Mainly sedentary. The most southern races may winter farther north. Largely nocturnal, but partly crepuscular.

FEEDING ECOLOGY AND DIET

Mainly insectivorous, but also takes small birds, mammals, reptiles, and bats, especially during the breeding season. Hunts from a perch in forest clearings and edges.



REPRODUCTIVE BIOLOGY

Nests in cavities, both natural and in man-made structures. Lays three to five eggs. Incubation is about 30 days. Chicks fledge at about five weeks. Young stay with parents for up to three months after fledging.

CONSERVATION STATUS

Not globally threatened. Widespread and generally common throughout most of its range, but vulnerable to habitat destruction that destroys preferred nesting sites in tree hollows.

SIGNIFICANCE TO HUMANS

None known. ◆

Short-eared owl

Asio flammeus

SUBFAMILY

Asioninae

TAXONOMY

Strix flammea Pontoppidan, 1763, Denmark. Ten subspecies are recognized.

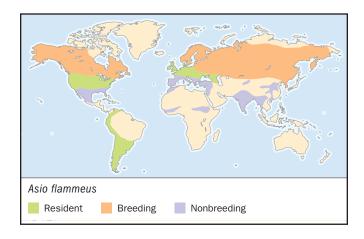
OTHER COMMON NAMES

French: Hibou des marais; German: Sumpfohreule; Spanish: Búho Campestre.

PHYSICAL CHARACTERISTICS

14.6–15.4 in (37–39 cm). Female, 9.9–17.6 oz (280–500 g). Male, 7.1–15.9 oz (200–450 g). Huge range gives wide differences in size. A medium-sized owl with a large, round head and very small ear tufts that are hard to see. Round, grayish white facial disc, white chin, and white, brown, and buff facial ruff and forehead. The yellow eyes are surrounded by black. Upperparts are brown and buff. Underparts are whitish to pale buff with vertical streaks. Large, buff wing patches on the up-

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per wings and dark wrist markings on the underwings. Feet and legs are whitish buff.

DISTRIBUTION

Canada and United States; northeast Venezuela, Guyana, Colombia, Ecuador, southern Peru, west-central Bolivia, Paraguay, and southeastern Brazil to Tierra del Fuego; Iceland, England, Europe below the tree line through Asia to Russia and China. Winters in India, Southeast Asia, southern China, and parts of Africa.

HABITAT

Marsh lands and grasslands, open areas, tundra, and moorland.

BEHAVIOR

Diurnal, crepuscular, and nocturnal. Very migratory. These birds are seen throughout the year in the southern part of the breeding range, although they may not be the same birds. Breeding areas are reliant on a good prey base. This owl will winter in groups and roost on the ground or in low trees.

FEEDING ECOLOGY AND DIET

One of the most aerial hunters, its light wing-loading allows this owl to hunt by quartering the ground in low-level flight seeking prey. Preys on small mammals, including mice, voles, shrews, moles and even young rabbits and hares; also small birds less frequently.

REPRODUCTIVE BIOLOGY

Males display to females with dramatic flights, aerobatics, and clapping of wings. This owl nests on the ground in cover—grasses, heather, reeds; some line the nest with grass and feathers, making this one of the very few owls to attempt any form of nest building. Lays five to 10 eggs. Increased clutch sizes in vole and lemming years. Incubation is 26–29 days. Young leave the nest before they can fly at about 12–18 days and hide in vegetation.

CONSERVATION STATUS

Not globally threatened, but probably declining slowly due to drainage of wetlands, human encroachment and disturbance. This owl occurs in a number of protected areas throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

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Jemima Parry-Jones, MBE Christine Jeryan, MLS

Caprimulgiformes (Nightjars)

Class Aves

Order Caprimulgiformes

Number of families 5

Number of genera, species 24 genera, 105 species

Photo: Tawny frogmouth (Podargus strigoides) pair in Queensland, Australia. (Photo by Jen & Des Bartlett. Bruce Coleman Inc. Reproduced by permission.)



Evolution and systematics

Anatomical and biochemical data suggest owls (Strigiformes) are the closest relatives of the Caprimulgiformes, with swifts (Apodiformes) and trogons (Trogoniformes) as more distant relatives. The oldest fossils of Caprimulgiformes are from the Eocene to Oligocene around 55-35 million years ago (mya), by which time representatives of the oilbirds (Steatornithidae), owlet-nightjars (Aegothelidae), frogmouths (Podargidae), potoos (Nyctibiidae), and true nightjars (Caprimulgidae) had emerged, along with several species of the long-extinct caprimulgiform family Archaeotrogonidae.

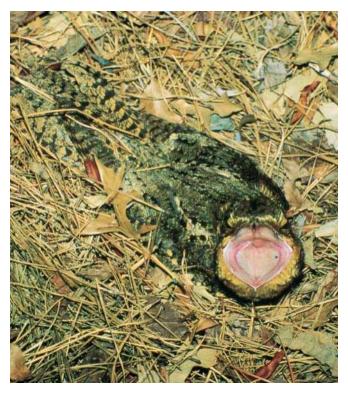
Inferences from the fossil record coupled with evidence from rates of DNA evolution suggest the initial divergence of these families from a common ancestor of all Caprimulgiformes occurred between the end of the Cretaceous around 65 mya and the middle Eocene (50.5-42.0 mya). Eocene or Oligocene fossils of most of these caprimulgiform families are known from Europe (although owlet nightjars and oilbirds are only tentatively identified), pointing to much wider geographical ranges for many of them in the past than at present because modern oilbirds and potoos are exclusively South and Central American, modern frogmouths are restricted to Asia and Australasia, and modern owlet nightjars are found only in Australasia.

Some doubt remains about the sequence in which the five living families of Caprimulgiformes diverged from each other. Recognition of two suborders, Steatornithi for the oilbird and Caprimulgi for all the others, implies that the oilbirds were the oldest group to diverge and that the ecology (fruiteating) and behavior (echolocation) of the living oilbird are so unique that they easily suggest ancient origins. However, DNA-hybridization evidence and some anatomical features suggest the owlet nightjars diverged from an ancestral caprimulgiform stock earlier than the oilbirds, especially because owlet nightjars have several owl-like features, including a well-developed facial disk. The three remaining families, the frogmouths, potoos, and true nightjars are all well-defined groups but apparently rather closely interrelated. Two of these families are divided into subfamilies, the frogmouths into an Asian group (Batrachostominae) and an Australasian group (Podarginae), the true nightjars into nighthawks (Chordeilinae) and nightjars (Caprimulginae).

Physical characteristics

Caprimulgiformes are small to rather large nocturnal birds (0.7-23.6 oz; 20-670 g), all of which have relatively large heads with large eyes, a wide to very wide gape, and very short legs. The bill is small and weak in nightjars, nighthawks, and potoos; not much stronger in owlet nightjars; relatively strong in the oilbird; but stout and wide in the appropriately named frogmouths. Strong rictal bristles (specialized feathers with elongated, tapering shafts and sometimes short barbs that surround a bird's mouth) occur at the base of the bill in many of the species, often accompanied by other facial bristles. However, within the Caprimulgidae the absence of rictal bristles is the main character distinguishing the nighthawk subfamily Chordeilinae from the nightjars of the Caprimulginae; most potoos also lack rictal bristles. Many forest-living

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A large, wide mouth is typical of the Caprimulgiformes, as shown in this chuck-will's-widow (*Caprimulgus carolinensis*). (Photo by R. & A. Simpson/VIREO. Reproduced by permission.)

Caprimulgiformes that feed by sallying from perches have short, rounded wings, but nightjars and nighthawks that feed in more sustained flights bear wings that are long and pointed, as does the strong-flying oilbird. The tail varies from short to long, with a rounded tip in most Caprimulgiformes but square or notched in some Caprimulgidae. Males of a few true nightjar species have wing feathers (innermost secondaries) or tail feathers that have been greatly modified as display plumes. Feet of Caprimulgiformes have four usually slender toes with the hallux (first toe) variously pointing forward, outward, or backward. A pectinate middle claw that is serrated or bears projections like the teeth of a comb occurs only in Caprimulgidae.

Like baby owls, Caprimulgiformes young hatch with a covering of soft down feathers. In the oilbirds, frogmouths, and owlet-nightjars, the first down is pale or white and succeeded by a second down plumage that is usually darker. In potoos and nightjars, however, the first down is often dark or patterned and is replaced directly by juvenal true feathers, which mainly resemble those of the adults in structure and coloration. Adult plumages of most species are marked in subdued shades of brown, gray, buff, rufous (rust-colored), or black, which provide beautifully elaborate concealing coloration. The wing and tail feathers are mainly dark or black, but in nightjars and nighthawks, signal markings are commonly hidden within them and consist of contrasting white, buff, or cinnamon patches that are revealed only when the wings or tail are spread.

Distribution

Caprimulgiformes are absent only from the Arctic, Antarctic, and sub-Antarctic and from most oceanic islands. They are most common in the tropics and subtropics, as expected for birds that mainly rely on large insect prey. Fossil records indicate the modern ranges of most of the families have contracted since the early Tertiary period, when subtropical forests were more widespread than today and included much of Europe and North America.

The oilbird has a modern range largely restricted to tropical South America; the potoos are also Neotropical with northern limits in Mexico, Hispaniola, and Jamaica and southern range limits in Uruguay. Owlet-nightjars have an Australasian range, from the northern Moluccas and New Guinea through Australia to Tasmania. The frogmouths include an Asian subfamily that ranges from southern India and Sri Lanka to Vietnam and southward to Java and the Philippines and an Australasian subfamily that ranges from New Guinea and the northern Solomon Islands through Australia to Tasmania. Only the Caprimulgidae has a nearly worldwide range, which spans from Canada to Argentina and northern Chile in the Americas; and, in the Old World, from Ireland, Scandinavia, and Siberia to South Africa, Sri Lanka, and through the East Indies to Australia and Tasmania, including most large islands. Of its two subfamilies, the Caprimulginae occupies almost all of this wide area, whereas the Chordeilinae are mainly American, with representatives that are tentatively classified alongside them from tropical Africa (brown nightjar Veles binotatus) and ranging from southern Asia to Australia (genus Eurostopodus).

Habitat

The ancestral habitat of Caprimulgiformes was apparently in tropical lowland forests, which still form the main habitat of the oilbird, owlet-nightjars, potoos, and frogmouths. At least a few of the species of the latter three families have extended into more open woodlands, savannas with trees, or scrub. Nevertheless, species of all these groups still rely heavily on trees, for food in the case of the oilbird and for perches and nest sites in the case of the others. Only the Caprimulgidae has occupied more open habitats, with many species inhabiting savannas and open woodlands, although some occupy grasslands or even semi-deserts and a few are restricted to closed forests.

Behavior

Although details of behavior of many of these secretive nocturnal birds are little known, at least one or a few species of each family have been studied sufficiently to allow generalizations that should apply more widely. Thus it is clear that most species are monogamous. The pair bond may be sustained with the birds living together in a territory for several years in succession (in tawny frogmouth *Podargus strigoides*) or the pairbond may be maintained only for one breeding season (European nightjar *C. europaeus*). Two African nightjars, in which the breeding males develop elaborate display plumes, are exceptional in being polygynous (mating with more than

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one female) (standard-winged nightjar *Macrodipteryx longipennis*, pennant-winged nightjar *M. vexillarius*). With these two species, the displaying males are visited by females to mate, after which the female alone is responsible for nesting and care of the young. A similar system apparently prevails with three South American nightjars (genus *Macropsalis*), in which males have elaborately elongated tail feathers.

Just as darkness hinders human observers watching nocturnal birds, it also limits the scope for visual display and communication among the birds themselves. Many Caprimulgiformes have therefore developed white or pale patches that can be exposed as effective signals in low light; these signal markings are often surrounded or contrasted with darker areas similar to the bold coloration in the American striped skunk (*Mephitis mephitis*). Movement also emphasizes the signal markings, such as when the bold white patches in the outer primaries and on outer tail feathers of male European nightjars are shown off in territorial display flights and their bold white throat patches are exposed as the head is lifted to give territorial songs. However, all these conspicuous markings can be hidden from predators during the day.

Sounds are much more effective than vision for communication at night, therefore it is perhaps unsurprising that many Caprimulgiformes appear to lack elaborate visual displays and to rely instead on vocalizations. Indeed, so far as known, all caprimulgiform species give distinctive calls or songs. In many cases, these provide the best means of detecting the birds' presence, and many are among the most beautiful, unusual, and distinctive of all bird sounds (e.g., the call giving rise to the mnemonic "Good Lord deliver us" of the African fiery-necked nightjar C. pectoralis); many are also well-known to local people (e.g., the onomatopeic, echoing, calls of the whip-poor-will C. vociferus). However, a few are monotonous drumming or hammering sounds (e.g., the monotonously repeated t-chop, t-chop, t-chop of the large-tailed nightjar C. macrurus) while a few are harsh or raucous (e.g., the loud guttural snoring of the great potoo Nyctibius grandis).

The nocturnal calls of many Caprimulgiformes undoubtedly function in advertisement or defense of territories because playback of recordings commonly results in a "song-duel" that may be accompanied or followed by rapid approach and aggressive displays. Tawny frogmouths are known to spend the whole year as pairs in well-defended territories, whereas some nightjars only advertise and defend territories for the duration of one breeding attempt. The territories of these birds not only provide much or all of the food for their owners, they also provide nesting and roosting sites, and presumably freedom from interference by conspecifics that might include illicit mating attempts. A few species are known to have territories of much more restricted extent, reduced in the colonial-nesting oilbird to the immediate vicinity of the nest. Since up to 10 male standard-winged nightjars may assemble to sing and display at a lek, which is visited by females, the territory in this species also must presumably be greatly reduced or absent.

The frogmouths, owlet-nightjars, and potoos that live year-round in the same territory appear to be among the most sedentary of all birds, with few or no records of extra-limital



A great potoo (*Nyctibius grandis*) in Venezuela. (Photo by Erwin & Peggy Bauer. Bruce Coleman Inc. Reproduced by permission.)

vagrancy. In contrast to these, some nightjars and nighthawks are long-distance migrants, and many others make shorter seasonal movements. Extreme examples of long-distance migration are provided by the European nightjar, which breeds widely across Europe and Siberia but vacates all of this area to spend the northern winter in Africa south of the Sahara, and the common nighthawk (*Chordeiles minor*), which breeds widely in North America north to southern Canada and winters in South America south to northern Argentina. Among many examples of shorter migrations, one of the best understood is with the pennant-winged nightjar, which breeds in savannas of Africa south of the equator but migrates to spend the nonbreeding season in the savannas north of the equator. Others, such as the standard-winged nightjar, move seasonally from one vegetation zone to another.

Activity patterns

Because so much of the activity of Caprimulgiformes occurs under cover of darkness, it was difficult to identify the birds' activity patterns until miniaturized radio-transmitters and other devices were used by researchers. It has, however,

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long been clear that all species of the order normally roost during the day, moving only when disturbed. Their activity commences at dusk and continues at least intermittently through the night until shortly before dawn. There often appear to be peaks in singing and other activity soon after dusk and before dawn, with less activity in the middle of the night. This crepuscular and nocturnal feeding undoubtedly gives these specialized birds access to much larger numbers of flying insect prey than are available during the day. Furthermore, potential predators such as hawks are inactive at night, although there is still a risk from owls. Radio-tracking studies tend to confirm that activity levels really are low in the middle of the night, when light levels may be too low for the birds to feed. However, at least some species show more activity throughout the night on moonlit nights, when feeding is presumably possible.

Several nightjar species have been shown to synchronize egg-laying with the phases of the moon, this having been demonstrated with the fiery-necked nightjar in Zimbabwe and the whip-poor-will in North America. The potential advantage of synchronizing egg-laying with a full moon is that better feeding conditions on moonlit nights will recur one month later when young are being fed by the parents and two months later when fledglings are beginning to feed themselves. It has been demonstrated that whip-poor-wills feed their young more often on moonlit nights than on dark nights.

The demonstration in 1948 that the common poorwill *Phalaenoptilus nuttallii* of the American Southwest hibernates in rock cavities astounded biologists. It has since been established that they may be dormant for months at a time during the winter, although they can become active briefly on warm days. When hibernating, the body temperature is reduced and the heart-rate is slowed, much as in hibernating mammals. The winter dormancy of the common poorwill allows it to survive through the months when there are few, if any, flying insects. Regular use of dormancy for much shorter periods of hours rather than weeks in order to survive cool conditions has been demonstrated in the common nighthawk, European nightjar, tawny frogmouth, and Australian owlet nightjar *Aegotheles cristatus*, therefore it appears widespread in the order.

Feeding ecology and diet

The oilbird feeds on fruits taken at night from forest trees. All other Caprimulgiformes feed largely or entirely on arthropods, mainly insects but also including spiders and sometimes millipedes. The larger species of frogmouths and potoos and the largest nightjar (Chuck-will's-widow *C. carolinensis*) also take a proportion of small vertebrates, such as frogs, small birds, bats, or mice.

The most widespread feeding technique in the order consists of sallying flights from a perch to capture prey on the ground, on vegetation, or in flight. Some species, such as the larger frogmouths, use this technique mainly to capture prey on the ground, while others, such as the potoos, rarely, if ever, visit the ground. However, many nightjars are more versatile. Many of the longer-winged species of nightjar and most

nighthawks feed on insects captured on more continuous hawking flights, often high above the ground.

Reproductive biology

The extent to which nests are built varies widely among the Caprimulgiformes. Australasian frogmouths build a small platform like a pigeon's nest; Asian frogmouths build a neat but tiny nest cup; the oilbird makes a rough cup on a ledge; owlet-nightjars accumulate at least a pad of material in the bottom of the nest hole. In contrast, no nest at all is built by the potoos, which lay in a crevice of a branch or stump, or by any of the nightjars or nighthawks, which nest on the ground, rarely in a crevice of a branch. In North America, the common nighthawk commonly nests on graveled roof tops.

Eggs are an unmarked white in oilbirds, frogmouths, and owlet-nightjars but somewhat spotted in potoos. A few of the nightjars and nighthawks have unmarked white eggs, but many species have them richly patterned with spots, blotches, or lines. The eggs of some, such as the Chuck-will's-widow, have a layer of calcium deposited after pigment has been deposited on the egg, giving them a "creamy" mottled appearance. Clutches are comprised of a single egg in all potoos, some small frogmouths, and many tropical nightjars; of two eggs in other nightiars and a few small frogmouths; but regularly of up to four eggs in oilbirds, tawny frogmouths, and Australian owlet-nightjars. The degree to which the sexes care for eggs and young varies widely in the order, from being a concern only of the female in the pennant-winged nightjar, to a fairly equal sharing in oilbirds, to incubation predominantly by the male with young fed by both sexes in frogmouths.

Conservation status

Eight species of Caprimulgiformes are listed by the IUCN as globally threatened, of which three are Critically Endangered (Jamaican poorwill Siphonorhis americana, Puerto Rican nightjar C. noctitherus, New Caledonian owlet-nightjar Aegotheles savesi), two are Endangered (white-winged nightjar C. candicans, Itombwe nightjar C. prigoginei), and three are Vulnerable (Heinrich's nightjar Eurostopodus diabolicus, Nechisar nightjar C. solala, Bonaparte's nightjar C. concretus). Several additional species are listed as Near Threatened or Data Deficient.

Significance to humans

Most species of the order are retiring nocturnal birds that are noticed only by their calls, if at all. A few, such as the whip-poor-will, large-tailed nightjar, and several potoos, have well-known voices, but calls of many others are regularly muddled with sounds from owls or nocturnal mammals. Voices of some are the subject of folklore and superstitions. How caprimulgiforms obtained their common names is also the stuff of legend and folklore. The ancient belief, dating to Aristotle's time, that the birds flew at dusk and sought out she-goats and cows to suck dry of milk, eventually killing them, gave rise to the name "goatsucker". The name "night-

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jar" undoubtedly has its origins in the loud, churring call made by the European nightjar that lasts several minutes and "jars one in the night." None of the species is of much economic significance, although nestling oilbirds were formerly collected for oil and several of their large colonies are nowadays significant as tourist attractions.

Resources

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David T. Holyoak, PhD

Oilbirds

(Steatornithidae)

Class Aves

Order Caprimulgiformes Suborder Steatornithes Family Steatornithidae

Thumbnail description

Medium-sized birds, rather like nightjars but with a sharply hooked bill; nocturnal, feed only on fruit; breed and roost gregariously in caves; navigate by echolocation; long development period, fatty young

Size

17-19 in (43-49 cm); 0.8-1 lb (375-455 g)

Number of genera, species

1 genus; 1 species

Habitat

Low and montane primary forests mainly along mountains; require existence of large caves or gorges for roosting and breeding

Conservation status

Not threatened



Distribution

Largely restricted to South America, from Guyana, Trinidad, and Venezuela in the north, south along the Andes of Colombia, Ecuador, Peru, and Bolivia; northern Brazil, near Venezuelan border

Evolution and systematics

The Steatornithidae is a monotypic family found only in South America. The family's sole member, the oilbird (Steatornis caripensis Humboldt, 1817), is unique among members of the order Caprimulgiformes because it feeds only on fruit, nests and roosts colonially in caves, and echolocates. Nevertheless, oilbirds are recognizably nightjar-like, and their anatomy and the structure of their egg albumin and DNA confirm their phylogenetic affinity to other species of the order. Researcher David Snow proposed that oilbirds evolved from nocturnal or crepuscular insectivorous ancestors that benefited from social feeding because of the patchy distribution of fruiting forest trees. He theorized that because nestling fruit-eating birds develop slowly, predation pressure led to seeking safer, deeper recesses; the perfection of echolocation allowed the birds to occupy the deepest caves.

Reconstruction of such a sequence of events is unlikely because the fossil record of the family is fragmentary. However, two nearly complete fossil skeletons of early Steatornithidae from the early Eocene Green River Formation of Wyoming

in the United States provide important evidence of the evolutionary origins of oilbirds. These extinct oilbirds (*Prefica nivea*) lived about 50 mya when the climate of western North America was subtropical and its landscape was similar to that of present day Neotropical savanna-woodland. The evidence suggests that the transition to fruit eating had taken place or was in the process of evolving by the early Eocene and that the lineage leading to *Steatornis* has been feeding on essentially the same specialized fruit diet for nearly 50 million years. In agreement with Snow's scenario, *P. nivea* was not yet adapted to cave life.

Oilbirds seem to be the extreme product of a limited offshoot that arose near the base of the caprimulgiform radiation. At the family level, the Steatonithidae should be regarded as a relict in South America rather than as an autochthonous endemic (a native that originated there).

Mitochondrial DNA analysis indicates that there is reduced genetic diversity among oilbird populations in Venezuela, possibly because the species has gone through a bottleneck. Alexander von Humboldt described oilbirds after

Family: Oilbirds Vol. 9: Birds II



Oilbird (Steatornis caripensis). (Illustration by Emily Damstra)

a visit, in 1799, to the now famous Cueva del Guácharo, near Caripe in northeastern Venezuela (hence its Latin name, *caripensis*). In Spanish, the common name for oilbirds is Guácharo.

Physical characteristics

Oilbirds have a hawk-like head with a strongly hooked bill but the body resembles that of a nightjar. Total length is 17–19 in (43–49 cm) and the wingspan is about 37.5 in (95 cm). Adult body mass is 0.8–1 lb (375–455 g). The plumage is rusty brown speckled with white dots. The wings are long, broad, and highly slotted and the wing-load is low, which allows birds to fly slowly in caves and to carry large loads. The tail is long and faintly barred black. At rest, the tail feathers form a tent-like inverted V, with the central feathers held higher and the outer feathers held lower. The legs are short and placed far forward so that at rest the head is held lower than the tail. As in other Caprimulgiformes, vibrissae (bristles on each side of the bill) are well developed. Plumage dimorphism is subtle, but males are slightly larger than females. Oilbirds do not cling to rock faces.

Distribution

Oilbirds are largely restricted to South America. They are locally distributed from Guyana, Trinidad, and Venezuela in the north, and along the Andes south through Colombia, Ecuador, Peru, and Bolivia. Oilbirds also inhabit northern Brazil on table-top tepuy mountains near the Venezuelan border. Wandering individuals have been recorded in Central America and on some Caribbean islands.

Habitat

Oilbirds inhabit evergreen lowland and montane forests. They require large expanses of forest where ripe fruit is available year round and nearby caves or gorges where they can nest and roost. They have an exceptionally broad altitudinal range that extends from sea caves to over 10,500 ft (3,200 m) in the Andes.

Behavior

Oilbirds are the only nocturnal fruit-eating birds in the world. They roost and nest colonially in caves in which they navigate by echolocation. Oilbirds are strongly gregarious, and thousands of birds can inhabit a single cave. Some of the

largest colonies in Venezuela may each have an estimated 10,000 birds.

Oilbirds spend the day sitting quietly on their nests or perched on ledges of a rock wall. Shortly before dusk they awaken and become noisy and restless until the darkness of night settles over the forest. Then they leave the caves to feed, and they seem to forage in groups.

Oilbirds can navigate in total darkness by echolocation. They utter echolocating clicks with a bilaterally asymmetrical bronchial (not tracheobronchial) syrinx (or vocal organ). Most of the acoustic energy of clicks lies between 1 and 15 kHz, which is almost entirely within the audible human range. Clicks typically last 40 to 80 ms and are produced at a rate of up to 10–12 per second. The frequency of clicks depends on a bird's proximity to obstacles, with the frequency increasing as the bird approaches the obstacle. Because oilbirds use low frequencies for echolocation, their sonar system is crude compared to those of many insectivorous bats. Among birds, oilbirds' ability to echolocate is shared only with some paleotropical swiftlets. In addition to echolocating clicks, oilbirds emit various harsh contact calls and high-intensity agonistic squawk-like vocalizations.

Feeding ecology and diet

Oilbirds are entirely frugivorous (fruit eating); adults and nestlings feed on fruit pulp only. They feed almost exclusively on the fruits of trees belonging to three plant families: Lauraceae (the avocado family), Arecaceae (palms), and Burseraceae. Oilbirds do not use their clicking echolocating call when foraging; instead, they seem to rely on their keen nocturnal vision and possibly on their sense of smell.

Oilbirds grab fruits on the wing and swallow them whole. After stripping the nutritious fleshy pulp they regurgitate seeds intact. Fruits are also fed whole to nestlings. The pulp of most fruit consumed by oilbirds is rich in fats and conse-



Oilbirds (*Steatornis caripensis*) nesting in their cave in Arima Valley, Trinidad. (Photo by John J. Bamgma. Photo Researchers, Inc. Reproduced by permission.)

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Oilbirds (*Steatornis caripensis*) navigate by echolocation in the caves in which they live. (Photo by Jan Lindblad. Photo Researchers, Inc. Reproduced by permission.)

quently in energy. The Lauraceae eaten by oilbirds in Venezuela average about 50% fat and 32 kJ per dry gram. Such a high-energy food allows oilbirds to forage over vast expanses of forest. During the nonbreeding season when most laurel fruit becomes scarce, birds fitted with radio harnesses in Venezuela have been recorded foraging over 70 mi (110 km) away from their daytime roosting cave. They also migrate seasonally between caves.

Reproductive biology

Oilbirds spend most of the day in pairs, even when they are not nesting; apparently they are monogamous and form permanent pair bonds. Pairs fiercely defend their nest but tolerate other established pairs even within bill distance.

Oilbirds typically build their nest on ledges 33–66 ft (10–20 m) above the cave floor, although researchers have seen them nesting on the ground in Andean caves. The nest is a cylindrical mound about 16 in (40 cm) in diameter made of regurgitated plant fiber compacted into a firm paste. Two to four white eggs are laid at intervals of two to five days. Both adults share in incubation, brooding, and feeding of the young. Incubation lasts 32–35 days and begins when the first egg is laid.

Newly hatched chicks (0.4–0.5 oz; 12–15.5 g) bear an egg tooth, are pinkish, are almost completely naked, and their eyes are closed. Chicks grow very slowly, leaving the nest when they are between 110 and 120 days old. By day 70, nestlings have an appearance similar to that of adults, except that the tail and wings are shorter. At this point they reach a peak weight of about 1.3 lb (600 g), nearly 50% above average adult weight (14.5 oz; 410 g). Afterwards, they are fed at a slower rate and lose weight until reaching adult mass at fledging. Such an unusual pattern of weight change seems to be related to oilbirds' frugivorous habits. Fruits eaten by oilbirds have a low protein-to-energy ratio, and it is presumed that to meet their protein requirements, nestlings must ingest an excess of energy that is temporarily stored as fat. The diet's low protein content might also account for oildbirds' slow rate of development.

Breeding is highly seasonal, largely coinciding with the rainy season, but the onset of breeding varies from place to place. In the Caripe Cave most egg laying occurs in the second half of April and May, which coincides with the fruiting peak of Lauraceae. In nearby Trinidad, breeding is less seasonal; a number of birds are likely to be found in several breeding stages at any time of the year.

Conservation status

Oilbird colonies are widespread but patchily distributed. Threats include poaching of nests and forest destruction. The species is not threatened, but its specialized diet and very large home range make it vulnerable to deforestation. Several colonies disappeared in Trinidad and Venezuela during the last decades of the twentieth century, but all of them were small. The species receives ample legal protection in several parks and conservation areas throughout South America.

Significance to humans

Oilbird nestlings are a rich source of energy and protein. At one time, throughout their range, native South Americans ate oilbird nestlings and used their fat for lamp oil. At the turn of the twenty-first century, oilbirds are legally protected in most countries where they are found.

Oilbirds are unique among birds and large oilbird colonies are one of the great ornithological spectacles of the world. Easily accessible oilbird caves such as the one in Caripe are important tourist attractions. Oilbirds have not successfully been kept in zoos, but at least one individual is known to have been kept as a pet for years.

Resources

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Carlos Bosque, PhD

Frogmouths (Podargidae)

Class Aves

Order Caprimulgiformes
Suborder Caprimulgi

Family Podargidae

Thumbnail description

Small to rather large nocturnal birds with strong wide beak, hooked at tip, large gap, cryptic coloration, rounded wings, and short legs

Size

7.5-24 in (19-60 cm); 1.5-23.6 oz (43-670 g)

Number of genera, species

2 genera; 13 species

Habitat

Forests, woodlands, scrub, plantations

Conservation status

Near Threatened: 5 species



Distribution

South Asia from India to Vietnam, Java, and Philippines; New Guinea and Solomon Islands to Australia and Tasmania

Evolution and systematics

The frogmouths form a well-defined group that clearly belongs within the Caprimulgiformes. The large strong beak with a very wide gape is the basis of the frogmouth name and provides an immediate distinction from the weaker-beaked owlet-nightjars (Aegothelidae), potoos (Nyctibiidae), and true nightjars (Caprimulgidae) that are their closest relatives. The earliest fossil frogmouths are known from the Eocene of France and Germany, providing evidence of the family's antiquity and adding to other information that implies they diverged from their closest relatives during the early Tertiary. Fossils from Europe also suggest that the modern range, from south Asia to Australia, is a relic of a formerly more extensive Tertiary range, presumably developed when subtropical forests covered much more of the Northern Hemisphere.

Asian frogmouths of the genus *Batrachostomus* are mainly smaller than the Australasian species of the genus *Podargus*, and differ somewhat in color and nest structure. But these groups have always seemed sufficiently similar to be regarded as closely related. It came as a surprise when DNA hybridization studies by Charles Sibley and Jon Ahlquist sug-

gested the two genera are so distantly related that they should be placed in separate families. Some recent publications have compromised by placing them in separate subfamilies, Batrachostominae for the Asian species and Podarginae for the Australasian species, and that arrangement is adopted here.

There is now little doubt that three species should be recognized in the Australasian *Podargus*: the marbled frogmouth (*P. ocellatus*), the tawny frogmouth (*P. strigoides*), and the Papuan frogmouth (*P. papuensis*). However, there is more doubt about how many species are represented among the less well-known Asian frogmouths of the genus *Batrachostomus*, particularly whether the Sumatran and Bornean populations of short-tailed frogmouth (*B. poliolophus*) are distinct species, and whether some of the more distinctive subspecies of Javan frogmouth (*B. javensis*) might be better treated as species than subspecies.

Physical characteristics

Frogmouths are rather stocky, compact birds that resemble other Caprimulgiformes in having a relatively large head

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A tawny frogmouth (*Podargus strigoides*) adult with young. (Photo by M.P. Kahl/VIREO. Reproduced by permission.)

with large eyes. The strong wide bill is the family's hallmark and is relatively even wider in the Asian than in the Australasian species. The base of the bill has strong rictal bristles; some Asian species also have other well-developed facial bristles, providing an assemblage of whiskers that is presumed to help direct prey into the gape and protect the eyes from impact with hard prey. Wings and tail are rather short to moderately long, but both are always rounded. Very short legs allow only a restricted shuffling gait. The claw of the middle toe lacks the serrated *comb* found in other Caprimulgiformes.

The Australasian species have rather variable brown, buff, or grayish coloration with predominantly streaked patterns, providing excellent camouflage at daytime roosts. Sexual differences in color are not large, although the female may be brighter than the male. In several Asian species the "reversed" sexual dichromatism (difference between sexes in coloration) is much greater, with mainly bright-rufous females having bold white signal markings on their underparts and wings, whereas males are mainly brown with intricately barred and streaked patterns. Some Asian frogmouth males incubate on the exposed nest during the daytime when concealment is most needed, whereas the female is active in nocturnal territorial advertisement. These reversed roles may explain the apparent reversal of the usual pattern of sexual dichromatism in birds.

Distribution

Asian frogmouths occur in forested regions from southern India and Sri Lanka and the southern slopes of the Himalayas east to Vietnam and the Philippines, and through the Indonesian islands to Java. They reach greatest diversity in Sumatra and Borneo, which have up to five species in low-land forests and two more in lower montane forests.

Three species of Australasian frogmouths range from New Guinea and its satellite islands and the northern Solomon Islands to Australia and Tasmania. Only the tawny frogmouth occurs in Tasmania and over most of Australia, but all three species are present in Queensland and two are widespread in New Guinea.

Although they can fly strongly, frogmouths are among the most sedentary birds. There are no migratory species, and there are no records of extralimital vagrancy for any species. The tawny frogmouth apparently remains on its territory throughout the year, with no seasonal wandering even in the arid regions of Australia. While there must undoubtedly be some dispersal of young birds, even this remains to be documented.

Habitat

Forests are the principal habitat of most frogmouths and the only habitat of many species. The tawny frogmouth alone has adapted to life in more open woodlands and scrub, allowing it to colonize large unforested areas of Australia that offer the minimum requirement of groves of trees or bushes in which to nest and roost, and perches from which to hunt.

Detailed differences in habitat preferences and body size among Asian frogmouths may contribute to the coexistence of several species in regions such as Borneo. There, montane forests are shared between the large Dulit frogmouth (*Batrachostomus harterti*) and the smaller short-tailed frogmouth; the primary lowland forests support the large frogmouth (*B. auritus*), the rather small Gould's frogmouth (*B. stellatus*), and the very small Javan frogmouth; and disturbed secondary forests in the lowlands have only the Sunda frogmouth (*B. cornutus*).

Behavior

All frogmouths roost during the day and are active from dusk through part or all of the night until around dawn. Daytime roosts of several species including the tawny frogmouth and Sri Lanka frogmouth (*Batrachostomus moniliger*) are on branches in trees or bushes, where the birds remain quiet and still unless approached so closely that they suddenly fly away to escape. They give an impression of remaining immobile if not asleep when approached, with the beautifully camouflaged plumage sleeked to aid concealment, but in fact they watch intruders through nearly closed eyes and keep them in view with very slow head movements.

There are a few reports of daytime roosting in tree holes by the marbled frogmouth (*Podargus ocellatus*) and large frogmouth, which, if observations are typical, may explain why these species are rarely encountered during the day. However, there have been other daytime sightings of Asian frogmouths in thick tangles of vines in forests, where a small motionless and well-camouflaged bird is remarkably inconspicuous.

Nocturnal activity consists largely of movements around the territory to hunt from different perches, and singing or calling to defend the territory. The Australasian species have sustained cooing or hooting songs that may be given as duets by paired birds. These are backed up by aggressive calls and loud bill-snapping if another bird of the same species enters the territory. Asian frogmouths are less well known, but females of several species give loud territorial whistling, mewing, or trilling calls, while the males have different and often more subdued calls.

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A tawny frogmouth (*Podargus strigoides*) adopts a rigid camouflage posture on its nest in Nocoleche Nature Reserve, Australia. (Photo by Wayne Lawler. Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Insects and other active invertebrates caught on sallving flights from a perch form the main prey of frogmouths, but the larger Australian species also take small vertebrates. Predominant insect prey are beetles, moths, orthopterans, stick insects, cicadas, bugs, and many other types, commonly supplemented with other arthropods such as spiders and millipedes. Recorded vertebrate prey include frogs and mice. Details of hunting behavior are unknown or poorly known for many species. However, the tawny frogmouth feeds mainly by swooping to the ground from a prominent perch to pick up moving prey in the beak, then shakes or beats large or tough prey against the perch to immobilize it. The small Javan frogmouth is thought to catch much of its insect food by sallying to flutter at leaves and trunks, a smaller proportion perhaps being obtained flycatcher-like in sustained flight or from the ground.

Several frogmouth species use prolonged gaping in threat display, but it is also possible that similar actions are used in passive *fly-trapping*. It is suggested that sticky or smelly saliva facilitates this feeding method, but there are few detailed observations and more study is needed.

Reproductive biology

Unlike most Caprimulgiformes, frogmouths build well-formed nests. Those of Australian frogmouths are small flat pads of twigs or tendrils placed among forking branches or on a flat branch, the structure reminiscent of a pigeon's nest and built by both birds of the pair. Asian frogmouths build relatively tiny nests on a branch or stem, the tiny cup made of moss or lichens interwoven with feathers plucked from the birds' own underparts.

Clutches are one or two eggs in most species, but three or sometimes four in the tawny frogmouth. The eggs are unmarked white, but camouflaged eggs are not needed because a beautifully concealed adult bird invariably covers the egg or eggs. So far as is known, daytime incubation is carried out exclusively by the male, although the female is known to take some part in nocturnal incubation in three species. The incubation period (around 30 days) is known only for the rather large tawny frogmouth.

At least in the Australian species, nestlings hatch with a coat of white down and later acquire a second coat of gray down before juvenal feathers develop. Small young are continuously brooded by the male in daytime, but fed by both parents at night on regurgitated food. The fledging period is known only for the tawny frogmouth (25–35 days), the young of which are fed for another one to two weeks after fledging, then remain in the company of their parents for several months.

Conservation status

No frogmouth species is listed as globally threatened, but undoubtedly there have been large declines in many species due to deforestation. Five species are considered Near Threatened—the large frogmouth, Dulit frogmouth, Bornean frogmouth (*B. mixtus*), short-tailed frogmouth, and Gould's frogmouth.

Significance to humans

Frogmouths are mainly unobtrusive forest birds commonly overlooked even by local people. Early European settlers in Australia were familiar with nocturnal calls of the tawny frogmouth, but it is evident from the given common name "Mopoke" or "Morepork" that there was confusion with the common small owl, the southern boobook (*Ninox boobook*).



1. Marbled frogmouth (*Podargus ocellatus*); 2. Female Sunda frogmouth (*Batrachostomus cornutus*); 3. Large frogmouth (*Batrachostomus auritus*); 4. Gould's frogmouth (*Batrachostomus stellatus*), dark morph; 5. Sri Lanka frogmouth (*Batrachostomus moniliger*); 6. Female Papuan frogmouth (*Podargus papuensis*); 7. Hodgson's frogmouth (*Batrachostomus hodgsoni*); 8. Tawny frogmouth (*Podargus strigoides*). (Illustration by Barbara Duperron)

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Species accounts

Marbled frogmouth

Podargus ocellatus

SUBFAMILY

Podarginae

TAXONOMY

Podargus ocellatus Quoy and Gaimard, 1830, Arfak Peninsula, New Guinea. Six subspecies.

OTHER COMMON NAMES

English: Little Papuan or plumed frogmouth; French: Podarge ocellé; German: Marmorschwalm; Spanish: Podargo Ocelado.

PHYSICAL CHARACTERISTICS

15–19 in (37–48 cm); 4.6–10.1 oz (130–286 g). Upperparts of males vary from dull gray-brown to deep rufous with varying amounts of streaks, marbling, and spots; underparts often have whitish barring and longitudinal dark streaks. Females are often darker than males.

DISTRIBUTION

Eastern Australia, New Guinea and satellite islands, north Solomon Islands.

HABITAT

Forests, rarely plantations.

BEHAVIOR

Usually roosts in thick vegetation during day, active in territory only at night. Pair defends territory with song and calls, backed up by bill-snapping when intruding birds enter territory.



FEEDING ECOLOGY AND DIET

Sallies to catch mainly insect prey from ground and tree trunks, using succession of perches on tree branches and stumps.

REPRODUCTIVE BIOLOGY

Breeding season in Australia from August to December, with a single brood each year. Nest is small platform in tree, with one or occasionally two white eggs. Male known to incubate and brood small young during day. Fledging period at least 31 days.

CONSERVATION STATUS

Not threatened overall but rare in Australia.

SIGNIFICANCE TO HUMANS

None known.

Papuan frogmouth

Podargus papuensis

SUBFAMILY

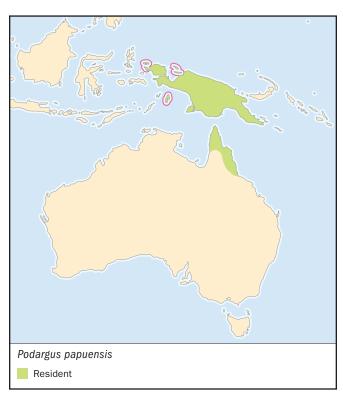
Podarginae

TAXONOMY

Podargus papuensis Quoy and Gaimard, 1830, Arfak Peninsula, New Guinea. Monotypic.

OTHER COMMON NAMES

English: Giant or great Papuan frogmouth; French: Podarge papou; German: Papuaschwalm; Spanish: Podargo Papú.



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PHYSICAL CHARACTERISTICS

18–24 in (45–60 cm); 9–20 oz (256–570 g). Largest member of its genus. Male's upperparts elaborately patterned in light and dark, but overall appear gray-brown; underparts are lighter brown-gray with white spots and bars and blackish streaking. Females are typically browner or more rufous than males.

DISTRIBUTION

Oueensland; New Guinea and satellite islands.

HABITAT

Forest, woodland, wooded savanna.

BEHAVIOR

Roosts by day in tree cover, often a pair together; active at night in territory.

FEEDING ECOLOGY AND DIET

Swoops from perch to catch prey mainly on ground, taking large insects and small vertebrates such as frogs and rodents.

REPRODUCTIVE BIOLOGY

Nests on a platform in tree, containing clutch of one or rarely two eggs. Daytime incubation by male; incubation and fledging periods unknown.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Known to tribespeople in New Guinea, who have given descriptions of a "gaping" posture, possibly used for fly catching. ◆

Tawny frogmouth

Podargus strigoides

SUBFAMILY

Podarginae

TAXONOMY

Caprimulgus strigoides Latham, 1801, New Holland. Three subspecies.

OTHER COMMON NAMES

English: Morepork, freckled or tawny-shouldered frogmouth; French: Podarge gris; German: Eulenschwalm; Spanish: Podargo Australiano.

PHYSICAL CHARACTERISTICS

13.5–21 in (34–53 cm); 6–24 oz (180–670 g). Male's upperparts are normally grayish with bold black streaks and intricate finer bars and lines; underparts are lighter grayish with blackish streaks, white barring, and variable brown to rufous suffusion. Female often darker with more rufous suffusion.

DISTRIBUTION

Australia and Tasmania.

HABITAT

Woodland, scrub, tree groves, plantations, gardens with trees.

BEHAVIOR

Daytime roosts are on tree branches; active at night in territory defended by pair of birds.

FEEDING ECOLOGY AND DIET

Feeds mainly by sallying from perch to take large insects, other arthropods, or small vertebrates from ground.



REPRODUCTIVE BIOLOGY

Nest a platform in tree or bush, usually containing clutch of one to three eggs. Daytime incubation by male, incubation period about 30 days. Young fed by both parents, fledging period 25–35 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Nocturnal calls familiar to rural Australians, but much confused in past with those of owls. ◆

Large frogmouth

Batrachostomus auritus

SUBFAMILY

Batrachostominae

TAXONOMY

Podargus auritus J. E. Gray, 1829, Sumatra. Monotypic.

OTHER COMMON NAMES

French: Podarge oreillard; German: Riesenfroschmaul; Spanish: Podargo Orejudo.

PHYSICAL CHARACTERISTICS

16–17 in (40–43 cm); 7.25 oz (206 g). Largest Asian frogmouth. Upperparts are chestnut to light brown with pale bars on scapulars and blackish-edged whitish spots on wing coverts; underparts are rufous brown with buff to white spots. Coloration of males and females is similar.

DISTRIBUTION

Thailand, Peninsular Malaya, Sumatra, and Borneo.

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HABITAT

Lowland rainforest.

BEHAVIOR

Little known; daytime roosts in canopy or tree-hole; active only at night.

FEEDING ECOLOGY AND DIET

Diet of insects including cicadas and grasshoppers.

REPRODUCTIVE BIOLOGY

Tiny nest on branch of shrub or sapling, with clutch of single egg.

CONSERVATION STATUS

Near Threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Gould's frogmouth

Batrachostomus stellatus

SUBFAMILY

Batrachostominae

TAXONOMY

Podargus stellatus Gould, 1837, Malacca, Peninsular Malaya. Monotypic.

OTHER COMMON NAMES

French: Podarge étoilé; German: Schuppenfroschmaul; Spanish: Podargo Estrellado.

PHYSICAL CHARACTERISTICS

8.3–9.9 in (21–25 cm); 1.7 oz (47–48.5 g). Two color morphs—chestnut and a rarer dark morph (almost blackish chestnut).

Both morphs have a whitish collar across the mantle, whitish spots on wing-coverts, and white or grayish white spots on scapulars. Sexes are similar.

DISTRIBUTION

Thailand, Peninsular Malaya, Sumatra, and Borneo.

HABITAT

Lowland rainforest.

BEHAVIOR

Little known; sings from branches in trees during night.

FEEDING ECOLOGY AND DIET

Little known; diet includes orthopterans.

REPRODUCTIVE BIOLOGY

The only nest reported in detail was tiny and placed on a low branch about 4.3 ft (1.3 m) above the ground beside a foot path running through primary forest. It contained a single white egg.

CONSERVATION STATUS

Near Threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Sri Lanka frogmouth

Batrachostomus moniliger

SUBFAMILY

Batrachostominae

TAXONOMY

Batrachostomus moniliger Blyth, 1849, Ceylon. Monotypic.

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OTHER COMMON NAMES

English: Ceylon frogmouth; French: Podarge de Ceylan; German: Ceylonfroschmaul; Spanish: Podargo de Ceilán.

PHYSICAL CHARACTERISTICS

8.7–9 in (22–23 cm). Males are brownish gray with black and white lines, a whitish collar across the mantle, and white spots on scapulars, wing-coverts, and underparts. Females are rufous or rufous-brown with reduced markings.

DISTRIBUTION

Southwest India and Sri Lanka.

HABITAT

Forests, woodland, second-growth.

BEHAVIOR

Roosts in dense cover by day, usually as pair together. Active in territory at dusk and during the night, but most details of behavior are unknown.

FEEDING ECOLOGY AND DIET

Catches insect prey on ground or on branches.

REPRODUCTIVE BIOLOGY

Nest a small circular pad on branch, containing clutch of single egg. Daytime incubation by male.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Hodgson's frogmouth

Batrachostomus hodgsoni

SUBFAMILY

Batrachostominae

TAXONOMY

Otothrix hodgsoni G. R. Gray, 1859, northern India. Monotypic.

OTHER COMMON NAMES

French: Podarge de Hodgson; German: Langschwanz-Froschmaul; Spanish: Podargo Colilargo.

PHYSICAL CHARACTERISTICS

8.7–10.6 in (22–27 cm); 1.8 oz (51 g). Distinct sexual dichromatism. Males have rufous brown upperparts with black markings and white spots; underparts are patterned in black, rufous, and white. Females are more rufous and have a reduced number of pale spots.

DISTRIBUTION

Sikkim, Bhutan, and Assam to Laos and central Vietnam.

HABITAT

Hill forests.

BEHAVIOR

Little known; roosts in thick cover during day.

FEEDING ECOLOGY AND DIET

Little known; feeds on moths, beetles, and other large insects.

REPRODUCTIVE BIOLOGY

Small nest on branch, with clutch usually of two eggs. Daytime incubation by male.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆



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Sunda frogmouth

Batrachostomus cornutus

SUBFAMILY

Batrachostominae

TAXONOMY

Podargus cornutus Temminck, 1822, Sumatra. Two subspecies.

OTHER COMMON NAMES

English: Long-tailed or horned frogmouth; French: Podarge cornu; German: Sundafroschmaul; Spanish: Podargo Cornudo.

PHYSICAL CHARACTERISTICS

9–11 in (23–28 cm). Plumage color highly variable. Two color morphs are known—black-and-white or brown-and-buff; intermediates also occur. Colors of males and females differ in both morphs.

DISTRIBUTION

Sumatra, Borneo, and small islands nearby.

HABITAT

Scrub, secondary forest.

BEHAVIOR

Roosts on low branches by day; active at night.

FEEDING ECOLOGY AND DIET

Little known; diet includes beetles.

REPRODUCTIVE BIOLOGY

Small nest on branch contained single egg. Adult reported to carry half-grown nestling in flight across a narrow road, apparently holding chick between its legs.



CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

Holyoak, D. T. "Frogmouths." In *Handbook of the Birds of the World*, Vol.5, *Barn-owls to Hummingbirds*, edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal. Barcelona: Lynx Edicions, 1999.

Holyoak, D. T. *Nightjars and their Allies*. Oxford: Oxford University Press, 2001.

David T. Holyoak, PhD

Owlet-nightjars (Aegothelidae)

Class Aves

Order Caprimulgiformes
Suborder Caprimulgi

Family Aegothelidae

Thumbnail description

Small to medium-sized, cryptically colored nocturnal birds that perch upright; have large heads, large forward-facing eyes within a facial disk, rounded wings, small legs and feet, and long toes that bear long claws

Size

7-12 in (18-30 cm); 1.0-3.5 oz (29-98 g)

Number of genera, species

1 genus; 7 species

Habitat

Forest, woodlands, scrub, and savannas

Conservation status

Critically Endangered: 1 species



Distribution

Northern Moluccas, New Guinea and satellite islands, Australia, Tasmania, and New Caledonia

Evolution and systematics

Owlet-nightjars are the most distinctive group in the order Caprimulgiformes, showing characteristics that to some extent link this order with the owls (Strigiformes). Similarities between owlet-nightjars and owls include the facial disk with eyes directed forwards, hole nesting, unmarked white eggs, and certain anatomical features. Furthermore, DNA-hybridization studies point to early evolutionary divergence of owlet-nightjars from the other Caprimulgiformes, perhaps not long after the early ancestors of the order diverged from ancestral owls. The earliest fossil owlet-nightjars are known from the Upper Eocene, suggesting that the family evolved in the early Tertiary.

As of 2001, all living species of owlet-nightjars are placed in the genus Aegotheles. There is some uncertainty about how many species should be recognized, particularly about whether spangled owlet-nightjars (Aegotheles tatei) should be regarded as a distinct species or as a subspecies of feline owlet-nightjars (A. insignis). Further studies of these poorly known birds may also suggest that certain populations of other species that are currently regarded as subspecies might be better elevated to species rank.

Physical characteristics

Like other members of the Caprimulgiformes, owletnightiars have a relatively large head, large eyes, and a wide gape. The small hooked bill has a wide base. Rictal bristles (the rictus is the gape of a bird's mouth) are well developed at the base of the bill and these along with other whiskers (facial bristles) are thought to function in directing prey into the mouth and in protecting the eyes from hard insect prey; a tactile function has also been suggested. Flank feathers are elongated. The wings are rather long but rounded and the tail is moderately long and wedge shaped. The legs are relatively short, but less so than in most other Caprimulgiformes, and the toes are long, slender, and bear claws. Aegotheles novaezealandiae, a species known only by fossils from the Quaternary of New Zealand, had much larger feet and legs than any living species and reduced wings, suggesting that it was more terrestrial than any living species. The rare New Caledonian owlet-nightjar (A. savesi) has legs and wings that approach the rather strong legs and reduced wings of the extinct New Zealand form, suggesting that it may also have come to rely more on walking and less on flying than other owletnightjars, but the habits of the living bird are almost unknown.

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The plumage coloration of owlet-nightjars consists of the beautifully marked shades of brown, gray, buff, rufous, and blackish that characterize the Caprimulgiformes and promote concealment from predators. Patterns of several species are dominated by fine dark barring whereas others have bold blotches or streaks, often with prominent facial stripes. Sexes are similar.

Distribution

Owlet-nightjars reach their greatest diversity in New Guinea, which has seven of the nine species. Among these are Archbold's (A. archboldi), barred (A. bennettii), and Wallace's (A. wallacii) owlet-nightjars, as well as a small population of the Australian owlet-nightjar (A. cristatus), which is the only species in Australia and Tasmania. The other two species are restricted to the Northern Moluccas (Moluccan owlet nightjar, A. crinifrons) or New Caledonia (New Caledonian owlet-nightjar). All species are sedentary, with movements apparently limited to local dispersal.

Habitat

Owlet-nightjars are mainly forest birds, with different species in New Guinea occurring in lowland rainforests, midmountain forests, or in montane forests up to the scrubby growths at the tree line. Only the Australian owlet-nightjar occurs extensively in more open habitats in addition to open forests and woodlands. They extend into scrub-covered country such as mallee in the Australian interior and into coastal mangroves and feed in grasslands that adjoin habitats with trees.

Behavior

Owlet-nightjars occupy concealed roosts during the day, commonly in holes in trees. Some species roost in the con-



An Australian owlet-nightjar (*Aegotheles cristatus*) at night. (Photo by R. English/VIREO. Reproduced by permission.)



A feline owlet-nightjar ($Aegotheles\ insignis$). (Photo by W. Peckover/VIREO. Reproduced by permission.)

cealment afforded by dense vines. Unless they are disturbed, all activity occurs in near-darkness between late dusk and the early predawn light. Flight is swift and direct but usually of short duration. Very little is known of the social organization and other aspects of behavior of most species. The broad outlines of behavior are clear only for the better-studied Australian owletnightjar. In that species, a pair of birds lives all year within a large territory. The pair roost in close proximity throughout the year, although roost sites are frequently changed.

Nocturnal calls provide the main evidence of the presence and identity of owlet nightjar species, and there can be little doubt that the voice is the main means by which these birds communicate with each other. Different species produce characteristic churring, snarling, or whistling sounds that evidently function in defense of territories. The full vocabulary is unknown for most species, but sounds given by some include hissing during threat displays from nest holes.

Feeding ecology and diet

The diet of most owlet-nightjars consists mainly of insects, supplemented by other small invertebrates such as spiders and

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millipedes. The mountain owlet-nightjar (*A. albertisi*) includes earthworms in its diet. The food of several species remains completely unknown. The main feeding technique consists of sallying from perches to capture prey in the bill, often from the ground, but also sometimes from tree trunks or by fluttering against foliage. Each prey item is swallowed whole.

Reproductive biology

For several species of owlet-nightjars, nests have not been discovered. All described nests have been in holes, mainly tree holes. Australian owlet-nightjars sometimes nest in cavities of banks or buildings. Clutches are of one to five, slightly glossy, unmarked white eggs that, for unknown reasons, have unusually thick shells. Young hatch with white down which is replaced by a second coat of gray down before the juvenal feathers grow. Details of breeding are known only for the Australian species, in which incubation takes 25–27 days and is carried out at least mainly by the female, eggs hatch over

several days, the young are fed by both parents, and fledging occurs after 21–32 days. No nest cleaning occurs so that droppings accumulate in the nest cavity.

Conservation status

New Caledonian owlet-nightjars were known only from a single specimen collected in 1880, and they were feared extinct until a sighting was reported in 1998. It is now regarded as Critically Endangered. None of the other species is thought to be seriously threatened, although several of those in New Guinea remain poorly known and susceptible to deforestation.

Significance to humans

The owlet-nightjars are among the most inconspicuous and retiring of nocturnal forest birds; even local tribespeople in New Guinea know little about them.



1. Mountain owlet-nightjar (*Aegotheles albertisi*); 2. Feline owlet-nightjar (*Aegotheles insignis*); 3. Australian owlet-nightjar (*Aegotheles cristatus*); 4. Barred owlet-nightjar (*Aegotheles bennettii*). (Illustration by Brian Cressman)

Species accounts

Feline owlet-nightjar

Aegotheles insignis

TAXONOMY

Aegotheles insignis Salvadori, 1875, Hatam, Arfak Mountains, New Guinea. Monotypic.

OTHER COMMON NAMES

English: Reddish or large owlet-nightjar; French: Grand égothèle; German: Käuzchenschwalm; Spanish: Egotelo grande.

PHYSICAL CHARACTERISTICS

12 in (30 cm); 2.1–3.5 oz (59–98 g). Two well-defined color morphs—rufous and brown; intermediates also occur. Upperparts have sparse whitish streaks or spots and prominent lateral crown stripes; throat is buff or white; underparts have bold whitish spots. Sexes are similar.

DISTRIBUTION

New Guinea.

HABITAT

Montane forests.

BEHAVIOR

Solitary, secretive, and little known.

FEEDING ECOLOGY AND DIET

Diet of insects, including beetles.

REPRODUCTIVE BIOLOGY

Nest and eggs unknown.



CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known.

Mountain owlet-nightjar

Aegotheles albertisi

TAXONOMY

Aegotheles albertisi Sclater, 1874, Arfak Mountains, New Guinea. Three subspecies.

OTHER COMMON NAMES

French: Égothèle montagnard; German: Bergschwalm; Spanish: Egotelo montano.

PHYSICAL CHARACTERISTICS

7–8 in (18–20 cm); 0.9–1.5 oz (25–43 g). Rufous and brown morphs; intermediates also occur. Sexes are similar.

DISTRIBUTION

New Guinea mountains.

HABITAT

Montane forests, extending to edges.

BEHAVIOR

Secretive, nocturnal, roosting in hollows during day.



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FEEDING ECOLOGY AND DIET

Catches food on ground beneath forest canopy and in clearings, taking insects and earthworms.

REPRODUCTIVE BIOLOGY

Nests in hole in tree stump; clutch apparently a single white egg.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Barred owlet-nightjar

Aegotheles bennettii

TAXONOMY

Aegotheles bennettii Salvadori and D'Albertis, 1875, Hall Sound, New Guinea. Five subspecies.

OTHER COMMON NAMES

English: Bennett's or collared owlet-nightjar; French: Égothèle de Bennett; German: Bennettschwalm; Spanish: Egotelo barrado.

PHYSICAL CHARACTERISTICS

8–9 in (20–23 cm); 1.6–1.7 oz (45–47 g). Upperparts are dark brown to blackish with narrow light lines; underparts are pale gray to whitish buff with broad bars and spots. Sexes are similar.

DISTRIBUTION

New Guinea.

HABITAT

Lowland forests.



BEHAVIOR

Little known; roosts by day in tree hollows.

FEEDING ECOLOGY AND DIET

Not known.

REPRODUCTIVE BIOLOGY

Nest sites undescribed; eggs white.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Australian owlet-nightjar

Aegotheles cristatus

TAXONOMY

Caprimulgus cristatus Shaw Smith & Hunter, 1790, New South Wales. Two subspecies.

OTHER COMMON NAMES

English: Owlet-nightjar, crested owlet-nightjar; French: Égothèle d'Australie; German: Baumschwalm; Spanish: Egotelo Australiano.

PHYSICAL CHARACTERISTICS

8.3–10 in (21–25 cm); 1.4–2.1 oz (39–60 g). Upperparts are dark gray with pales lines and spots; underparts are paler with narrow brown lines. Sexes often similar but females vary between a gray morph and a rufous morph (with intermediates). The extreme rufous morph does not seem to occur in males, although intermediate males are known.

DISTRIBUTION

Australia, Tasmania, and southeastern New Guinea.

HARITAT

Open forests, woodlands, scrub, and mangroves.



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BEHAVIOR

Sedentary in pairs. Roosts by day, usually in tree holes.

FEEDING ECOLOGY AND DIET

Feeds mainly on insects, most of which are caught by swooping (sallying) to ground from low perch.

REPRODUCTIVE BIOLOGY

Nests in hole, usually in tree. Clutches of two to five white eggs laid between August and December. Young hatch with white down which is replaced by gray down before juvenal feathers grow. Incubation period 25–27 days, fledging period usually 21–29 days.

CONSERVATION STATUS

Not threatened, although suffers mortality from domestic cats and road kills.

SIGNIFICANCE TO HUMANS

Mentioned in the legends of aboriginal Australians. •

Resources

Books

Holyoak, D.T. "Owlet-nightjars." In *Handbook of the Birds of the World.* Vol. 5, *Barn-owls to Hummingbirds*, edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal. Barcelona: Lynx Edicions, 1999.

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David T. Holyoak, PhD

Potoos (Nyctibiidae)

Class Aves

Order Caprimulgiformes
Suborder Caprimulgi
Family Nyctibiidae

Thumbnail description

Medium-sized, cryptically colored, nocturnal birds with large head, poorly developed facial bristles, long wings and tail, and short legs

Size

8-23 in (21-57 cm); 1.6-22 oz (46-624 g)

Number of genera, species

1 genus; 7 species

Habitat

Forest, woodlands, wooded savannas

Conservation status

Not threatened



Distribution

Central and South America from Mexico to Uruguay, Hispaniola, and Jamaica

Evolution and systematics

Potoos are a well-defined group of Caprimulgiformes that are now restricted to the Neotropics. They are perhaps most closely related to the true nightjars of the family Caprimulgidae, from which they appear less distinct than do the owletnightjars (Aegothelidae) or frogmouths (Podargidae). A fossil leg bone from the early Tertiary (Upper Eocene or Oligocene) of France demonstrates the antiquity of potoos and also that they formerly had a much more extensive range.

Although the seven species are normally placed within a single genus they differ markedly in size and color, with small rufous potoos (*Nyctibius bracteatus*) being only a tenth the mass of great potoos (*N. grandis*), so that taxonomists may eventually subdivide the genus. Some specimens of northern potoos (*N. jamaicensis*) and gray potoos (*N. griseus*) are almost identical in external appearance; the division into two separate species had to await description of the striking differences in their voices.

Physical characteristics

Potoos have a small body, a disproportionately large head with large eyes, a small but wide-based bill with a huge gape,

long rounded wings, a long tail, and proportionately very small legs and feet. Except in the rufous potoo, facial bristles are less developed than in most other Caprimulgiformes. Unlike true nightjars, potoos lack comb-like serrations on the claw of the middle toe.

Plumage coloration involves the drab hues and cryptic patterns found in other Caprimulgiformes, with gray, buff, rufous, or brown dominant in different species. Several of the smaller potoos have bold white spots or wing patches, but the two largest species are rather uniformly colored with closely barred and streaked patterning.

Distribution

Most potoo species are found in tropical South America, but the overall range of the family extends from subtropical areas in Mexico, Hispaniola, and Jamaica south to southern Brazil and Uruguay. All species are thought to be sedentary.

Habitat

Potoos are mainly forest birds, with different species characteristic of lowland or montane forests. Several species

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A gray potoo (*Nyctibius griseus*) in Mexico. (Photo by Patricio Robles Gil. Bruce Coleman Inc. Reproduced by permission.)

extend into woodlands, plantations, or even groves of trees in savannas or partly deforested areas.

Behavior

Potoos spend daylight hours almost motionless on a branch or tree stump, where their immobility and cryptic coloration render them almost invisible. When disturbed they reinforce the camouflage by flattening their plumage and adopting an erect concealment posture so that their outline merges with that of a snag on a branch or the top of a stump. Although birds thus concealed have their eyelids closed, two small notches in the eyelids (the so-called magic eyes) allow vision without spoiling the bird's camouflage by opening the large shiny eyes.

If undisturbed, activity occurs only from dusk until dawn, when the birds sing and hunt from exposed perches and fly about their territories. They are most conspicuous by their loud songs, which are different in each species and vary from a long whistled glissando in the white-winged potoo (*Nyctibius leucopterus*) to a loud guttural snoring in the great potoo.

Singing birds approach aggressively when recordings of their songs are played, suggesting that the songs function in advertisement and defense of territories.

Feeding ecology and diet

The main food items of potoos are flying insects, particularly beetles, moths, orthopterans, and termites. There are a few records of the larger potoos (great potoos) taking small bats, and once a small bird (white-throated seedeater, *Sporophila torqueola*) was found in the stomach of a northern potoo. Prey is captured by sallying flights from exposed perches such as tree stumps, branches, or fence posts. Prey items are mainly caught in the air, less often taken from vegetation, and apparently not taken from the ground.

Reproductive biology

Potoos are monogamous. They do not build a nest; instead a single egg is laid in a natural hollow on top of a branch or on a high tree stump. The egg is oval-elliptical or elliptical with white color and spots of brown or gray. Incubation and care of the young is carried out by both sexes, although details are poorly known. The few data on the incubation period show that it may last 30–33 days in the gray potoo, which has fledging periods of 40–51 days. The larger great potoo has a fledging period of at least 55 days. Young have pale down when hatched. Adult birds incubating eggs



A great potoo ($Nyctibius\ grandis$) is well camouflaged while sitting on a dead tree branch in Colombia. (Photo by T. McNish M./VIREO. Reproduced by permission.)

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or brooding small young freeze in place when disturbed so that they blend in well, like potoos at their normal daytime roosts. By the time nestlings have most of their early down replaced by juvenal feathers they are no longer brooded by a parent and they also freeze if disturbed.

Conservation status

No potoo species is regarded as globally threatened, but several have suffered large declines in populations as a result of deforestation. In particular, populations of white-winged potoos in the forests of the Bahia region of southeastern Brazil must now be endangered if they are not already extinct, and the widespread long-tailed potoo (*Nyctibius aethereus*) is reported to be rare in most parts of its range.

Significance to humans

Potoos have little economic importance. Their loud nocturnal voices are well known to local people, although potoos' calls are often attributed to other animals such as sloths. Potoos formerly figured in superstitions and folklore at least in rural Brazil, where the melancholy song of gray potoos was believed to be a sad lament from the reincarnation of one of a pair of separated, widowed, or unrequited lovers. The harsher voice of the great potoo, on the other hand, was sometimes considered a sign of bad luck or impending death.



1. Great potoo (Nyctibius grandis); 2. Rufous potoo (Nyctibius bracteatus); 3. Gray potoo (Nyctibius griseus). (Illustration by Bruce Worden)

Vol. 9: Birds II Family: Potoos

Species accounts

Rufous potoo

Nyctibius bracteatus

TAXONOMY

Nyctibius bracteatus J. Gould, 1846, Colombia. Monotypic.

OTHER COMMON NAMES

English: Colombian potoo; French: Ibijau roux; German: Tropfentagschläfer; Spanish: Nictibio rufo.

PHYSICAL CHARACTERISTICS

8.3–9.8 in (21–25 cm); 1.6–2.0 oz (46–58 g). Coloration is atypical for a potoo. Overall the bird is deep orange-rufous with large white spots bordered in black; long bristles spring from the loral area. Sexes similar.

DISTRIBUTION

South America from Colombia and Guyana south to eastern Peru and northern Brazil.

HABITAT

Lowland rainforests.

BEHAVIOR

A little-known, nocturnal bird of the forest understory and middle story.

FEEDING ECOLOGY AND DIET

Catches insects on sallying flights from a perch.



REPRODUCTIVE BIOLOGY

Only nest reported was on top of a broken palm stub inside forest, with a single blotched egg. Nestling was later tended by both parents and fledged before reaching adult size.

CONSERVATION STATUS

Probably not threatened overall, but undoubtedly declining due to forest destruction.

SIGNIFICANCE TO HUMANS

None known. ◆

Gray potoo

Nyctibius griseus

TAXONOMY

Caprimulgus griseus Gmelin, 1789, Cayenne. Two subspecies.

OTHER COMMON NAMES

English: Common potoo; French: Ibijau gris; German: Urutau-Tagschläfer; Spanish: Nictibio urutaú.

PHYSICAL CHARACTERISTICS

13–16 in (33–41 cm); 5–7 oz. (145–202 g). Plumage varies from reddish brown to gray-brown. Sexes are similar.



Family: Potoos Vol. 9: Birds II

DISTRIBUTION

Central and South America from Costa Rica and Panama south to Uruguay.

HABITAT

Forest, woodland, plantations, and savanna with scattered trees.

BEHAVIOR

Roosts singly and quietly on branch during day. Active at night, when song of four to seven whistled notes is emitted.

FEEDING ECOLOGY AND DIET

Feeds on insects, including beetles, moths, grasshoppers, bugs, and termites, caught by sallying from perch.

REPRODUCTIVE BIOLOGY

Lays single egg in depression in sloping branch or near forking branches. Incubation by both sexes, lasts for 30–33 days. Young brooded by either parent when small, fledging period variously estimated as 40–51 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Like other potoos, the subject of myths and superstitions in some rural areas. ◆

Great potoo

Nyctibius grandis

TAXONOMY

Caprimulgus grandis Gmelin, 1789, Brazil and Cayenne. Two subspecies.

OTHER COMMON NAMES

English: Grand potoo; French: Grand ibijau; German: Riesentagschläfer; Spanish: Nictibio grande.

PHYSICAL CHARACTERISTICS

19–23 in (48–57 cm); 12.7–22 oz (360–624 g). The largest member of its genus. Overall color ranges from buff-brown to nearly white; the palest and most variable species of potoo. Sexes are similar.

DISTRIBUTION

Central and South America from southern Mexico to southeastern Brazil.

HABITAT

Forests, woodlands, and plantations.

BEHAVIOR

Roosts high in trees during day, active at dusk and during night. Calls most actively on moonlit nights, giving loud



guttural snoring sound from perch that functions in territorial defense.

FEEDING ECOLOGY AND DIET

Sallies for flying prey from an exposed perch, taking mainly insects such as beetles and moths, but sometimes also small bats.

REPRODUCTIVE BIOLOGY

Clutch of a single egg is laid in depression in branch of tree. Incubation by both sexes reported, period unknown. Fledging period of one nestling was at least 55 days.

CONSERVATION STATUS

Not threatened overall, but has doubtless declined in many regions because of deforestation.

SIGNIFICANCE TO HUMANS

Subject of mythology and superstition in rural areas. ◆

Resources

Books

Cohn-Haft, M. "Family Nyctibiidae (Potoos)." In *Handbook of Birds of the World*. Vol. 5, *Barn-owls to Hummingbirds*, edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal. Barcelona: Lynx Edicions, 1999.

Holyoak, D.T. Nightjars and Their Allies. Oxford: Oxford University Press, 2001.

Skutch, A. "Common Potoo." In *Birds of Tropical America*. Austin: University of Texas Press, 1983.

David T. Holyoak, PhD

Nightjars (Caprimulgidae)

Class Aves

Order Caprimulgiformes
Suborder Caprimulgi
Family Caprimulgidae

Thumbnail description

Small to medium-sized nocturnal and crepuscular birds with small bill, large gape and eyes, long wings and tail, short legs, cryptic coloration, and comb-like serrations on the claw of middle toe

Size

6-16 in (15-40 cm); 0.7-6.6 oz (20-188 g)

Number of genera, species

19 genera; 77 species

Habitat

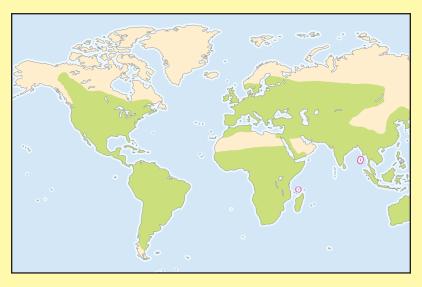
Semi-desert, grassland, savanna, woodland, and forest

Conservation status

Critically Endangered: 2 species; Endangered: 2

species; Vulnerable: 3 species; Near

Threatened: 4 species



Distribution

Nearly cosmopolitan, but absent from Arctic, Antarctic, and most oceanic islands

Evolution and systematics

Fossils of a single undescribed species of Caprimulgidae have been reported from the Middle Eocene (50.5–42 million years ago) oil shales at Messel in Germany, providing the only fossil record of a true nightjar from the Tertiary. Other fossils suggest that the closest relatives of the nightjars, the potoos (Nyctibiidae) and frogmouths (Podargidae), had diverged by the Eocene, and estimates based on differences in their DNA structures likewise point to early Tertiary origins of the nightjars.

Division of the Caprimulgidae into two subfamilies, the nighthawks (Chordeilinae) and nightjars (Caprimulginae), is based on several characters, of which the absence of rictal bristles in nighthawks is the most obvious (the rictus is the gape of a bird's mouth). Compared to the nightjars, nighthawks tend to have longer wings and tail and more often have a notched or forked tail, but there are exceptions. Originally, the Chordeilinae was established only for several American genera of nighthawks, but the African brown nightjar (Veles binotatus) and the Asian to Australasian eared nightjars (genus *Eurostopodus*) show similar characters, so these also should probably be included in the Chordeilinae. However, the so-called nacunda nighthawk (Podager nacunda) has well-developed rictal bristles and other characters like those of the true nightjars, so it seems best placed in the Caprimulginae.

The elaborately lined plumages of nightjars differ little between some species, yet other species are variable in color. It is therefore often difficult to classify nightjars into species and there is a tendency to rely on differences in songs and other evidence in seeking the best possible treatment, especially when similar forms occur in neighboring regions without range overlap. Such unsolved problems in the classification of species exist with the African fiery-necked nightjar (*Caprimulgus pectoralis*) and the closely related black-shouldered nightjar (*C. nigriscapularis*), which differ very slightly in appearance and have slightly different songs. Likewise, treatment of the eastern and western American forms of the whip-poor-will (*Caprimulgus vociferus*) as subspecies of a single species remains tentative because they are very similar in coloration but have slightly different voices.

Physical characteristics

Nightjars are small to rather large Caprimulgiformes with a relatively large head, large eyes, short neck, and very short legs. Although the bill is tiny, the huge gape allows large insects to be swallowed whole. The base of the bill often has strong rictal bristles (lacking in Chordeilinae), which may serve to direct prey into the gape, to protect the eyes from hard prey, or both. Wings are long to very long and more or less pointed, and the tail can be rather short to long with a graduated, rounded, square, notched, or forked tip. Toes are slender, and the claw of the middle toe has comb-like serrations that provide a unique feature of the Caprimulgidae within the order Caprimulgiformes.

A few species have elaborate long plumes that probably serve to exaggerate displays. In three South American species

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Profile of a whip-poor-will (*Caprimulgus vociferus*). (Photo by A. Morris/VIREO. Reproduced by permission.)

of the genus Macropsalis, adult males have deeply forked tails with greatly elongated outer feathers, which converge at their tips in the swallow-tailed nightjar (M. segmentata) and longtrained nightjar (M. forcipata) but converge subapically then diverge slightly at the extreme tips in the lyre-tailed nightjar (M. lyra). Adult males of two African species develop a single greatly elongated inner secondary feather that is retained only for part of each year. In the standard-winged nightjar (Macrodipteryx longipennis) the elongated feather consists only of a wire-like shaft except near the tip where it widens into a broad standard so that when the bird flies it seems to be closely followed by two large dark butterflies. The closely related pennant-winged nightjar (M. vexillarius) has the inner secondary modified to form a long narrow streamer. The exaggerated display plumes of the genera Macropsalis and Macrodipteryx appear to be associated with lek displays (a lek is a mating ground) in these species, which are the only polygynous (more than one female mate at a time) nightjars.

Nightjar plumages are marked in mainly somber shades of brown, gray, buff, tawny, or rufous and are often beautifully patterned with bars, streaks, and blotches to give some of the finest examples of concealing coloration of any animals. Thus, desert birds such as the aptly named golden nightjar (*Caprimulgus eximius*) tend to be pale to match the prevalent substrate, whereas birds of the dark forest interior

such as the brown nightjar are predominantly very dark brown or blackish. White or pale signal markings used in nightjar displays are normally kept concealed inside closed wings or tail or beneath the throat when the birds are at rest; they are revealed during nocturnal display flights or when singing.

Distribution

The range of caprimulgids is much wider than that of any other family in the order Caprimulgiformes, and many of the species are migratory, unlike the essentially sedentary birds in other families. Only the Arctic, Antarctic, and remote oceanic islands lack nightjars. The greatest diversity of species occurs in the tropics and subtropics. In North America the common nighthawk (*Chordeiles minor*) extends far north into Canada. In the Old World the European nightjar (*Caprimulgus europaeus*) extends north to the boreal forests of Finland and east to the semi-desert steppes of Mongolia. In the Southern Hemisphere, the band-winged nightjar (*Caprimulgus longirostris*) ranges south to Chile.

The diet of flying insects prevents most nightjars from remaining all year in regions with cold winters, although the common poorwill (Phalaenoptilus nuttallii) does so by hibernating. Other species that breed at high latitudes are longdistance migrants, the most striking examples being the common nighthawk, which leaves North America to winter in South America as far south as northern Argentina, and the European nightjar, which leaves Europe and Asia to winter in Africa south of the Sahara. Shorter migrations are undertaken by species such as the red-necked nightjar (Caprimulgus ruficollis), which breeds in Spain and winters south of the Sahara in west Africa, and the rufous-cheeked nightjar (C. rufigena), which breeds in South Africa and neighboring countries but migrates to spend the southern winter in tropical and subtropical countries of central Africa, especially Cameroon. Other species make seasonal movements from one vegetation zone to another within the tropics.

Habitat

Nightjars and nighthawks occupy a much broader range of habitats than do members of other families of Caprimulgiformes, which are often closely restricted to the ancestral rainforest habitats of the order. Instead of requiring trees for nest sites and hunting perches, the Caprimulgidae have evolved a predominance of ground nesting, and many species have the ability to hunt in sustained flight or by sallying from the ground, which enables them to live in grasslands, steppes, semi-deserts, savannas, and open woodlands. Few nightjar and nighthawk species live in closed forests, including both lowland and montane rainforests, and it is likely that species inhabiting such forests have reinvaded from more open habitats.

Several species have become urban dwellers, finding suitable nest sites on flat roofs of city buildings and plenty of insects to hunt around street lights and high in the air. Common nighthawks have adopted many North American cities over

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The white-throated nightjar (*Eurostopodus mystacalis*) chick exhibits a cryptic down color and frigid posture to avoid predation as it waits for its parents to return with insects for food (Mount Beerwah, Australia). (Photo by Wayne Lawler. Photo Researchers, Inc. Reproduced by permission.)

the twentieth century, and band-winged nightjars have colonized Rio de Janeiro (Brazil), Madagascar nightjars (*Caprimulgus madagascariensis*) occur in towns in Madagascar, and savanna nightjars (*C. affinis*) are at home in such large Indonesian cities as Jakarta and Surabaya.

Behavior

Like other Caprimulgiformes, nightjars and nighthawks are essentially crepuscular and nocturnal birds that sit quietly in roosts during the day and become active from around dusk until dawn. The timing of activities varies among species, season, and sometimes according to phase of the moon. The common nighthawk begins feeding much earlier in the evening than most nightjars, often hunting in the last of strong daylight well before dusk. Other species commonly remain immobile until little light is left and human observers can scarcely distinguish colors in the twilight; the late start to activity presumably serves to reduce risks of predation. Many nighthawks and nightjars do not hunt during the middle hours of moonless nights, apparently because they are unable to see prey when there is insufficient light; this hypothesis seems to be confirmed by the fact that some feed for much longer on moonlit nights.

Common poorwills are able to become torpid and hibernate for months in a rock crevice during cold winter conditions, but there is no evidence that any other species of the family makes such extensive use of torpor. Nevertheless, torpor lasting at least several hours has been reported from common nighthawks, lesser nighthawks (*Chordeiles acutipennis*),

and European nightjars that were cold, hungry, or both. It seems likely that entering torpor to reduce energy requirements is among the adaptations of Caprimulgidae that enable them to cope with an uncertain food supply.

Most nightjars have striking territorial songs that vary from clear loud whistles or whistled phrases to sustained churring, knocking, or purring sounds. The name nightjar derives from the prolonged jarring chur of the European nightjar, and the nocturnal vocalizations provide the first indication of the presence of most nightjar species for layman and ornithologist alike. Besides the song, the vocabulary of several of the better-known species includes a range of calls. The European nightjar uses at least 10 different types of calls, among which are special flight, alarm, threat, mating, brood-summoning, and food-begging calls. Mechanical wing clapping is also a feature of territorial display in the European nightjar and many other species.

Feeding ecology and diet

The diet of nightjars and nighthawks consists largely of insects. It typically includes beetles, moths, bugs, orthopterans, flies, termites, and flying ants, most if not all of which are caught in flight. Some nightjars take a small proportion of food from the ground or pick it from vegetation while hovering, and this behavior doubtless accounts for occasional wingless beetles, ants, or caterpillars that are eaten. Besides insects, spiders are occasionally eaten and there are a few records of centipedes, millipedes, and small snails in nightjar stomach contents. The rare records of seeds and other vegetable matter, however, may represent material accidentally ingested along with insects. The largest of all the nightjars, the chuck-will's-widow (Caprimulgus carolinensis), rarely eats tree frogs and very small birds, mainly warblers (Parulidae).

Two principal feeding techniques are used by nightjars and nighthawks, both of which lead to seizing prey in the bill while in flight and swallowing it whole. Hawking involves sustained flights during which the bird may catch numerous insects, often high in the air, but sometimes also low over the ground or water. Sallying involves a shorter flight from a perch or from the ground to catch an insect before returning to a perch. Most nighthawks and some nightjars rely almost exclusively on hawking for food, their long wings and strong flight evidently being adaptations for this. On the other hand, many nightjars of wooded or forest habitats rely mainly or exclusively on sallying. Others use both techniques. The European nightjar apparently chooses between them according to abundance and location of prey.

Because most feeding takes place in near-darkness, there has been much misunderstanding of how it is carried out. Many old accounts implied that nightjars fly about with the bill open, using it in the manner of a net to scoop up insects. This may occasionally be true, as when the bird flies through dense swarms of tiny insects such as mosquitos, but it is not the usual technique. Detailed studies of common nighthawks, common poorwills, and European nightjars show that individual insects are targeted and the bird only opens its bill to

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A group of sand-colored nighthawks (Chordeiles rupestris). (Photo by P. Robles Gil/VIREO. Reproduced by permission.)

seize them when they are closely approached. There seem to be clear preferences for larger insects, and limitations of the birds' eyesight may preclude feeding on the smallest prey (as opposed to considerations of cost-effectiveness).

Nightjars are adept at locating concentrations of insects prey and taking advantage of local superabundances of insects. Swarms of winged ants and termites, emerging caddis-flies, and mayflies at lakes may be targeted. Concentrations of insects around streetlights provide attractive food sources and artificial light may allow feeding later into the night than is possible under natural conditions. Nightjars also feed on insects flushed by grass fires in savanna regions of Africa and in open pine forests of the southeastern United States.

Reproductive biology

Most nightjars are monogamous, with pairs mating for life or breeding together for one season. Occasionally they may change partners between clutches in the same season. The pennantwinged and standard-winged nightjars have a different breeding strategy from other nightjars and are probably polygynous.

Breeding seasons of Caprimulgidae appear to be timed to coincide with presence of abundant flying insects needed to feed young. Species with northern ranges, such as common nighthawks or European nightjars, are rather late arriving as spring migrants and do not lay eggs until late spring. In tropical savannas, breeding typically occurs as the flush of new vegetation following seasonal rains allows a peak of insect abundance. The breeding season may be more prolonged in regions of the tropics with rain for much of the year, although caprimulgids usually avoid breeding in the months with high rainfall.

Unlike several other families of Caprimulgiformes, none of the nighthawks or nightjars makes a nest. Most choose a simple hollow in the ground, apparently without deliberately deepening it. A few species nest in depressions in tree branches, high above the ground in the case of short-tailed nighthawks (*Lurocalis semitorquatus*). The only account of the nest of the brown nightjar was of a bird apparently incubating or brooding on top of an arched frond of a *Raphia* palm in the Central African Republic. Nesting above ground is rare in Caprimulgidae and is apparently a secondary development from ground nesting, as no nest-building or other special adaptations are known to be involved.

Clutches are of one or two eggs, typically a single egg in tropical species and two eggs or variably one or two in others. Eggs are unmarked white in some species (for example most eggs of common poorwills), but more often they are spotted or blotched with shades of brown, gray, lavender, or black, which promotes concealment. Nevertheless, it is likely that there is little need for concealing coloration with eggs of most nighthawks and nightjars because an incubating adult bird would normally cover them almost continuously.

The role that males and females play in incubation varies considerably among species. In freckled nightjars (*Caprimulgus tristigma*) and fiery-necked nightjars, males incubate at night and the more cryptically colored females do so by day. In European nightjars, the male takes only a short stint at dusk and dawn while the female is away feeding. In polygynous pennant-winged and standard-winged nightjars, only the female incubates eggs. Incubation periods are unknown for many species, but typically they last about 17–20 days.

Young hatch with a covering of soft down that is replaced by the emerging juvenal feathers after about a week. Small Vol. 9: Birds II Family: Nightjars



Nacunda nighthawk (*Podager nacunda*) in flight. (Photo by T.J. Ulrich/VIREO. Reproduced by permission.)

young in down are brooded most of the time, but when they grow juvenal feathers they are typically brooded only when it is cold or wet. Even quite small young commonly walk from the original nest site and after a few days they may be many yards away from it. Fledging is a gradual process in that development of flying skills is progressive, with weak flapping usually possible after about two weeks but strong flight and independent feeding not until the fourth week. Typically, both parents are involved in brooding the young and feeding them on regurgitated insect food, but only the female carries out these duties in polygynous species.

Several of the nightjars are known to raise two broods each breeding season, and most if not all will lay replacement clutches if the first is lost. The two broods in European nightjars somewhat overlap, a response to the short northern breeding season. This is achieved because the male takes full charge of the young of the first brood while the female incubates the second clutch.

Many nightjar eggs and young are lost to predators, including birds such as crows, mammals such as rats and mice, and snakes. Much of the breeding behavior of nightjars is adapted to reduce risks of predation. For example, incubating birds crouch motionless with eyes almost closed, unwilling to leave the nest until almost trodden upon. When detected at the nest, adult nighthawks and nightjars commonly show threat or distraction displays intended to intimidate or distract potential predators. These displays have been well studied in lesser nighthawks; ground predators or less

dangerous intruders such as sheep or rabbits are confronted with a threat display in which the bird faces the intruder, erects its plumage with spread wings and tail, and at high intensity gapes and hisses. Walking humans or crows are met with distraction displays of disablement-lure type, in which the adult bird typically flutters along the ground as if injured, with trailing wings or flopping flight, attempting to lure the intruder away from eggs or chicks.

Conservation status

Two nightjar species are Critically Endangered: Jamaican poorwill (Siphonorhis americana; last reliably recorded in 1859) and Puerto Rican nightjar (Caprimulgus noctitherus). Two species are Endangered: white-winged nightjar (C. candicans) and Itombwe nightjar (C. prigoginei). Three species are listed as Vulnerable: Heinrich's nightjar (Eurostopodus diabolicus), Bonaparte's nightjar (C. concretus), and nechisar nightjar (C. solala). Four species are classified as Near Threatened: Salvadori's nightjar (C. pulchellus), sickle-winged nightjar (Eleothreptus anomalus), Chocó poorwill (N. rosenbergi), and plain-tailed nighthawk (Nyctiphrynus vielliardi). An additional three species are listed as Data Deficient.

Significance to humans

No nightjar species is of much economic importance and many of them are retiring birds that are little known to local people. However, their strange and often beautiful nocturnal



Common nighthawks (*Chordeiles minor*) mating. (Photo by T. Fink/VIREO. Reproduced by permission.)

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voices attract attention, and several species are the subject of folklore. A recurrent theme is the myth that nightjars suck milk from the teats of goats, resulting in widespread use of names such as goatsucker in English, Ziegenmelker in German, and Succiacapre in Italian. The scientific name of the principal nightjar genus, *Caprimulgus*, has the same origin, being formed from the Latin words *capra* for a goat and *mulgere* to milk. The basis for this groundless belief may lie in the frequent observation of milk on the ground near goats with newly-born kids coupled with presence of nightjars feed-

ing on insects near the animals at night and the fact that nightjars have an immensely wide mouth.

Other widespread beliefs are that the nocturnal calls of various nightjars are bad omens that may even foretell death. One local name for the European nightjar, the German *Todtenvögel*, means death bird. Elsewhere, the number of successive calls given by some South American nightjars was believed to foretell the number of years for which the listener would live, and other nightjar species were thought to represent spirits of the dead.



1. Standard-winged nightjar (*Macrodipteryx longipennis*); 2. Chuck-will's-widow (*Caprimulgus carolinensis*); 3. Fiery-necked nightjar (*Caprimulgus pectoralis*); 4. Gray nightjar (*Caprimulgus indicus*); 5. Common poorwill (*Phalaenoptilus nuttallii*); 6. European nightjar (*Caprimulgus europaeus*); 7. Whip-poor-will (*Caprimulgus vociferus*); 8. Common nighthawk (*Chordeiles minor*); 9. Large-tailed nightjar (*Caprimulgus macrurus*); 10. Spotted nightjar (*Eurostopodus guttatus*). (Illustration by Brian Cressman)

Family: Nightjars Vol. 9: Birds II

Species accounts

Common nighthawk

Chordeiles minor

SUBFAMILY

Chordeilinae

TAXONOMY

Caprimulgus minor J.R. Forster, 1771, South Carolina. Nine subspecies.

OTHER COMMON NAMES

English: Nighthawk, American or booming nighthawk; French: Engoulevent d'Amérique; German: Falkennachtschwalbe; Spanish: Añapero Yanqui.

PHYSICAL CHARACTERISTICS

8.7–9.7 in (22–25 cm); 1.4–3.8 oz (40–107 g). Dark brown, buff, grayish white, and cinnamon cryptic coloration. Sexually dimorphic.



DISTRIBUTION

Breeds over much of North and Central America from Canada to Panama; winters in South America from Ecuador to northern Argentina.

HABITAT

Mainly in open habitats, including woodland clearings, prairies, savannas, sand dunes, and cities.

BEHAVIOR

Active from well before dusk until after dawn, often flying high in air. Commonly in flocks outside breeding season, sometimes of up to a thousand birds. Displaying male makes booming sound as air rushes through primaries during aerial dive.

FEEDING ECOLOGY AND DIET

Catches diet of insects mainly on wing during continuous hawking flight; regularly takes insects that have been attracted to street lights.

REPRODUCTIVE BIOLOGY

Unlined nest site on ground (or flat roof of building) with clutch of two eggs. Incubation usually by female for a period of 18–20 days. Young have cryptically patterned down, are fed by both parents, and fledge at 25–30 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

More often noticed by humans than most other nightjars in North America because of habit of nesting on flat roofs of buildings in towns and cities and activity and calls during twilight or even daylight. ◆

Spotted nightjar

Eurostopodus guttatus

SUBFAMILY

Chordeilinae

TAXONOMY

Eurostopodus guttatus Vigors and Horsfield, 1826, New South Wales. Monotypic.

OTHER COMMON NAMES

English: Spotted eared-nightjar; French: Engoulevent argus; German: Argusnachtschwalbe; Spanish: Chotacabras Argos.

PHYSICAL CHARACTERISTICS

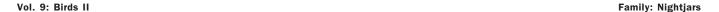
11.5–13.2 in (29–33 cm); 2.8–3.7 oz (80–104 g). Grayish brown, grayish white, tawny, and buff cryptic coloration. Sexes are similar.

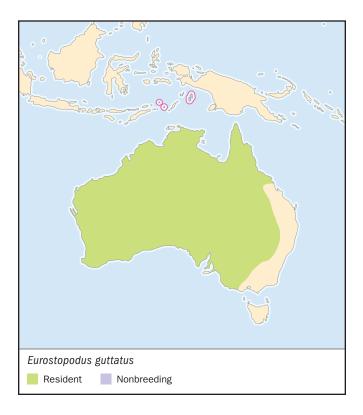
DISTRIBUTION

Breeds over much of Australia west of the Great Dividing Range; winters mainly in north of breeding range, but migratory stragglers recorded from islands north of Australia.

HABITAT

Open woodlands, grasslands.







Roosts on ground during daytime; active from dusk until before dawn. Musical song advertises territories. Song commences with two to five up-slurred units then concludes with eight to 15 higher-pitched clinking double units, all on the same pitch.

FEEDING ECOLOGY AND DIET

Feeds on insects, mainly caught in sustained hawking flight over the territory after dusk and before dawn.

REPRODUCTIVE BIOLOGY

Nest is an unlined scrape in ground with clutch of single egg. The egg is greenish with dark spots. Small young have reddish brown down. Incubation apparently by both sexes, period unknown. Young can flutter short distances after 18–20 days.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

A retiring nocturnal bird of the Australian outback, unfamiliar even to most country dwellers except by its nocturnal calls. According to the superstition of some Australian aboriginals, this species took away babies during the night. ◆

Common poorwill

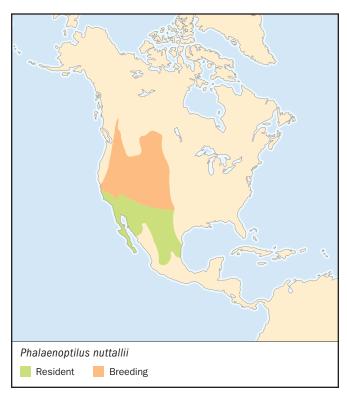
Phalaenoptilus nuttallii

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus nuttallii Audubon, 1844, eastern side of the upper Missouri River. Five subspecies.



OTHER COMMON NAMES

English: Poorwill; French: Engoulevent de Nuttall; German: Winternachtschwalbe; Spanish: Chotacabras Pachacua.

PHYSICAL CHARACTERISTICS

6.7–8.7 in (17–22 cm); 1.1–2.0 oz (32–58 g). Grayish brown, grayish white, blackish brown, and buff cryptic coloration. Sexes marginally dimorphic.

DISTRIBUTION

Breeds in western North America from southern Canada to northern Mexico, leaving northern part of range for winter.

HABITAT

Open woodland, scrub, prairies, canyons.

BEHAVIOR

Roosts on bare ground during day, becoming active from around dusk until before dawn. May become torpid and hibernate in rock crevice for months during winter. Song sounds like "poor-will-ip."

FEEDING ECOLOGY AND DIET

Catches insect prey mainly on short sallying flights from low perch or ground.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two unmarked, white eggs. Incubation period 20–21 days; both sexes incubate. Small young have vinaceous-buff down with dark markings. Young make first flight at 20–23 days old.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Living birds poorly known even to local people. Species has become famous among ornithologists as best example of a bird that hibernates. •

Family: Nightjars Vol. 9: Birds II

Chuck-will's-widow

Caprimulgus carolinensis

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus carolinensis Gmelin, 1789, South Carolina. Monotypic.

OTHER COMMON NAMES

English: Carolina chuck-will, chuck; French: Engoulevent de Caroline; German: Carolinanachtschwalbe; Spanish: Chotacabras de la Carolina.

PHYSICAL CHARACTERISTICS

11–23 in (28–33 cm); 3.3–5.2 (94–147 g). Brown, blackish brown, buffish white, and white cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Breeds in eastern and southeastern USA; winters from Florida and West Indies through Central America to Colombia and northern Venezuela.

HABITAT

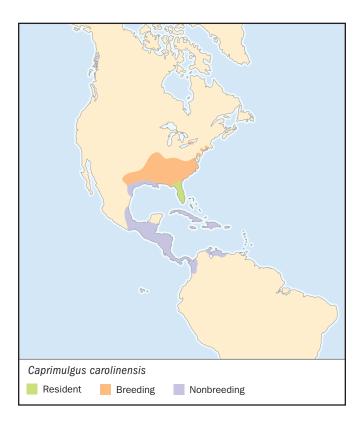
Woodland and forests. Often sits and calls at night from gravel roads

BEHAVIOR

Roosts during day; active mainly at dusk and before dawn. Song "chuck willow willah" is basis of English name, the initial "chuck" is often inaudible.

FEEDING ECOLOGY AND DIET

Feeds mainly on insects caught on sallying flights from ground or perch. Occasionally recorded feeding on small birds.



REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two eggs that are cream with dark blotches and spots. Incubation by female for period of around 20 days. Small young are golden-brown, paler beneath. Young can fly when 16–17 days old.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Rarely noticed by humans, except for its distinctive nocturnal song. ◆

Whip-poor-will

Caprimulgus vociferus

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus vociferus Wilson, 1812, eastern United States. Six subspecies.

OTHER COMMON NAMES

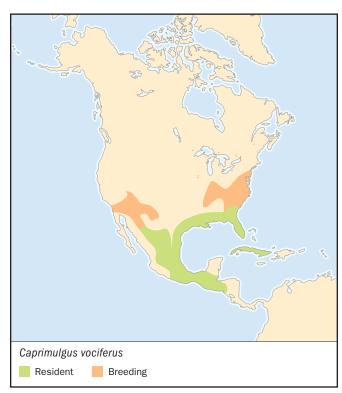
French: Engoulevent bois-pourri; German: Schwarzkehlnachtschwalbe; Spanish: Chotacabras Cuerporruín.

PHYSICAL CHARACTERISTICS

9–10 in (23–26 cm); 1.5–2.4 oz (42–69 g). Grayish brown, blackish brown, tawny, buff, and whitish cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Breeds in eastern North America from southern Canada southwards, in Cuba, and in Central America south to Honduras; migrates from northern part of range for winter.



Vol. 9: Birds II Family: Nightjars

HABITAT

Forests and open woodlands.

BEHAVIOR

Roosts during day; active from dusk until before dawn. Distinctive nocturnal song "whip' poor weel'" is basis of English name.

FEEDING ECOLOGY AND DIET

Feeds on insects caught in flight, often on short sallying flights from a perch.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two eggs. Eggs are white to pale cream, usually with spots or small blotches of gray and brown. Incubation mainly by female for period of 19–20 days. Small young have pale buff to yellowish brown down. Young can first fly when about 20 days old.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Rarely noticed by humans, except for its distinctive nocturnal calls. lacktriangle

Gray nightjar

Caprimulgus indicus

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus indicus Latham, 1790, India. Five subspecies.

OTHER COMMON NAMES

English: Japanese, jungle, or migratory nightjar; French: Engoulevent jotaka; German: Dschungelnachtschwalbe; Spanish: Chotacabras de Jungla.

PHYSICAL CHARACTERISTICS

8.3–11.4 in (21–29 cm); 2.4–3.8 oz (69–107 g). Grayish brown, blackish brown, buff, tawny, brown, and grayish white cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Breeds in southern and eastern Asia from India to northeast China and Japan; northern populations migrate to winter south to Java.

HABITAT

Open forests, woodlands, scrub, and farmland.

BEHAVIOR

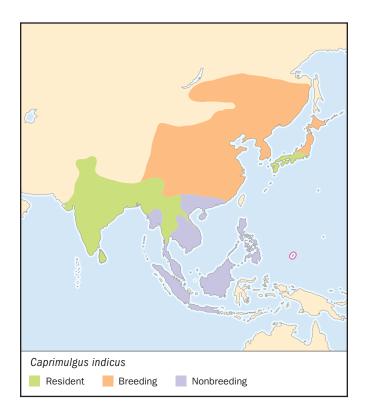
Roosts during day; active mainly at dusk and before dawn. Territorial song a long series of rapidly repeated knocking sounds.

FEEDING ECOLOGY AND DIET

Catches insect prey in sustained hawking flight and by shorter sallying flights from perches.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two eggs. Eggs are white, pale cream, or pale gray, marbled with dark brown or grayish, with overlying spots of clear gray. Incubation mostly



by female, for period of 16–17 days. Small young have tawny down. Fledging period probably about 18 days.

CONSERVATION STATUS

Species is not threatened, but endemic subspecies in Palau Islands is uncommon and declining.

SIGNIFICANCE TO HUMANS

Infrequently noticed by local people, except for nocturnal songs. \spadesuit

European nightjar

Caprimulgus europaeus

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus europaeus Linnaeus, 1758, Sweden. Six subspecies.

OTHER COMMON NAMES

English: Common goatsucker; French: Engoulevent d'Europe; German: Ziegenmelker; Spanish: Chotacabras Europeo.

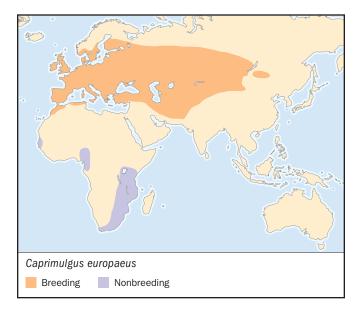
PHYSICAL CHARACTERISTICS

10–11 in (25–28 cm); 1.2–3.6 oz (35–101 g). Grayish brown, blackish brown, buff, brown, and whitish cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Breeds across most of Europe and North Africa and east across Asia to Outer Mongolia; all populations migrate to winter in Africa south of Sahara.





HABITAT

Breeds in open woodland, heath, sand dunes, steppe, and semidesert; winters in savannas and woodlands.

BEHAVIOR

Roosts during daytime; active from before dusk until dawn. Prolonged churring song serves to advertise territory. Song is a sustained tremolo, alternating between lower-pitched screeches and slower, higher-pitched screeches, and ending in a quiet bubbling trill, the whole often lasting five minutes.

FEEDING ECOLOGY AND DIET

Catches insect prey in sustained hawking flights or in short sallying flights from perches.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two eggs. Eggs are pale gray to cream with dark blotches and spots. Incubation mainly by female for 17 days. Small young have cream-buff down. Young tended by one or both parents; able to fly when about 17 days old.

CONSERVATION STATUS

Not globally threatened, but declining in some European countries such as Ireland.

SIGNIFICANCE TO HUMANS

Infrequently noticed by local people, except for its churring nocturnal song. ◆

Large-tailed nightjar

Caprimulgus macrurus

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus macrurus Horsfield, 1821, Java. Seven subspecies.



OTHER COMMON NAMES

English: Horsfield's or long-tailed nightjar; French: Engoulevent de Horsfield; German: Langschwanz-Nachtschwalbe; Spanish: Chotacabras Macruro.

PHYSICAL CHARACTERISTICS

10–13 in (25–33 cm); 1.9–2.7 oz (55–78 g). Grayish brown, blackish brown, buff, and white cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Southern Asia from northeast Pakistan to Hainan, south through East Indies to northern and eastern Australia.

HABITAT

Open forests, woodland, scrub, and plantations.

BEHAVIOI

Roosts during daytime, usually on ground. Active from dusk until before dawn. Territorial song a monotonous "t-chop" repeated in long series.

FEEDING ECOLOGY AND DIET

Hunts for insect prey using prolonged hawking flights and by shorter sallying flights from perches or ground.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch of two eggs. Incubation at least mainly by female. Eggs are pale cream to dull buff with blackish brown spots. Incubation period is 21–22 days; fledging period is about three weeks. Small young have buff down.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Noticed mainly by nocturnal song, from which local names such as axe-, carpenter-, or hammer-bird are derived. ◆

Vol. 9: Birds II Family: Nightjars

Fiery-necked nightjar

Caprimulgus pectoralis

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus pectoralis Cuvier, 1816, Western Cape, South Africa. Four subspecies.

OTHER COMMON NAMES

English: Pectoral nightjar; French: Engoulevent musicien; German: Pfeifnachtschwalbe; Spanish: Chotacabras Músico.

PHYSICAL CHARACTERISTICS

9–10 in (23–25 cm); 1.2–2.5 oz (35–70 g). Dark brown, grayish brown, brownish white, buff, tawny, and white cryptic coloration. Sexually dimorphic.

DISTRIBUTION

Africa from Kenya and Angola south to South Africa.

HABITAT

Woodlands and forest edges.

BEHAVIOR

Roosts on ground during day; active mainly from dusk to dawn. Distinctive territorial song a whistled phrase rendered as *Good Lord deliver us*.

FEEDING ECOLOGY AND DIET

Catches insect prey on sallying flights from perches.

REPRODUCTIVE BIOLOGY

Unlined nest on ground with clutch usually of two eggs. Eggs are white to pale pink, usually with brownish spots. Incubation by female during day, by male at night, period 18 days. Small

Caprimulgus pectoralis

■ Resident

young have brownish down. Young able to fly when about 18 days old.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

Usually not noticed by local people, except for its nocturnal songs. lacktriangle

Standard-winged nightjar

Macrodipteryx longipennis

SUBFAMILY

Caprimulginae

TAXONOMY

Caprimulgus longipennis Shaw, 1796, Sierra Leone. Monotypic.

OTHER COMMON NAMES

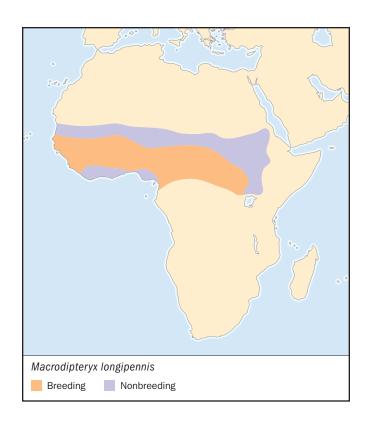
French: Engoulevent à balanciers; German: Fahnennachtschwalbe; Spanish: Chotacabras Portaestandarte.

PHYSICAL CHARACTERISTICS

8–9 in (20–23 cm), excluding long standards on wings of breeding male; 1.3–2.3 oz (37–65 g). Sexually dimorphic. Variable cryptic coloration; males often blacker with whiter speckles, while females are more buffy or sandy. Breeding males have unmistakable standards (extremely elongated second innermost primaries) on wings.

DISTRIBUTION

West and central Africa from the Gambia to southwest Sudan.



Family: Nightjars Vol. 9: Birds II

HABITAT

Lightly wooded or bushy savannas.

BEHAVIOR

Roosts on ground during day; active from dusk until before dawn. Males assemble to display at leks that are visited by females.

FEEDING ECOLOGY AND DIET

Feeds on insects caught in sustained hawking flights.

REPRODUCTIVE BIOLOGY

Unlike most members of the Caprimulgidae, probably polygynous. Unlined nest on ground with clutch of one or two eggs.

Eggs are pale pink to buff-gray or brown, with dark spots of blotches. Incubation and care of young carried out by female alone. Small young have down that is buff, mottled with black on upperparts.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

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David T. Holyoak, PhD

Apodiformes

(Swifts and hummingbirds)

Class Aves

Order Apodiformes

Number of families 3

Number of genera, species 121 genera; 431 species

Photo: White-whiskered hermit hummingbird (*Phaethornis yaruqui*) in Ecuador. (Photo by Anthony Mercieca. Photo Researchers, Inc. Reproduced by permission.)



Evolution and systematics

Eighteenth-century classification kept swifts and hummingbirds well apart. Swifts and swallows were usually placed in the same family, while hummingbirds were often linked with other birds with fine bills, such as hoopoes or sunbirds. By the mid-nineteenth century, a relationship between swifts and hummingbirds was generally, although not universally, accepted. In 1892, Ridgeway wrote: "The Humming Birds and Swifts…agree in numerous anatomical characters, and there can be no doubt that they are more closely related to each other than are either to any other group of birds."

Even with a lack of fossil evidence for hummingbirds, morphological similarities, together with the results of biochemical analysis, unite modern ornithologists in treating swifts, treeswifts, and hummingbirds as monophyletic. Sibley and Ahlquist used DNA analysis to support their conclusion that the families diverged in the late Cretaceous or early Tertiary Period (65–70 million years ago). Schuchmann concurs, identifying the breaking off, from Gondwana, of a tectonic plate that became South America as the physical moment of divergence.

The Apodiformes are divided into three families. The suborder Apodi contains both the true swifts Apodidae and the treeswifts Hemiprocnidae. The latter family—whose name derives from *hemi progne*, meaning "half swallow"—has significant anatomical features that distinguish it from true swifts, including the presence of a non-reversible hind toe, soft feathering with down on the flanks, and the absence of a claw on the manus. The Apodidae are generally divided into two sub families. The Cypseloidinae are considered the most primitive. They do not use saliva in nestbuilding, possess two carotid arteries, and have a simple palate. Relationships among the 17 genera and species within the more advanced Apodinae are the subject of some disagreement.

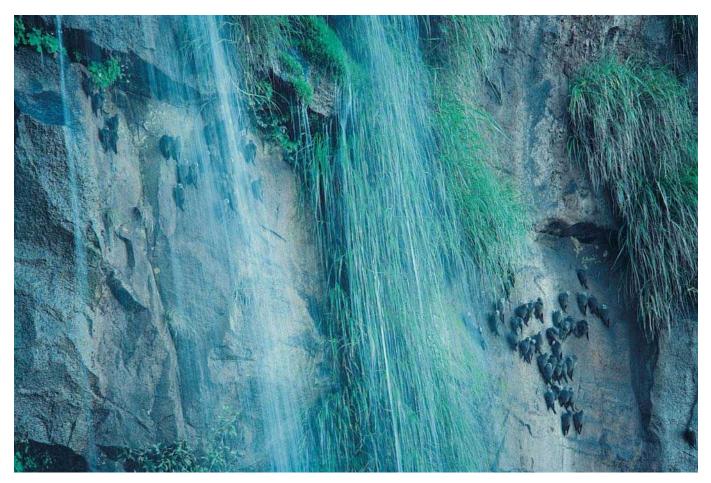
Classification of hummingbirds is even more controversial. The crude division proposed by Gould in 1861 is still accepted (as of 2001). This separates the subfamily Phaethornithinae, comprising the hermits, from the Trochilinae, or typical hummingbirds.

Physical characteristics

All Apodiformes are small to very small birds. Morphologically, the most striking shared feature is the wing structure. The sternum is long and, in the case of hummingbirds, deeply keeled. The coracoid bones linking the sternum and the humerus are particularly strong. Apodiformes are unique in having shallow ball and cup sockets connecting the coracoids to the sternum. The humerus, radius, and ulna are all relatively short, but the carpal bones are exceptionally long. The total length of the "hand" bones is nearly twice that of the "arm" bones. The corresponding wing feathers are also a distinctive feature of this order. Apodiformes have 10 long primaries and normally six to seven short secondaries. In swifts, the longest primary is three times the length of the shortest secondary.

Although all Apodiform wing structures are very similar, different methods of flight mean that flight musculature is adapted accordingly. Hummingbirds' reliance on hovering flight with rapid wing beats means that they need extremely powerful flight muscles. The flight muscles make up 30% of a hummingbird's body mass. By comparison, swifts rely far more on gliding, rather than flapping, flight. The flight muscles of the Alpine swift (*Tachymarptis melba*), for example, make up only 16% of its body mass.

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Great dusky swifts (Cypseloides senex) at rest behind a waterfall at Iguassu, Brazil. (Photo by M.P.L. Fogden. Bruce Coleman Inc. Reproduced by permission.)

The tail of a typical Apodiform has 10 rectrices. In most swifts and some hummingbirds, it is forked, and in a number of species, the tail feathers may be longer than the body length. The tail feathers play a critical part in steering; swifts are able to make slight directional adjustments at speed, while hummingbirds tilt their tails to lift, lower, and brake. Longtailed swifts such as needletails also use their stiffened tail feathers to provide support when clinging to vertical surfaces.

Apodiformes have small feet that are useless for walking. The genus name *Apus* is from the Greek *a pous*, meaning "without foot," but this is misleading. The small, strong, sharp claws are well adapted to clinging on vertical surfaces, with the hind toe in line so that all four toes face forward to secure a better grip. Hummingbird feet are too small and weak for walking or climbing. The birds' reliance on hovering flight, and the aerodynamic difficulties that would be posed by having larger feet, mean that tiny hummingbird feet are only suitable for perching.

In plumage, swifts and hummingbirds offer a huge contrast. Swift body plumage is usually glossy, with predominantly drab brown or black feathers. Conversely, body feathers of male hummingbirds offer a dazzling display of iridescent colors. Female hummingbird plumage is normally cryptic to aid in concealment when nesting. Males rely on

bright plumage both for self-advertisement to potential mates and to warn off intruders from their territory.

All Apodiformes show similar, or shared, physiological adaptations for their extreme lifestyles. They have a relatively short gut and the caecum, which is important in plant-eating bird species, is either absent or vestigial. The three families share a unique type of malate dehydrogenase, an enzyme that catalyzes the formation of hydrogen. Erythrocytes in the blood of swifts tend to be large, enabling the birds to maximize oxygen intake from air at high altitudes. Hummingbirds have the highest known density of erythrocytes in any bird taxon, with 6.59 million per cubic milliliter. They also have the largest relative heart size and fastest heartbeat—1,260 beats per minute in the blue-throated hummingbird (*Lampornis clemenciae*). All these features allow hummingbirds to process large amounts of oxygen to sustain their energy-demanding flight.

At least two swift species share with hummingbirds and some Caprimulgiformes the ability to enter periods of torpidity to conserve energy. The white-throated needletail's (*Hirundapus caudacutus*) body temperature has been recorded dropping from 101°F (38.5°C) to 82°F (28°C) overnight. It is possible that future research will show that the white-throated swift (*Aeronautes saxatalis*) is not the only other swift

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to achieve a state of torpidity. This energy-saving mechanism exists in possibly all Neotropical hummingbirds. Nocturnal torpor may lower the body metabolism by 80–90%, with body temperature held at 64–68°F (18–20°C) and heartbeat reduced to about 50 beats per minute.

Distribution

Apodiformes are highly specialized feeders and this governs their distribution. Although hummingbirds are found from southernmost South America to Alaska, their dependence on nectar for food means that they are absent from tundra areas of Alaska and northern Canada. Swifts have successfully colonized most land areas of the planet, but their reliance on aerial plankton excludes them from the coldest parts of the Arctic and Antarctic, as well as the most arid desert areas. Food that is only seasonally available forces species breeding in north temperate areas to migrate south for the winter.

Habitat

Most swifts are highly mobile aerial feeders, hunting for insects over a wide range of terrestrial habitats, from marshy meadows to city office blocks. During the breeding season, swifts in temperate areas may travel great distances to escape severe weather—common swifts (*Apus apus*) have been recorded making round trips of up to 1,242 mi (2,000 km). Only a small number of Apodi are confined to particular habitats, including wholly tropical forest-dwelling species such as the whiskered treeswift (*Hemiprocne comata*). Most species of swiftlet appear to be sedentary, using the same caves or places nearby for roosting and nesting.

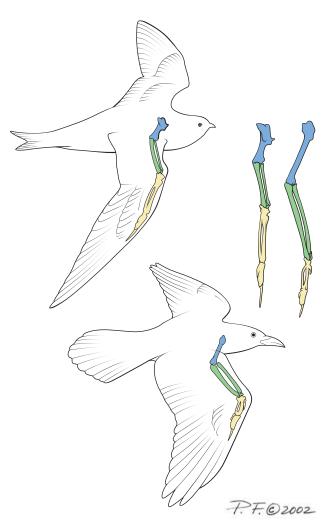
Hummingbirds have adapted successfully to everywhere in the New World where there are sources of nectar. Even in the high Andes mountains, helmetcrests and hillstars are able to exploit nectar, while adapting physiologically to extreme weather conditions.

Behavior

In behavior, swifts and treeswifts are often diametrically opposed to hummingbirds. Social organization in hummingbirds is non-existent, except for the brief mating period. Otherwise, they tend to be solitary, with males of many species aggressively defending feeding territories, often using a range of chase calls to warn off intruders. Swifts, by contrast, are usually highly gregarious, feeding, roosting, and nesting in colonies, which can be large. One Oregon autumn roost of Vaux's swift (*Chaetura vauxi*) had around 25,000 birds. These behavioral differences are adaptive: individual hummingbirds guard sources of nectar; swifts feeding on aerial insects and roosting or nesting on cave or cliff ledges are generally not competitive, and may benefit by sharing sometimes-limited nest caves and perhaps in locating concentrations of flying insects.

Feeding ecology and diet

Among Apodiformes, hummingbirds are the most specialized feeders. They drink nectar by probing plant corollas using an extended biforked tongue, usually in a long bill. The



The humerus bone is colored blue; the radius and ulna are green; and the carpus is yellow in this illustration. A swift (top) has a longer carpus, with longer primaries attached to the carpus compared to a passerine bird (bottom). (Illustration by Patricia Ferrer)

specialization is such that thousands of plants are exclusively ornithophilous—dependent on hummingbirds for pollination. The birds also glean insects and spiders from leaves and flowers, an essential protein supplement to their diet. Swifts eat only insects and arachnids, almost always taken in the air. The size of prey taken is related to the size of the bird, with larger swifts taking fewer, bigger prey items. The gape is wide, with guard feathers in front of large, deep-set eyes. These feathers are moved by muscles and probably serve to cut glare from the sun.

Swifts and hummingbirds share a cervical muscular adaptation that enables them to make rapid head movements. The relatively long splenius capitus muscle enables Apodiformes to move their heads quickly to catch insects in fast flight.

Reproductive biology

Apodiformes breed during periods of peak food availability. In hummingbirds, this is usually when the greatest number of Order: Apodiformes Vol. 9: Birds II

bird-pollinated plants are in flower. In swifts it is during the temperate summer or the tropical wet season when insects abound. Aerial displays play a significant role in courtship. Swifts are monogamous, with pair bonds lasting through the nesting season, as both parents tend the young. Hummingbirds are polygamous; once mated, the male plays no further part in care of the young.

Most apodiform nests are open cup constructions, held together, in the case of hummingbirds, by spiders' webs; in swifts with saliva. Because of their high dependence on flight, Apodiformes invariably build their nests with clear flightpaths in front of them. The eggs are white and oval, and most species have a clutch of one or two eggs. Some *Chaetura* and *Hirundapus* swifts are exceptional in having up to seven. Once hatched, the naked, or near-naked, young remain as nestlings for a comparatively long period in relation to the birds' size: this may be to compensate for irregular food supplies, as adults are away from the nest for long periods. Young swifts are fully independent once fledged, while hummingbirds rely wholly on the adult female for food for at least 18 days after leaving the nest.

Conservation status

Fewer than a tenth of Apodiformes are under a serious level of threat, ranging in increasing degree from Endangered and Vulnerable to Critically Endangered. Downward population trends are evident for 24 of these species. An additional 22 species are classified as Near Threatened.

Historically, none of the species in this order appears to have been regarded as any economic threat. Exploitation for financial gain, however, has been widespread and, in the case of swiftlets, continues. Numbers of Mascarene (*Collocalia francica*) and Seychelles (*Collocalia elaphra*) swiftlets have been seriously reduced by collection of nests for birds' nest soup, a dish popular in southeast Asia.

Habitat degradation and destruction are the biggest threats facing Apodiformes today, with hummingbirds in Central and South America particularly threatened. Lower montane forests are being logged and cleared to make way for such diverse activities as cattle ranching; coffee, coca, marijuana, sugarcane, and citrus plantations; mining; and charcoal. The cutting of roads through previously inaccessible areas and subsequent forest destruction are now affecting species such as the chestnut-bellied hummingbird (Amazilia castaneiventris) of Colombia and the Peruvian piedtail (Phlogophilus harterti). Human encroachment onto the upper forest slopes continues, with a number of endangered species, such as the royal sunangel (Heliangelus regalis) and violet-throated metaltail (Metallura baroni), being affected by accidental fires, which are started when vegetation below the treeline is burned off to promote fresh growth of grass for grazing. Modern machinery is enabling logging of some upper montane areas, threatening species such as the white-tailed hummingbird (Eupherusa poliocerca).

Island endemics are often at risk from introduced predators. Such a threat faces a number of Apodiformes: the Tahiti swiftlet (*Collocalia leucophaeus*) is probably affected by common mynas, swamp harriers, and possibly other introduced species.

The Guam swiftlet (*Collocalia bartschi*) is hunted by the introduced brown tree snake, and the Juan Fernandez firecrown (*Sephanoides fernandensis*) is killed by rats, cats, and coatis. Tiny endemic populations are also vulnerable to pressure from tourism. The caves of both the Atiu (*Collocalia sawtelli*) and Mascarene swiftlet have been disturbed by an increase in human visitors.

The effects of intensive agriculture on apodids are less easy to quantify. There may be visible impacts on island and restricted-range species; for example, the use of pesticides and drainage of wetlands have probably reduced the numbers of Seychelles swiftlets. But accurately monitoring wide-ranging, aerial plankton feeders is difficult.

Conservation efforts to alleviate the problems facing Apodiformes are fraught with difficulty. Many well-forested areas are relatively inaccessible by virtue of geography or political instability, making true assessments of population levels impossible. Targets set by BirdLife International for species such as the black inca (*Coeligena prunellei*) start with the need for full monitoring.

Even when population ranges are known, and protected areas are established, conservation attempts to safeguard key areas are often hampered by an inability to enforce legal protection. Whitehead's swiftlets (*Collocalia whiteheadi*) on the Mount Matutum Reserve in the Philippines are vulnerable to illegal logging, and the mangrove hummingbird (*Polyerata boucardi*) is threatened by cutting of mangroves in Costa Rica, even though such activity is banned.

Significance to humans

Their distinctive habits and appearance have given hummingbirds significant roles in the cultures of native American peoples for millennia. The North American Cherokee, Fox, and Creek people have stories related to the birds' speed. Numerous ingenious legends revolve around their feeding techniques; the Ge people of Brazil had a legend in which a bird sucked a biting ant out of the inside of a man's ear. The most famous hummingbird legends are associated with the Aztecs, whose most important god, Huitzilopochtli, has a name that translates as "Hummingbird from the left." This god was depicted as wearing the head of a hummingbird as his helmet. Warriors who fell in battle were believed to resurrect as hummingbirds. The Aztec king Montezuma wore hummingbird feathers as part of his elaborate headdress. Europeans continued the fascination with and desire to collect colorful hummingbird feathers, most destructively in the nineteenth and early twentieth centuries, when millions of hummingbirds were slaughtered for their feathers. Between 1904 and 1911, 152,000 hummingbirds were imported from North America to London to adorn ladies' hats. Today, direct persecution of hummingbirds is rare. Thousands of backyard feeders throughout North America testify to the birds' popularity with humans.

The word swift is derived from the Old English *swifan*, meaning fast. The dark, screaming, sickle-shaped common swift inspired both fear and awe in medieval Europe. In Eng-

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land, it was known as the devil bird. Yet in their nesting habits, many species of swift have enjoyed a physically close association with humans. The common and chimney (*Chaetura pelagica*) swifts rarely choose anything but artificial nest sites.

The nests of swiftlets in southeast Asia have been prized as food by humans for at least a thousand years. The trade is still enormously popular. In the 1980s, Hong Kong alone imported nests worth up to an estimated \$39 million.

Resources

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Derek William Niemann



Class Aves

Order Apodiformes

Suborder Apodi

Family Apodidae

Thumbnail description

Small to medium-sized, fast flying birds with narrow swept-back wings, square to deeply forked tails, small bills and feet, and sometimes distinctive screaming vocalizations

Size

3.4-9.6 in (9-25 cm); 0.2-7.6 oz (5-205 g)

Number of genera, species

18 genera; 99 species

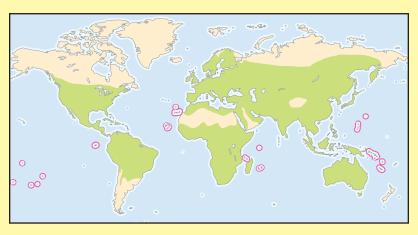
Habitat

Wide-ranging aerial foragers, but dependent on cliffs, hollow trees, or caves for nesting and roosting sites

Conservation status

Endangered: 1 species; Vulnerable: 5 species; Near Threatened: 5 species; Data deficient: 6

species



Distribution

Nearly worldwide except for coldest and treeless areas of northern hemisphere; most numerous in warmer tropical regions

Evolution and systematics

Swifts are highly specialized, generally fast flying, aerial foragers that rarely come to earth except at nest or roost sites. There have been suggestions of a swift-swallow relationship and an affinity between swifts and hummingbirds. Caprimulgids have also been frequently mentioned as a possibly closely allied group. The view that swifts and hummingbirds are related is influenced by the greatly shortened humerus and elongated distal portion of the wings. More recent DNA evidence has supported this.

The intrafamilial relationships of the swifts have also been debated over the years. Today, consensus supports there being three subfamilies: Cypseloidinae, Chaeturinae, and Apodinae. The Cypseloidinae (two genera; 12 species), with the least derived, or shortened, humerus, are presumed to be the most primitive of the swifts and are today confined to North and South America and the West Indies. Their distinctive habit of nesting and roosting in dark damp areas near or behind waterfalls or in sea caves set them apart from the other swifts.

The Chaeturinae are often called spinetails as many have stiffened shafts with bare tips to the tail feathers and use them for support while perching on vertical surfaces. This subfamily consists of 58 species in 10 genera. It includes the bewildering array of morphologically similar swiftlets or cave swiftlets of Southeast Asia, northern Australia, and many islands in the Indian and Pacific oceans. Determining the species limits among this group has been considered to be among the most daunting in ornithology and has led to most

of the variation in the number of species, from 90–99, attributed to the family. Their use of echo-location and the commercial exploitation of their nests further contributes to the uniqueness of the swiftlets.

The Apodinae have a unique lateral grasping foot where toes one and two oppose toes three and four. The Apodinae, the second largest subfamily, consists of 29 species in six genera, including the widespread genus *Apus* as well as five species of palm-swifts.

Physical characteristics

Swifts are true masters of the aerial environment. With their long narrow swept-back wings, their flight is rapid with frequent changes in direction to capture prey. In some, the rushing noise of their wings or screaming cries announce their presence even before they come into view. Swifts are similar in having narrow-pointed wings with seven to nine secondaries and 10 primaries, the outermost being greatly elongated and more than twice the length of the innermost. They have different tail shapes with many being slightly rounded, square, or shallowly notched, while others are deeply forked. Swifts also differ greatly in size. Body lengths vary from 3.5-9.8 in (9-25 cm) and weights from about 0.17-7.2 oz (5 g-205 g). Among the smallest are the pygmy swiftlet (Collocalia troglodytes) of the Philippines and the pygmy palm-swift (Micropanyptila furcata) in Venezuela. The white-naped swift (Streptoprocne semicollaris) of western Mexico and the purple needletail (Hirundapus celebensis) from the Celebes vie for

Family: Swifts Vol. 9: Birds II



A chimney swift (*Chaetura pelagica*) adult feeding chicks at the nest. (Photo by Ron Austing. Photo Researchers, Inc. Reproduced by permission.)

honors as the largest, while the widespread and familiar white-collared swift (*Streptoprocne zonaris*) in the Neotropics and the alpine swift (*Apus melba*) are intermediate in mass between these extremes.

Generally, swifts are dull-colored creatures with only the chestnut-collared swift (*Cypseloides rutilus*) and Tepui swift (*Cypseloides phelpsi*) having a rich chestnut red in addition to the browns, grays, black, and varying amounts of white found in other species. Several swifts have a faint to pronounced greenish irridescent sheen to their freshly molted feathers, but this is largely unobservable except for birds in the hand. In all but a few species, males and females are not separable by external appearance and, in nearly all, there is no appreciable difference in size or mass. The bill of all swifts is small but the gape is large, facilitating capture of aerial prey.

Distribution

Swifts are decidedly more common in the tropical parts of the world where up to eight or nine resident species may occur sympatrically. However, one or more species are also found at high latitudes on all continents other than Antarctica. They

are found nesting from sea level to several thousand feet/ meters elevation in mountainous regions of Europe, North America, and in the Andes of South America. Three swifts, the common swift (Apus apus), alpine swift (Apus melba), and pallid swift (Apus pallidus), occur as breeding species in Europe and migrate to Africa in the winter. In North America, three species similarly migrate south in winter, two of which, the chimney swift (Chaetura pelagica) and black swift (Cypseloides niger), travel all the way to South America. The white-throated swift similarly migrates from the more northerly portions of its range but is a permanent resident in much of the southwestern United States and Mexico. Two Asiatic breeding swifts, the white-throated needletail (Hirundapus caudacutus) and fork-tailed or Pacific swift (Apus pacificus), make extended migrations to winter in Australia and New Zealand, and occasionally reaching sub-Antarctic Macquarie Island.

Habitat

Swifts occur in a wide variety of habitats from densely forested tropical areas to nearly the limit of suitable nest trees in northern Scandanavia. Others that depend more on rock cliff, or manmade equivalents, for nest sites can utilize extensive nearby open savanna or grassland habitats.

Behavior

Swifts typically leave their nesting and roost sites at dawn and in many cases do not return until dusk. Swifts spend their entire day aloft, only landing at nest sites when feeding young or at nighttime roosts. The daily foraging range of these highly mobile birds has not been adequately studied, but some species may regularly forage in excess of 30–38 mi (50–60 km) from nest or roost sites. Although they may occur singly or in small groups, swifts are highly social birds and flocks of hundreds are often found in suitable feeding areas. During migration, huge flocks of swifts can occur.

Nesting is largely dependent on the nest-type and location; some species such as the lesser swallow-tailed swift (Panyptila cayennensis) build solitary nests under rock clefts or under large limbs of forest trees. Others, notably some of the swiftlets, may nest in dense aggregations where more than 100,000 individuals utilize a single cave system. Swifts conduct much of their courtship and social activities on the wing. The common swift in Europe is noted for its ability to spend nights aloft. These same swifts make extended movements away from breeding areas during spells of cold rainy weather and seek out food by following high-pressure zones; their chicks back in the nest may drop their body temperature and go torpid until both warmer weather and the adults return. Social interactions include a lot of high-speed, usually noisy, aerial chases with intermittent glides and raised-wing displays. In spring, interlocked birds sometimes make dramatic tumbling display falls of nearly 200 ft (60 m) or more which have been interpreted, at least in the white-throated swift (Aeronautes saxatalis), as aerial copulation.

Among the most interesting capacities of the swiftlets in the genus *Aerodramus* is the ability to echolocate, which means

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A chimney swift (*Chaetura pelagica*) colony roosts in a hollow beech tree in Ohio. (Photo by Maslowski. Photo Researchers, Inc. Reproduced by permission.)

they emit sharp pulses of sound, or clicks, and utilize the echo of these sounds to enable them to navigate to and from nest or roost sites in the inner regions of caves. These syringeally-produced sounds are typically brief audible clicks ranging from 2–10 kHz in frequency, with most of the sound energy between 2 and 5 kHz. Repetition rates vary between five and 20 clicks per second. Click rates are lowest in the twilight zone at the cave entrance and increase abruptly when the swiftlets enter the zone of total darkness. The sensitivity of this echolocation system does not allow them to discriminate targets much below 0.19–0.23 in (5–6 mm), which precludes them using it to locate food items.

Vocalizations in swifts are not particularly elaborate or even musical. They range from staccato chatter or chippering in such as the chimney swift to the more drawn out screams of *Apus* and *Aeronautes* swifts. Social screaming parties are a familiar sight and sound at dawn and dusk near breeding sites of the common swift in towns throughout much of Europe. The call of the greater swallow-tailed swift (*Panyptila sanctihieronymi*) in southern Mexico may be an exception in that it has been described as a high clear and descending musical whistle.

Swifts show an extreme long-term fidelity to breeding sites; some are regularly or continuously used for a half century or more. In some cases, nests are used again and again by the same pair of swifts year after year, with only the addition of some new nest material. Others build less durable nests that have to be built anew each season. Swifts are long-lived and generally monogamous. Life-spans may approach 15–20 years or more; annual survival rates can exceed 80%, although they are lower in some of the highly migratory species.

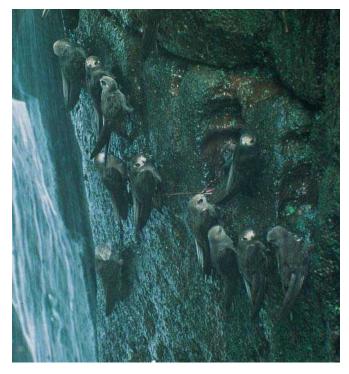
Feeding ecology and diet

Swifts gather all of their arthropod food on the wing, most of which are insects supplemented by the occasional spider.

The specific items taken vary extensively from place to place and even from day to day, particularly in temperate areas where substantial differences in local weather conditions occur. Swifts tend to forage at higher altitudes and take larger food items on bright sunny, warm days when more potential prey are carried aloft in wind currents and thermals. During cooler, overcast or rainy weather, they forage lower and seek out areas of continued insect productivity, such as lakes and settling ponds. Food for the young is generally carried in the mouth and consolidated into a bolus with the addition of a sticky glue-like substance produced by seasonally enlarged salivary glands. A given bolus may contain as many as 1,500 individual insects representing perhaps 50-60 different species. Swifts are quick to exploit local abundances of prey as found in the mating swarms of mayflies, termites, ants, and other insects. The foraging ecology of cypseloidine swifts is substantially different in that they appear to specialize in feeding on the swarms of winged reproductive ants and termites. They also store these prey in the esophagus thus enabling them to forage more widely in search of patchily distributed swarms of these energy-rich prey and then return with a larger load than a single bolus. Their chicks are provisioned only once or twice a day compared to the one to three times per hour for the other swifts. However, they may receive multiple regurgitations on each return of the adults to the nest.

Reproductive biology

Breeding in tropical swifts usually coincides with the onset of the seasonal rains and a flush of insect prey. In swifts in the temperate zone, it begins with the longer and warmer days of late spring and summer, and chick provisioning and



Great dusky swifts (*Cypseloides senex*) perch on the side of a cliff at a waterfall. (Photo by K. Schafer/VIREO. Reproduced by permission.)

Family: Swifts Vol. 9: Birds II

fledging occurs when aerial food supplies are near their peak. This timing is also important to adults that must increase fat reserves prior to their lengthy migrations.

The nests of swifts are highly variable and have proven useful in assessing intrafamilial relationships. The very large needletail swifts (Hirundapus) build no nest at all and lay their eggs in a scrape in the detritus at the bottom of hollow trees, and the white-naped swift utilizes a scrape in the sand on ledges in caves. The Horus swift (*Apus horus*) usurps burrows of bee-eaters and othe burrowing birds while two other African species, the white-rumped swift (Apus caffer) and Bates's swift (Apus batesi) utilize old swallow nests that they reline with feathers. The most elaborate structures are the tubular nests of the swallow-tailed swifts (Panyptila) of Central and South America, which are made of plant seed floss glued together with salivary cement into a felt-like material. In the chaeturine swifts in the genera *Chaetura*, *Telecanthura*, and Neafrapus, and presumably other spinetails, the nest is a neat half-saucer of twigs glued to the inside of a hollow tree. Other swifts build simple or bulky nests of plant material and feathers glued together and located on cliffs, in crevices, or, in the case of the palm swifts, attached to the hanging palm fronds. The cypseloidine swifts are unique in that their nests are a simple pad or cone of mosses or seaweed placed in a damp dark niche near or even behind waterfalls or in sea caves. The swiftlets include varying amounts of plant material and feathers in their nests along with copious amounts of salivary cement. Some such as those of the edible-nest swiftlet (Aerodramus fuciphagus) are made entirely of salivary secretions and are the highly prized ingredient of birds-nest soup and extensively harvested for this delicacy.

Swift eggs are almost uniformly ovate and glossy white in color. Clutch sizes range from only one or two in the cypseloidine swifts and swiftlets to as many as five to seven in some species of Chaetura and Aeronautes. Incubation periods tend to be long, ranging from 19-20 days to about 28 days. Newly hatched chicks are blind, helpless, and devoid of any natal down. A fluffy down-like semi-plume covering starts growing within a few days, which precedes the growth of the first typical contour plumage. Development of the chicks is slow compared to other similar-sized birds and takes from four to six and a half weeks (an extraordinary nine weeks in the spot-fronted swift [Cypseloides cherriei]). In many of the spine-tailed swifts (Chaetura), the young may leave the crowded nest and cling to the walls of the hollow tree nest site for a week or more before actually fledging. Others such as the cypseloidine swifts and cave-inhabiting swiftlets remain in the nest until fledging.

The molt period in swifts is generally prolonged with only a few flight feathers being replaced at the same time. This necessitates extensive overlap of breeding and molt periods in temperate zone species that complete their molt prior to fall migration. Others delay the molt until reaching the wintering ground, or interrupt it shortly after its start to accommodate the energy cost of migration.

Conservation status

Because of their highly specialized nesting requirements, a number of swifts have been included on various lists of threatened or vulnerable species. Destruction or disturbance of localized nesting areas, especially caves, can have an appreciable negative impact on populations of these birds, particularly island populations. A deficiency of detailed information on the breeding biology and status of a number of species of swifts has led to their being tentatively included on lists of those possibly needing protection. One species (Guam swift, *Collocalia bartschi*) is listed as Endangered by the IUCN. An additional five species are considered Vulnerable and another five species are deemed Near Threatened. Detailed information is badly needed for other poorly studied species.

Significance to humans

Swifts are often found nesting in close association with humans and common swifts used to be encouraged to nest in manmade rooftop compartments where the young could be harvested for food. Even today, swiftlet nests are widely harvested for food and perceived medicinal properties. The feather-free "white" nests of the edible-nest swiftlet (Aerodramus fuciphagus), which are made entirely of the sticky secretions of the salivary glands, are important economic assets throughout their range in the oriental region. So-called "black" nests of the black-nest swiftlet (Aerodramus maximus), which contain substantial amounts of feathers intermixed with the salivary secretions, are also harvested but command a much lower price. Today, the harvest of these nests is closely monitored and regulated. Properly managed, this can be a renewable resource providing a sustained yield year after year. However, illegal harvesting and excessive disturbance threaten the long-term viability of some colonies and the nest-collecting industry. Cross-fostering of young edible-nest swiftlet chicks into nests of other species as a means of establishing new colonies in places where a carefully regulated harvest will be possible is a promising new program.



1. Edible-nest swiftlet (*Aerodramus fuciphagus*); 2. White-collared swift (*Streptoprocne zonaris*); 3. Alpine swift (*Apus melba*); 4. Common swift (*Apus apus*); 5. White-throated needletail (*Hirundapus caudacutus*); 6. White-rumped swiftlet (*Aerodramus spodiopygius*); 7. Black swift (*Cypseloides niger*); 8. Chimney swift (*Chaetura pelagica*); 9. African palm swift (*Cypsiurus parvus*). (Illustration by Bruce Worden)

Family: Swifts Vol. 9: Birds II

Species accounts

White-collared swift

Streptoprocne zonaris

SUBFAMILY

Cypseloidinae

TAXONOMY

Hirundo zonaris Shaw, 1796, no locality although assumed to be Brazil. Nine subspecies.

OTHER COMMON NAMES

English: Cloud swift, Antillean cloud swift; French: Martinet & agrave collier blanc; German: Halsbandsegler; Spanish: Vencejo Grande.

PHYSICAL CHARACTERISTICS

8.5 in (22 cm); 3.2–4.0 oz (85.8–107.3 g). Blackish plumage and a distinctive white collar.

DISTRIBUTION

Widespread in Central and South America from northern Mexico south to southern Bolivia and northwestern Argentina; also in Greater Antilles. Extralimital in California, Michigan, Texas, and Florida.

HABITAT

Occurs over all terrain and habitats from sea level to 13,000 ft (4,000 m) in highlands. More typical in highlands and less common in more arid regions.



BEHAVIOR

A seemingly very social species often occurring in large flocks of 100–300. Daily foraging flights appear to be lengthy.

FEEDING ECOLOGY AND DIET

Tends to specialize on swarming insects, particularly winged ants and termites; other insects also taken.

REPRODUCTIVE BIOLOGY

Nests of mossy material in dense colonies where conditions permit. Two eggs are laid; incubation takes 30–35 days and chicks are fledged after 45–55 days.

CONSERVATION STATUS

Inaccessibleness of most nest and roost sites makes them less subject to human activities. No conservation measures identified or proposed.

SIGNIFICANCE TO HUMANS

None known. ◆

Black swift

Cypseloides niger

SUBFAMILY

Cypseloidinae

TAXONOMY

Hirundo nigra Gmelin, 1789, Hispaniola. Three subspecies.

OTHER COMMON NAMES

English: American black swift; French: Martinet sombre; German: Schwarzsegler; Spanish: Vencejo Negro.

PHYSICAL CHARACTERISTICS

6.9 in (18 cm); 1.5–1.9 oz (41–51 g). Dark plumage usually with white fringe on underparts; females have broader white fringe on underparts.

DISTRIBUTION

Widespread but highly localized breeder in western United States and southern Canada and Alaska, south through Central America to Costa Rica; also breeds in northern West Indies; as yet unidentified wintering ground in South America.

HABITAT

Forages widely at higher elevations; less common in drier areas away from mountain waterfall and sea cave nesting sites.

BEHAVIOR

Leaves nest and roost site at first light and only returns at dusk; forages at high altitudes; may nest in larger numbers at a single site.

FEEDING ECOLOGY AND DIET

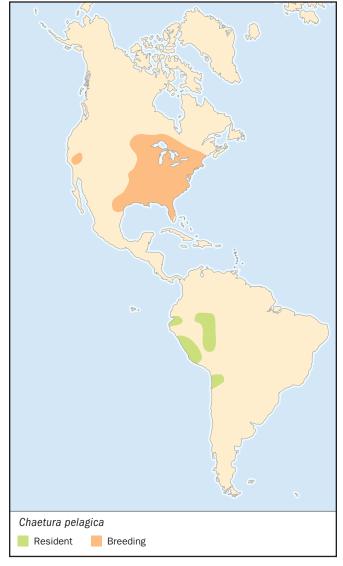
Insects and spiders; specializes on swarming insects, particularly winged reproductive ants.

REPRODUCTIVE BIOLOGY

Nest and the single white egg located in a cool damp dark area adjacent to water; incubation takes 24–27 days and fledging and additional 45–50 days.

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CONSERVATION STATUS

Nest sites largely free of human disturbances; some traditional breeding sites in coastal California have been unoccupied in recent years; on the list of Species of Special Concern in California, but this is currently under review.

SIGNIFICANCE TO HUMANS

None known. ◆

Chimney swift

Chaetura pelagica

SUBFAMILY

Chaeturinae

TAXONOMY

Hirundo pelagica Linnaeus, 1758, South Carolina, USA. Monotypic

OTHER COMMON NAMES

French: Martinet ramoneur; German: Schornsteinsegler; Spanish: Vencejo de Chimenea.

PHYSICAL CHARACTERISTICS

4.6–5.4 in (12–14 cm); 0.8–1.0 oz (21.5–28.0 g); average mass of 0.7–1.0 oz (20–23 g) during breeding season, and 0.9–1.0 oz (26–28 g) during pre-migration period. Sooty gray upperparts; dark gray-brown underparts with lighter throat.

DISTRIBUTION

Eastern North America west to Rocky Mountains; occasional breeder in California and southwest in recent years. Migrates through Central America to wintering grounds in Peru and northern Chile. Extralimital in Galapagos, West Indies, Bermuda, and British Isles.

HABITAT

Widespread occurring over open country, forested areas, and urban centers.

BEHAVIOR

Makes dashing flights in small groups and rapid chippering vocalizations; nests in chimneys more often than in hollow trees. Helpers at nests of breeding pairs may be young pre-breeders or failed breeders. Family: Swifts Vol. 9: Birds II

FEEDING ECOLOGY AND DIET

A wide variety of insects taken, including aerial insects and some spiders.

REPRODUCTIVE BIOLOGY

Nest of twigs glued together and to the wall of the hollow tree or chimney with salivary cement. Clutch is two to seven eggs, more typically four to five, laid between May and mid-July. Incubation takes 19–21 days and chicks fledge after an additional 28–30 days, although they may have vacated the crowded nest as much as a week earlier.

CONSERVATION STATUS

Although still common to abundant in most parts of its breeding range, population numbers appear to be declining, probably due to closure or screening of chimney nest sites in urban and suburban areas. Construction of artificial chimney-like structures as alternative nest sites is proving effective.

SIGNIFICANCE TO HUMANS

None known. ◆

Edible-nest swiftlet

Aerodramus fuciphagus

SUBFAMILY

Chaeturinae

TAXONOMY

Hirundo fuciphaga Thunberg, 1812, Java. Eight subspecies.

OTHER COMMON NAMES

English: Gray-rumped swiftlet, white-nest swiftlet, Hume's swiftlet; French: Salangane à nid blanc; German: Weißnest-salangane; Spanish: Salangana Nidoblanco.

PHYSICAL CHARACTERISTICS

4.6 in (12 cm); 0.4–0.6 oz (10–15 g). Glossy blackish brown upperparts sometimes with lighter rump; underparts are mostly brownish gray with lighter throat and blackish undertail-coverts.



DISTRIBUTION

Southeast Asia and Indonesia, from Andaman and Nicobar Islands through coastal south Thailand, Malaysia, Sumatra, Java, and Borneo to Lesser Sundas.

HABITAT

Widespread in coastal lowlands but in some places at elevations to 3,280–9,000 ft (1,000 to 2,800 m). Coastal mangroves, cultivated areas, and lowland forest.

BEHAVIOR

Gregarious and often associates with other swiftlets and swallows when foraging.

FEEDING ECOLOGY AND DIET

Aerial arthropods, including a wide array of insects and spiders.

REPRODUCTIVE BIOLOGY

Breeding season is lengthy and peaks in the dryer season of the year. Nests are self-supporting brackets made almost completely of the sticky salivary mucilage. Usually two eggs are laid and incubation period is 25.5 days for the first egg and 22.5 days for the second; the fledging period is 43 days.

CONSERVATION STATUS

In areas where unregulated repetitive nest harvesting is taking place, populations as well as harvesting yields are sharply declining by as much as 85% over a 12-year period.

SIGNIFICANCE TO HUMANS

Nest-harvesting provides substantial economic benefits to local human populations. ◆

White-rumped swiftlet

Aerodramus spodiopygius

SUBFAMILY

Chaeturinae

TAXONOMY

Macropteryx spodiopygius Peale, 1848, Samoa Islands. Eleven subspecies.

OTHER COMMON NAMES

Gray swiftlet, Pacific white-rumped swiftlet; French: Salangane à croupion blanc; German: Weißbürzelsalangane; Spanish: Salangana Culiblanca.

PHYSICAL CHARACTERISTICS

3.3–4.4 in (10–11.5 cm); 0.3 oz (8.2 g). A highly polytypic species. All have a pale rump, but the degree of paleness varies geographically.

DISTRIBUTION

Extensive range on oceanic islands in Papuasia, Melanesia, and Polynesia from island groups off New Guinea eastward to New Caledonia, Fiji, Tonga, and Samoa; New Zealand.

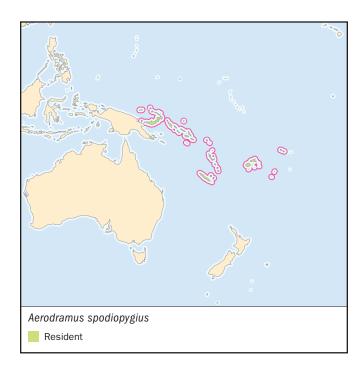
HABITAT

Island-inhabiting species occurring widely. Generally found in lowlands but sometimes to 5,250–5,900 ft (1,600–1,800 m) on larger islands.

BEHAVIOR

Feeds in association with other swiftlets and swallows: utilizes echolocation to access nest sites.

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FEEDING ECOLOGY AND DIET

Wide array of insects, including aerial insects and spiders.

REPRODUCTIVE BIOLOGY

Nest is of fine plant material and mosses held together with salivary cement and attached to the wall of a cave. Clutch size is one or two eggs. Incubation period is 22–25 days; fledging period is 45–46 days. Lost eggs and sometimes lost broods are usually replaced in 9–14 days.

CONSERVATION STATUS

A high fledging success rate suggests stable populations.

SIGNIFICANCE TO HUMANS

None known. ◆

White-throated needletail

Hirundapus caudacutus

SUBFAMILY

Chaeturinae

TAXONOMY

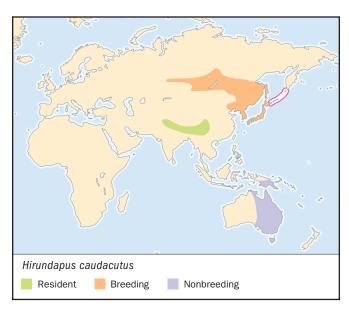
Hirundo caudacuta Latham, 1801, New South Wales, Australia. Two subspecies.

OTHER COMMON NAMES

English: Spine-tailed swift, needle-tailed swift, northern or Asiatic needletail; French: Martinet épineaux; German: Stachelschwanzsegler; Spanish: Vencejo Mongol.

PHYSICAL CHARACTERISTICS

7.3–7.6 in (19–20 cm); 4.0–5.2 oz (109–140 g). Brown body with off-white mantle and white throat, forehead, and markings on flanks and undertail-coverts; dark wings with blue gloss fading to green on remiges and coverts. Juveniles have black terminal tips to some of the undertail-coverts.



DISTRIBUTION

Forested areas from central Siberia east to Sachalin, Kurile Islands, and northern Japan; southern Himalayas; wintering in Australia and New Zealand, and to sub-Antarctic Macquarie Island. Accidental in Seychelles, western Europe, and British Isles. Only North American records in Pribiloff Islands.

HABITAT

Dense old-growth forest with abundance of dead and hollow trees; occasionally roosts in large eucalyptus groves.

REHAVIOR

Often occurs in large flocks; sometimes forages close to trees, even striking the vegetation to flush out insect prey. Considered to be one of the fastest flying birds, reaching speeds in excess of 100 mi/hr (170 km/hr).

FEEDING ECOLOGY AND DIET

A wide diversity of insects and spiders.

REPRODUCTIVE BIOLOGY

Uses hollow interior of large forest trees as nest sites. Clutch ranges from two to seven eggs, which are incubated starting with the first egg causing hatching to be asynchronous. Breeding in late May through the middle of June; migration begins in late September and early October.

CONSERVATION STATUS

Species is not in need of any conservation measures.

SIGNIFICANCE TO HUMANS

None known. ◆

Common swift

Apus apus

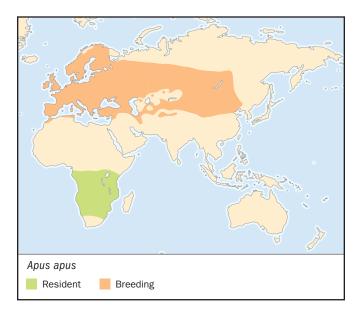
SUBFAMILY

Apodinae

TAXONOMY

Hirundo apus Linnaeus, 1758, Sweden. Two subspecies.

Family: Swifts Vol. 9: Birds II



OTHER COMMON NAMES

English: Eurasian, European, northern swift; French: Martinet noir; German: Mauersegler; Spanish: Vencejo Común.

PHYSICAL CHARACTERISTICS

6.1–6.5 in (16–17 cm); 1.3–1.9 oz (36–52 g). Juvenile similar to adult; sexes alike. Overall black-brown plumage with small, off-white throat patch.

DISTRIBUTION

Western Europe to eastern Asia and from northern Scandanavia and northern Siberia to North Africa, Himalayas, and central China; winter in southern Africa. Accidental in Spitzbergen, Iceland, Bermuda, and Seychelles.

HARITAT

Occurs in all but driest parts of extensive breeding range. Nests in woodpecker holes, hollow trees, and natural cliffs as well as buildings and other manmade structures.

BEHAVIOR

Regularly makes dashing flights accompanied by its drawn-out rattling screams. During prolonged cold weather, adults may temporarily abandon the chicks and make lengthy flights to warmer, food-rich areas. Annual molt is usually delayed until they are on the wintering grounds.

FEEDING ECOLOGY AND DIET

Aerial insects and spiders taken on the wing.

REPRODUCTIVE BIOLOGY

Lay from one to four eggs, most commonly two, and incubation takes about 19–20 days; fledging takes an additional 27–45 days. Nesting success varies from 58% to 65%.

CONSERVATION STATUS

Most populations seem to be healthy and not in need of particular conservation efforts.

SIGNIFICANCE TO HUMANS

None known. ◆

Alpine swift

Apus melba

SUBFAMILY

Apodinae

TAXONOMY

Hirundo melba Linnaeus, 1758, Gibraltar. Ten subspecies.

OTHER COMMON NAMES

French: Martinet à ventre blanc; German: Alpensegler; Spanish: Vencejo Real.

PHYSICAL CHARACTERISTICS

7.8–8.5 in (20–22 cm); 2.8–4.5 oz (76–120 g); largest swift of Europe and throughout most of its range. Olive-brown upperparts; underparts have a large white oval patch encircled by olive-brown breast band, flanks, and undertail-coverts; white throat.

DISTRIBUTION

Widely distributed in mountainous areas and along coastal cliffs from Pyrenees and Alps of western Europe eastward to the Himalayas and peninsular India; mountainous areas of east and southern Africa, Madagascar, and Arabian peninsula; winters in central and western Africa. Accidental in Scandinavia, British Isles, Iceland, and Caribbean.

HABITAT

Occurs widely at higher elevations; forests, cultivated areas, and highly urbanized sites.

BEHAVIOR

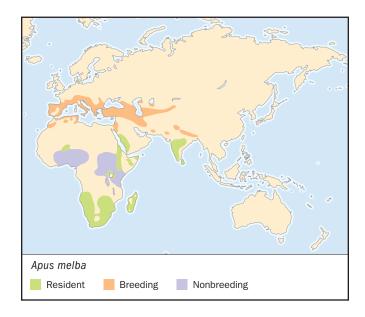
Screaming parties around breeding areas are common. Mating takes place on the wing as well as in nest chamber.

FEEDING ECOLOGY AND DIET

Wide array of aerial insects and spiders.

REPRODUCTIVE BIOLOGY

Nests are small pads of plant material and feathers in a cliff or natural cavity. Normally three eggs are laid, but sometimes as few as one or as many as four. Incubation period is 17–23 days: fledging at an age of 53–66 days.



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CONSERVATION STATUS

Conservation efforts have increased populations in some areas.

SIGNIFICANCE TO HUMANS

None known. ◆

African palm swift

Cypsiurus parvus

SUBFAMILY

Apodinae

TAXONOMY

Cypselus parvus Lichtenstein, 1823, Nubia. Eight subspecies.

OTHER COMMON NAMES

English: Palm swift, Old World palm swift; French: Martinet des Palmes; German: Palmensegler; Spanish: Vencejo Palmero Africano.

PHYSICAL CHARACTERISTICS

6.1 in (16 cm); 0.4–0.5 oz (10–14 g). One of the smallest African swifts. Pale gray-brown upperparts with head and wings appearing darker; underparts very pale with some streaking on the throat. Males have whiter throats than females.

DISTRIBUTION

Widespread in sub-Saharan Africa, including Madagascar.

HABITAT

Local foraging species in open areas in the vicinity of palms; generally forages at low to medium heights.

BEHAVIOR

Close association with palms which provide year-round roosting and nesting sites. Vocalizations a soft high-pitched scream.

FEEDING ECOLOGY AND DIET

Aerial arthropods, including diverse small insects and spiders, as well as winged ants, termites, and beetles.



REPRODUCTIVE BIOLOGY

Nests are small elongate pads of plant floss and feathers glued to the surface of hanging palm fronds. Clutch sizes are usually one or two eggs, rarely three. Incubation is typically 20 days. Chicks grow slowly and fledge after a period of 31–33 days.

CONSERVATION STATUS

Plantings of both native and exotic palms in suburban areas has resulted in a stable population.

SIGNIFICANCE TO HUMANS

None known. ◆

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Tree swifts (Hemiprocnidae)

Class Aves

Order Apodiformes

Suborder Apodi

Family Hemiprocnidae

Thumbnail description

Small to medium-sized birds with long, narrow, swept-back wings, deeply forked tail, and elaborate forehead crest or elongate feathered "whiskers"

Size

5.8-11.5 in (15-30 cm); 0.8-2.9 oz (21-79 g)

Number of genera, species

1 genus; 4 species

Habitat

Lowland forests and forest openings, river edges, and open grasslands and croplands where some trees remain

Conservation status

Not threatened



Distribution

Indian subcontinent, Indochina, Malay Peninsula, Indonesia, New Guinea, Bismarck, and Solomon Islands

Evolution and systematics

The tree swifts have always been recognized as separable from the other "true" swifts due to their brighter coloration, crest and whiskered ornamentation, and habit of perching and sally-flight foraging. Morphologically their wings do not show the extreme shortening of the humerus found in the swifts (Apodidae). Even so, the general resemblances between the swifts and tree swifts, backed up by skeletal anatomy and, more recently, DNA evidence, supports their being separate families within the suborder Apodi. The extinct fossil family Aegialornithidae from Europe is currently thought to be most closely related to the tree swifts and is sometimes considerd to be a subfamily of the Hemiprocnidae.

Physical characteristics

Tree swifts are truly flamboyant compared to swifts. Their brighter plumage with bright sheens to the blue and green coloration, chestnut facial patterns, along with their erectile forehead crests or elongate "whiskers" make them distinctive. Their long, narrow wings and deeply forked tails also serve

to set them apart. Sexually dimorphic plumages are also not typical of the swifts. Tree swift chicks have natal down and a highly motted cryptic juvenal plumage.

Distribution

The crested tree swift (Hemiprocne coronata) has a wide-spread distribuution on the Indian subcontinent from the foothills of the Himalayas through much of peninsular India and Sri Lanka and southeast through Indochina, Cambodia, and Vietnam. The closely related gray-rumped tree swift (H. longipennis) replaces it in the Malay Peninsula and parts of Indonesia and broadly overlaps with the whiskered tree swift (H. comata). The moustached tree swift (H. mystacea) is found farthest east in eastern Indonesia, New Guinea, and the Bismarck and Solomon Islands.

Habitat

Although tree swifts forage widely over forested and savanna areas, they seem to prefer forest openings and edges and

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A crested treeswift (*Hemiprocne coronata*) chick. (Photo by Doug Wechsler/VIREO. Reproduced by permission.)

river edges where the bare twigs of emergent trees provide suitable perches from which to make their dashing foraging flights. They are typically birds of lowland areas below 3,300 ft (1,000 m) but are occasionally recorded at higher elevations.

Behavior

Tree swifts are usually found singly or in pairs but some also occur in small groups of up to 10–12 individuals. They are not particulary gregarious and do not readily socialize with other tree swifts where their ranges overlap. They are quite vocal and have an array of harsh, rasping chatters and screams that are given both at rest and in flight. They have a characteristic upright stance when perched, with the crest, which is depressed in flight, usually erected. They are quick to use their flight skills in mobbing birds of prey.

Feeding ecology and diet

All dietary items are captured on the wing and presumably include an array of insects and possibly spiders. They feed most actively at dawn and dusk when loose flocks dash about at high speed.

Reproductive biology

The nests of tree swifts are among the most remarkable of birds. The tiny nest, barely large enough to hold the single white egg, is made of small chips of tree bark, feathers, and plant floss glued with salivary cement on the side of a narrow horizontal branch as much as 13-60 ft (4-18 m) above the ground. This most inconspicuous nest is difficult to detect and looks more like a slight natural knob on an othewise bare twig perch than a nest. Only careful observation of adults returning repeatedly to the same perch reveals the presence of a nest. The chick is equally cryptic in appearance with a lichen-like covering of natal down followed by the first contour plumage, characterized by broad mottled or whitish edges to the body feathers. This again makes the chick in its stationary upright resting posture strongly resemble a broken twig. The incubation period appears to be 21-26 days; the combined incubation and fledging period seems to be close to 50 days but detailed observations are lacking. Both sexes incubate and brood the chick, but females appear to spend more time in these activities.

Conservation status

Tree swifts can be found in suburban areas where suitable trees remain. However, their populations in some of these areas appear to be declining. The causes are unknown and no critical conservation issues have been identified.

Significance to humans

None known.

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Species accounts

Crested tree swift

Hemiprocne coronata

TAXONOMY

Hirundo coronata Tickell, 1833, Jungles of Borabhum and Dholbhum, India. Formerly considered conspecific with gray-rumped tree swift, *Hemiprocne longipennis*. Monotypic.

OTHER COMMON NAMES

English: Indian tree swift; French: Hémiprocné courounné; German: Kronenbaumsegler; Spanish: Vencejo Arborícola Coronado.

PHYSICAL CHARACTERISTICS

8.8 in (23 cm); 0.7-1.0 oz (20-26 g). Plumage largely blue-gray above with darker green-blue forehead crest and black eye patch and, in male, a reddish orange patch behind eye on ear coverts extending to side of throat. Throat and upper breast bluegray; rest of undersides white. Wing feathers dark blackish brown and darker than body; tertials pale gray. Wings long and narrow, tail deeply forked.



Hemiprocne coronata

DISTRIBUTION

From foothills of Himalayas and peninsular India, including Sri Lanka, east through Bangladesh to coastal areas of Thailand, Cambodia, and Vietnam. Replaced by gray-rumped tree swift in Malay Peninsula.

HABITAT

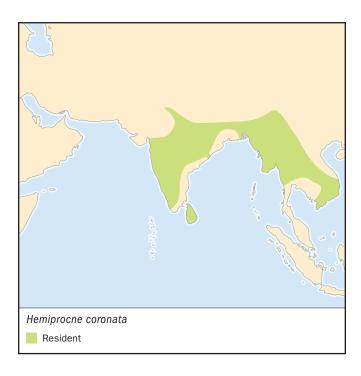
Forages over forested and open areas mostly at lower elevations. Prefers bare twigs on tops of emergent forest trees as perching site from which to forage.

BEHAVIOR

Makes short swooping flights in search of aerial insects, often returning to original perch. Uses distinctive upright stance with erected crest when perched. Gives rasping calls when perched and in flight. Not particularly gregarious but may join others, particularly at roosts and during active feeding periods at dusk and dawn. Flight fast with much intermittent gliding in manner of bee-eaters or wood swallows.

FEEDING ECOLOGY AND DIET

Feeds on a presumably wide array of aerial insects gathered in flight.



REPRODUCTIVE BIOLOGY

Builds tiny nest glued to small exposed horizontal branch typical of the family. The single egg takes 3+ weeks to hatch and incubation and fledging period combined takes approximately 50 days. The nest and chick are cryptically colored. The natal down of the chick is followed by a mottled cryptic contour plumage.

CONSERVATION STATUS

No conservation issues identified.

SIGNIFICANCE TO HUMANS

None known. ◆

Whiskered tree swift

Hemiprocne comata

TAXONOMY

Cypselus comatus Temminck, 1824, Sumatra. Two subspecies.

OTHER COMMON NAMES

English: Lesser tree swift; French: Hémiprocné coiffé; German: Ohrenbaumsegler; Spanish: Vencejo Arborícola Chico.

PHYSICAL CHARACTERISTICS

5.85 in (15 cm); 0.8–1.0 oz (21–26 g). Head and sides of throat glossy blue-black (with greenish gloss when fresh), body bronze olive, wing and tail dark. Short forehead crest and long lanceolate feathers in facial region forming two white stripes from lores over the eye to nape and from chin along jawline to side of neck. Ear coverts glossy blackish in females and rufous in males.

Family: Tree swifts Vol. 9: Birds II

DISTRIBUTION

Peninsular Thailand and Malaysia, Sumatra, Borneo, and Philippines except Palawan.

HABITAT

Forages over canopy and edge areas of lowland forests. Utilizes midlevel bare twigs of forest trees as perches from which to make brief foraging flights.

BEHAVIOR

Has characteristic upright stance when perched with short crest erected. Makes swooping flights in search of aerial prey, often returning to



Hemiprocne comata

original perch. Appears to be territorial year-round only sharing foraging area with newly fledged young. Not as social as other tree swifts which may at times gather in larger groups. Utilizes lower perches than gray-rumped tree swift when inhabiting same area.

FEEDING ECOLOGY AND DIET

Feeds on presumably a large array of aerial insects taken on the wing.



REPRODUCTIVE BIOLOGY

Makes tiny nest glued to horizontal branch characteristic of the family. The single white egg is incubated for about 21 days and the combined incubation and fledging period takes approximately 50 days.

CONSERVATION STATUS

No conservation issues identified.

SIGNIFICANCE TO HUMANS

None known. ◆

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Charles T. Collins

Hummingbirds

(Trochilidae)

Class Aves

Order Apodiformes

Suborder Trochili

Family Trochilidae

Thumbnail description

Small to very small birds, extensive metallic plumage, bill thin, extremely different in shape, feet tiny

Size

2-8.7 in (5-22 cm); 0.07-0.7 oz (1.9-21 g)

Number of genera, species

102 genera; 328 species

Habitat

Wide variety of habitats, arid zones, temperate, subtropical, and tropical forests, mountain regions to snow line

Conservation status

Endangered: 7 species; Critical: 8 species; Vulnerable: 12 species; Near Threatened: 7

species



Distribution

North, Central (including Caribbean islands), and South America

Evolution and systematics

Hummingbirds comprise a distinctive and most homogeneous group of New World birds. Although they form an undisputed phylogenetic unit, their relationship with other bird families is still debated. Traditionally trochilids are placed within the swifts (Apodiformes), together with the treeswifts (Hemiprocnidae) and the true swifts (Apodidae). This classification is mainly based on anatomical and morphological characters, such as modified cervical muscles, the skeleton of the flight apparatus, wing muscle innervation, or feather tracts. The question still remains whether these similarities are due to convergence or to common ancestry. This debate has led some classifiers to place hummingbirds in an order of their own, Trochiliformes. Recent biochemical studies favor the traditional classification: swifts and hummingbirds share a unique form of the enzyme malate dehydrogenase. This relationship is corroborated by the DNA comparisons of Sibley and his coworkers (1988). However, affinities to nightjars and their allies (Caprimulgiformes) based on patterns of feather growth (pterylosis), to mousebirds (Coliiformes) from intestinal tract comparisons, and even to the songbirds (Passeriformes), derived from feather structure and egg-white protein analysis, have been suggested by various systematists. Here we follow the treatment suggested by Schuchmann (1999) and give hummingbirds the rank of a family (Trochilidae) comprising two subfamilies (the hermits or phaethornithines, Phaethornithinae; and the nonhermits or trochilines, Trochilinae) within the order Apodiformes. The taxonomic treatment used herein distinguishes a total of 102 genera and 328 species (subfamily Phaethornithinae: 34 species; subfamily Trochilinae 294 species) with over 680 subspecies.

Generic limits and species relationships within the trochilines are still poorly understood. Indeed, many non-hermit genera are based on the same characters that are used to define species. In recent checklists and classifications the lack of synapomorphies at the genus level in trochilines is expressed by over 50% of monotypic genera. All this taxonomic uncertainty presents a considerable challenge for future systematic research.

Despite this problem, several major clades have been identified among trochilines. Based on the variation of a single wing muscle, the Musculus tensor patagii brevis, three groups

within the non-hermits have been proposed. The first unit covers those genera with a primitive muscle state: Androdon, Doryfera, Florisuga, Colibri, Anthracothorax, Eulampis, Chrysolampis, Polytmus, Topaza, and Heliothryx. A more advanced muscle state was found in the following genera: Campylopterus, Orthorbyncus, Stephanoxis, Lophornis, Discosura, Chlorostilbon, Cynanthus, Cyanophaia, Thalurania, Panterpe, Damophila, Lepidopyga, Hylocharis, Amazilia, Trochilus, Lampornis, and all Andean and North American taxa. The category "highly advanced" muscle state comprises members of the genera Calliphlox and Chaetocercus.

This single-character arrangement is surprisingly consistent when compared with morphological, morphometric, and behavioral information. Using these data sets, 11 distinct taxa can be clustered based on such characteristics as coloration, display and song structure, flight pattern, musculature, and nest structure and site. It should be noted that some of these genera are so closely related that their separate generic status is doubtful.

Patterns of tail-feather coloration, display and song structure, and a primitive cross-structure feature of the hindneck muscle (Musculus splenius capitis), place the "tooth-bills" Androdon and Doryfera at the base of the trochiline assemblage. They are followed by a more derived taxon containing the "sabrewing-and-mango" genera Campylopterus (including Phaeochroa, Eupetomena, Aphantochroa), Florisuga (including Melanotrochilus), Colibri, Anthracothorax (including Avocettula), Topaza, Eulampis, Chrysolampis, Orthorbyncus, Klais, Stephanoxis, and Abeillia. This assemblage is characterized by complex cervical musculature, similar patterns of song syntax, and small compact nests of little variation in form and structure, often placed on leaves or saddled on horizontal branches. Probably closely related to the "sabrewing-andmango" genera are the "coquettes" Lophornis and Discosura (including Popelairia), based on nest shape and male frontal display patterns.

The next taxon comprises the "true emeralds" Trochilus and Chlorostilbon (including Chlorestes). Biogeographical history and plumage feathers in both males and females already suggested close affinities between members of the West Indian taxa of Trochilus and Chlorostilbon, an assumption supported by a typical song pattern, exhibited during the male display, and also by similarities of nest structure and site. Based on the color patterns of the rectrices and other morphological features, their closest relatives are most likely the "emeralds" Panterpe, Elvira, Eupherusa, Goethalsia, and Goldmania, followed by the "woodnymph-and-sapphire" clade Cynanthus, Thalurania, Damophila, Lepidopyga, Hylocharis, and Chrysuronia. This latter assemblage shows distinctive cervical musculature, unique flight patterns in the male display, and nest structures with close affinities to the emeraldines. Another unit consists of the "amaziline emeralds" Leucochloris, Polytmus, Leucippus, Amazilia, Agyrtria, Polyerata, and Saucerottia. Typical nest forms, nest sites, and a cervical musculature pattern characterize this clade.

Another distinct taxon also derived from plumage comparisons are the "mountain gems" *Microchera*, *Anthocephala*, *Lampornis*, *Basilinna* (formerly treated under *Hylocharis*), and

Lamprolaima. The "brilliants" Clytolaima, Heliodoxa (including Polyplancta), Hylonympha, and Sternoclyta comprise a further assemblage of closely related taxa. This group is united by typical morphological features like feathered upper and lower mandibles, throat coloration, song and display patterns.

The large "Andean clade" consists of five sub-units: the first contains Urochroa, Boissonneaua, and Aglaeactis; the second Oreotrochilus, Lafresnaya, Coeligena, Ensifera, Pterophanes, Patagona, and Sepahnoides; the third Heliangelus, Eriocnemis, Haplophaedia, Urosticte, and Ocreatus; the forth Lesbia, Sappho, Polyonymus, and Ramphomicron; and the fifth Oreonympha, Oxypogon, Metallura, Chalcostigma, Opistoprora, Taphrolesbia, and Aglaicercus. This arrangement is based on the following common features: open wing presentations after perching (especially members of the first, second, and third groups); distress calls; perching displays; advertisement songs; plumage characteristics; nest shape; and nest site.

Finally, another distinct assemblage, the "starthroat-and-woodstar" group, containing *Heliomaster*, *Rhodopis*, *Thaumastura*, *Tilmatura*, *Doricha*, *Calliphlox* (including *Philodice*), *Microstilbon*, *Calothorax*, *Mellisuga*, *Archilochus*, *Calypte*, *Atthis*, *Stellula*, *Myrtis*, *Myrmia*, *Chaetocercus* (including *Acestrura*), and *Selasphorus*. Some of these share similarities in plumage characteristics, notably an eclipse plumage; display pattern features; song structure; flight displays; nest shape; and nest-site.

During the period 1946–1995, 23 hummingbird species new to science were described—eight in Phaethornithinae and 15 in Trochilinae. After critical revision only one of the hermits, Koepcke's hermit (*Phaethornis koepckeae*), was considered a valid species, while only four remained on the list of trochilines, namely the royal sunangel (*Heliangelus regalis*), colorful puffleg (*Eriocnemis mirabilis*), and Perija (*Metallura iracunda*) and Neblina metaltails (*Metallura odomae*). The others turned out to be subspecies, hybrids, aberrant individuals, immatures, or synonyms of known subspecies. The Chiribiquete emerald (*Chlorostilbon olivaresi*) is considered a valid species but may in the future end up being treated only as a subspecies of the bluetailed emerald (*Chlorostilbon mellisugus*), once more detailed information on geographical character variations are available and zones of contact within this complex are better understood.

Physical characteristics

Hummingbirds are extremely small. The majority of species are between 2.4 and 4.7 in (6–12 cm) in size and have a body mass of around 0.09–0.2 oz (2.5–6.5 g). The reddish hermit (*Phaethornis ruber*) from Guyana and Brazil and the Cuban bee hummingbird (*Mellisuga helenae*) weigh less than 0.07 oz (2 g), while members of the genera *Eutoxeres, Ensifera*, and *Pterophanes* are heavier than average at 0.42–0.49 oz (12–14 g). As its name suggests, the largest of all is the giant hummingbird (*Patagona gigas*) weighing 0.67–0.74 oz (19–21 g), comparable in size to a swift.

Trochilids are highly evolved nectarivores, depending almost completely on the carbohydrate-rich sugar secretions (nectar) of ornithophilous flowering plants (approximate composition of diet being 90% nectar, 10% arthropods and pollen). They reach this liquid food with specialized tongues



Hummingbird bills are adapted to feeding at different flowers: 1. Ruby-throated hummingbird (*Archilochus colubris*) at a hibiscus; 2. Purple-crowned fairy (*Heliothryx barroti*) at heliconia (*Panterpe insignus*); 3. Broad-billed hummingbird (*Cynanthus latirostris*) at feeder; 4. Sword-billed hummingbird (*Ensifera ensifera*) at trumpet flower; 5. Green hermit (*Phaethornis guy*) at lobster claw heliconia. (Illustration by Patricia Ferrer)

and thin, elongated bills of various shapes, protecting their long and sensitive tongues. Their feeding behavior necessitates hovering flight, which allows them to remain apparently motionless in the air when feeding on exposed flowers, but due to this unique foraging behavior, they can no longer walk or climb with their feet, which serve only for perching. During hovering, their pointed, uncambered wings are moved mainly in the horizontal plane, describing with their tips a flat figure of eight, in the manner of a variable-pitch rotor. By slightly altering the wing angle, this technique allows all kinds of controlled forward, sideward, and backward movements in the air, including upside-down maneuvers.

While hovering, the wingbeat in smaller trochilids like the amethyst woodstar (*Calliphlox amethystinus*) averages 70–80 per second compared to 10–15 in the giant hummingbird (*Patagona gigas*). During the courtship flights of some North

American trochilids such as the ruby-throated hummingbird (*Archilochus colubris*) and the rufous hummingbird (*Selasphorus rufus*) wingbeat rates of over 200 per second have been reported. The humming sound produced by the wings during hovering has given the family its English name.

Flying speeds under controlled laboratory conditions range roughly from 30 to 53 mph (48–85 kph). For the green violet-ear (*Colibri thalassinus*) in the wild a velocity of 60 mph (96 kph) has been recorded, and during short chase flights up to 93 mph (150 kph). The homing pigeon, one of the most skilful and rapid fliers among birds, travels at speeds of around 40 mph (64 kph).

The unique flight mode involves specific skeletal and flight muscle features. The deeply keeled and elongated hummingbird sternum is relatively large compared with those of other



Newly hatched Allen's hummingbird (*Selasphorus sasin*) chick in Los Osos, California. (Photo by George D. Lepp. Photo Researchers, Inc. Reproduced by permission.)

flying birds. Eight pairs of ribs, two more than in most birds, help to stabilize the body during flight. Exceptional in structure are the strong coracoids of the pectoral girdle. Only hummingbirds and swifts have a shallow cup-and-ball joint where the coracoids are connected to the sternum. Tendons connect the flight muscles with the humerus.

The arm bones of all trochilids, consisting of the humerus, radius, and ulna, are much shortened, with a result that over 70% of the wing skeleton size is attributable to the elongated hand bones, homologous to the second, third, and fourth finger of the tetrapod hand. The hand bones bear 10 large flight feathers—the primaries—generally increasing progressively in size from the inner portion of the wing towards the tip. The modified humerus bone of hummingbirds moves freely at the shoulder joint, permitting optimal wing movement in all directions, including axial rotations of nearly 180 degrees. It is only the humerus that moves at this joint.

Hummingbirds use the upstroke and downstroke almost equally for powered flight, in contrast to most other birds, which mainly employ the downstroke for their powered flight. Both flight muscles together make up over 30% of the body mass of a hummingbird, much more than in other strong fliers such as migratory birds, in which these muscles account for about 20% of body mass.

As tiny endotherms, hummingbirds suffer from low thermal inertia and high heat loss. Flapping flight is energetically expensive, and convective cooling caused by wing and air movements can further exacerbate energy loss. Energy conservation during flight is thus an important physiological problem for hummingbirds. Studies by Peng Chai and his coworkers revealed that trochilids clearly use the heat produced in flight to contribute to their thermoregulatory requirements during hovering. Heat production by contraction of the flight muscles is employed as a substitute for regulatory thermogenesis to compensate for heat loss during exposure to cold.

Hummingbird flight muscles are extremely oxygendependent. Mitochondrial volume density in these muscles can account for 35% of their volume; this figure may represent an upper limit because any further increase would reduce space for the muscle fiber necessary for mechanical work. However, even during hovering, trochilids are operating within a reasonable physiological safety margin. These physiological reserves are essential for maintaining fitness parameters.

Another special trochilid muscle is the heart. It amounts to about 2.5% of their body mass. Wheras in small songbirds, like the house sparrow (*Passer domesticus*), it contributes 1.3% of the weight (only 0.5% in primates). A hummingbird's heart beats 500–600 times per minute while resting, and over 1,000 times per minute during aggressive encounters. In a ratite like the ostrich (*Struthio camelus*) the normal heart rate ranges from 40 to 180 beats per minute.

Hummingbirds' tails differ greatly in size and shape. They can be forked, V-shaped, rounded, or wedge-shaped. In several species of the genera Lesbia, Trochilus, and Thaumastura, for example, some of the tail feathers are strikingly elongated, the same length or even twice as long as the actual body size of the bird. Others, like *Discosura longicauda* and *Ocreatus* carry little flags at the end of a single pair of extended rectrices. A major feature of trochilid plumage is the striking iridescent colors of crests, gorgets, rectrices, and other feather structures. In contrast to colors generated by pigments, iridescence is of a physical nature, caused by the structure of platelets in the feather barbules. Beneath the upper surface of these platelets we find thin elliptical melanin bodies filled with air bubbles. These form a mosaic-like non-homogenous layer of up to 10, stacked one above the other within a barbule. C. Greenewalt discovered by electron microscopy that the thickness of the platelets influences not only the properties of the perceived light, but also those of the air held inside each pigmented body, thus causing variations in interference effects. Each pigmented body within a platelet can produce different colors depending on the angle from which it is viewed. Thus, a hummingbird's throat may appear metallic golden if a beam of light comes from directly behind the observer, but will shift to almost black if the angle of view is changed.

Hummingbird coloration is related to behavior. Generally two broad groups of coloration characteristics can be distinguished in birds: those promoting concealment and those enhancing conspicuousness. The majority of trochilid females exhibit a cryptic coloration, since all activities associated with nesting and the rearing of the young are carried out by the

female alone. Conspicuous female coloration would easily betray the bird and the nesting site to potential predators. Males of many species of open habitats exhibit phaneric coloration, i.e., the opposite of cryptic. As part of their territorial and polygamous life-history, bright, light-dependent iridescent colors on throats, crests, or backs play an important role as visual threat signals for territorial defense, self-advertisement during display, or species-specific recognition cues. In forest-dwelling species, like most members of the Phaethornithinae, sex-specific phaneric iridescent coloration is absent, probably due to the dimly lit undergrowth of tropical forest habitats and to their non-territorial foraging behavior.

The plumage of male and female immatures is mainly similar to, but duller than, that of adult females. Immatures molt into adult plumage in their first year. In only a few sexually dimorphic species—like the Jamaican streamertails (*Trochilus polytmus*, *T. scitulus*) and the Juan Fernandez firecrown (*Sephanoides fernandensis*)—male and female nestlings can already be clearly separated by their plumage, which is similar to that of adults but less bright in coloration.

Hummingbirds have a single complete annual molt, starting soon after the breeding season. Replacement is slow and takes several months. Postjuvenile molt, which is absent in the Central American long-tailed hermit (*Phaethornis longirostris*, formerly considered as *P. superciliosus*) and possibly in other lekking tropical species, takes around four months, annual molt about four to five months. Molt of iridescent feather parts on throat, chin, forehead, and crown of males is often completed several weeks after renewal of primaries. It has been suggested that the delayed molt of brightly colored feathers ensures that the bird enters the subsequent breeding season in optimal plumage condition.

Nectar supplies the necessary energy for the highly evolved muscular system of trochilids. Hummingbirds take up nectar using their extendable biforked tongue, which is forced out of the bill by the hyoid apparatus stretched around the posterior part of the skull. The proximate half of the muscular tongue is partly cartilaginous. The distal half is divided lengthwise, forming two separate membranous curled troughs. This frontal part is essential in nectar drinking, since the liquid nectar is carried into the external troughs by capillary action. The rate of tongue licking varies from three to 13 licks per second. In nature, corolla curvature, position, and nectar volume are important factors in determining nectar extraction rate from flowers. As a general rule, hummingbirds drink their body mass of nectar in several hours. In order to meet their daily energy needs, hummingbirds must consume the nectar of about 1,000-2,000 flowers each day.

The first ornithologists to study hummingbirds supposed that the forked tip of the tongue had a sticky surface working as a glue to trap insects. However, this nectar-specialized feeding apparatus is completely unsuited for the capture of insects hidden inside flowers. Insects providing most of the protein in the hummingbird diet are either caught by hawking, or by gleaning from vegetation or spider webs.

Nectar also supplies the necessary energy for growth and renewal of body tissue, maintenance of body temperature at



A little hermit hummingbird (*Phaethornis longuemareus*) feeds on a *Heliconia* flower in Madre de Dios, Peru. (Photo by François Gohier. Photo Researchers, Inc. Reproduced by permission.)

104–107.6°F (40–42°C) (endothermy) and other important biological functions including reproduction. Since humming-birds have the highest mass-specific basal metabolic rates of all birds, their digestive system is well adapted to break down food as quickly as possible and to absorb its nutrients.

Due to their energy-demanding hovering flight, hummingbirds have the highest oxygen requirements of all vertebrates. Their respiratory system, two compact symmetrical lungs for gas exchange and nine thin-walled air sacs acting as bellows for their ventilation, is adapted to utilize high gas volumes. At rest, the breathing rate is 300 times per minute, which may rise under heat conditions or during hovering flight to over 500 per minute, whereas a starling or a pigeon breathes roughly 30 times, and man about 14–18 times per minute.

Small endotherms like hummingbirds are under considerable time pressure; not only must they meet their daily food requirements, but they must also accumulate sufficient energy reserves to survive their nocturnal starvation. The following factors are therefore of decisive importance for extremely small hummingbirds: quality and accessibility of food, and mechanisms to reduce energy consumption. In trochilids, these mechanisms are long periods of inactivity between daily meals and torpor.

During torpor, gaseous metabolism and body temperature are adjusted to the levels of ambient temperature and regulated to remain within the range of 64.4–68°F (18–20°C). In torpor, hummingbirds become lethargic and incapable of reacting in a coordinated way to external stimuli. Energy savings during this immobile state are considerable; up to 60% of the total energy accumulated for the nocturnal resting phase. During observations on Nearctic migratory hummingbirds an irregular occurrence of torpor was noted. Birds reacted only with torpor when energy levels fell below lower limits during the night. According to these studies, torpor is

an energy-regulating mechanism that is triggered below a threshold value, equivalent to a physiological regulation pattern coming into force in extreme conditions. As reasons for the irregularity of torpor, physiologists cite the risks and energetic costs of the lethargic state. The risks involved include the danger of predation while immobile, and insufficient residual energy for thermoregulation which could prevent awakening from torpor.

Laboratory research on Neotropical trochilids from a wide range of climatic zones and altitudes shows that in all species torpor occurs nocturnally. Regular occurrence of torpor has not been observed in Nearctic hummingbirds. An explanation could be that these trochilids enjoy long daylight conditions in their northern summer quarters (14–16 hours) during which to feed, resulting in a positive energy balance. Changes in levels of metabolism and body temperature only occur when the lower energy balance threshold is crossed.

Distribution

Hummingbirds are restricted to the New World. They reach their highest species diversity at tropical and subtropical latitudes in the montane zones of northern South America (Venezuela, Colombia, Ecuador, Brazil). Here, the species number reaches over 170 taxa. An abrupt decrease of species density can be observed on passing eastwards from the Andes to the extensive lowlands of that continent. A similar trend is seen at temperate latitudes in North America. Seven species of hummingbirds are found regularly in the western United States, whereas only one species, the ruby-throated hummingbird (Archilochus colubris), occurs in the eastern United States. Besides the west-east decrease of species richness, there is a general trend of species decline with increasing latitudes. At the northern and southern tip of both New World continents (Alaska and Tierra del Fuego) only one species exists. Hummingbirds in most temperate climate zones are migratory.

Habitat

Hummingbirds live in an extremely wide range of New World habitats. Some species—like the helmetcrests (Oxypogon) in western Venezuela and Colombia and the hillstars (Oreotrochilus) in Ecuador south to Chile—can be encountered at over 13,100 ft (4,000 m) on the verge of Andean snowfields and glaciers, where in wind-sheltered and sun-exposed canyons a relatively species-rich community of bird and insect-pollinated alpine flora flourishes. These high-altitude trochilids forage among dense stands of year-round flowering Scrophulariaceae, Asteraceae (Compositae), and Gentianaceae, which provide nectar and attract the insects that supplement their diet. Nocturnal frosts, occasional snowstorms, and daily temperatures of a few degrees above zero are the environmental conditions in these Andean regions. Helmetcrests and hillstars rarely leave this alpine habitat, except for periods of longer snow cover. Then they shift to the upper páramo, an open, grass-dominated vegetation with scattered stands of small trees and shrubs, only a few hundred meters below their native habitats. Often they leave the

páramo plateaus again after a few hours and return to the rocky heights when weather conditions are favorable again. During frosty nights, trochilids of alpine Andean regions seek shelter in caves or under overhanging vegetation on the steep slopes. The members of these two hummingbird genera only are able to inhabit the extreme habitats of the high Andes on a regular basis. Here they are physiologically well adapted, reproduce successfully without facing strong competition for nesting sites and food from other trochilids, and, equally important, are not exposed to predation.

Penetrating drizzle, sometimes turning into snow, and a constant dense fog cover that leaves everything dripping wet, is the characteristic weather of the Andean páramos from Ecuador north to western Venezuela. Although grass tufts carpet the ground at these altitudes, numerous taller herbaceous plants form the typical landscape, like man-sized giant Espeletia species (Asteraceae), locally called frailejones, and terrestrial bromeliads of the genus Puya (Bromeliaceae). In addition, a large number of other herbaceous flowers and woody plants-belonging to many different families, like Rosaceae, Myrtaceae, Ericaceae, and Melostomataceaeoften occur in wind-sheltered ravines. In this border zone between small patches of forest thickets and open páramo, over half a dozen trochilid species, including the genera Aglaeactis, Chalcostigma, Metallura, Ramphomicron, Lafresnaya, Eriocnemis, and sometimes Chaetocercus, occur year-round. During the major flowering period from the end of June to August, many more hummingbirds from lower elevations temporarily visit the páramos due to the superabundant nectar supply in the dense stands of angiosperms dependent on trochilids for pollination. Then large numbers of sparkling violet-ears (Colibri coruscans) from the lower Andean valleys, and occasionally, during warmer sunny days, even green hermits (Phaethornis guy) from the upper tropical rainforest may be encountered on the páramo. However, these species disappear in the afternoons, obviously returning to lower elevations again.

The mostly dry and windy puna zone of the Peruvian and Bolivian Andes is less favorable for hummingbirds than the northern wet páramo at similar altitudes. In the puna trochilids are much more confined to edges of *Polylepis-Gynoxys* woods and to sheltered gullies with bushy vegetation than to open grassland. The giant hummingbird (*Patagona gigas*) and the Andean hillstar (*Oreotrochilus estella*) occur regularly in the open grasslands of the southern high Andes mainly during the flowering period of the arborescent puya (*Puya raimondii*). A typical open puna species, the olivaceous thornbill (*Chalcostigma olivaceum*), frequently perches on grass tussocks from where it sallies for flying insects.

At 11,500 ft (3,500 m), the páramo and puna are sharply replaced by shrubs and trees of the upper Andean forest. Where these habitats merge, the hummingbird community comprises almost a dozen sympatric species foraging for nectar from a highly diverse angiosperm assemblage comprising many taxa of vines, shrubs, and woody plants with brightly red or orange-colored tubular flowers, a major visual cue for their minute avian visitors. From Venezuela to the yungas of Bolivia this life zone forms the upper distribution limit of the

sword-billed hummingbird (*Ensifera ensifera*). Also occupying the same habitat is the great sapphirewing (*Pterophanes cyanopterus*), as well as other closely related long-billed allies from the inca and starfrontlet group (*Coeligena*), together with pufflegs (*Eriocnemis*) and sunangels (*Heliangelus*).

The most hummingbird-rich altitudinal region is the transitional zone between the Andean forest and the adjacent lower submontane forest, roughly between 5,900 and 8,200 ft (1,800–2,500 m). Here the daily temperature is fairly constant, ranging from 53.6° to 60.8°F (12–16°C). Daily cloud cover, especially in the afternoon, brings the moisture that sustains a rich plant life of ferns, shrubs, trees, vines, and especially ephiphytes, like orchids, bromeliads, gesneriads, and ericads. As diurnal endotherms, trochilids are the most successful organisms serving the cloud forest plants as pollen vectors. At these altitudes, heterothermic insect pollinators are dependent on favorable temperature and weather conditions, which limits their flight activity to a few, often unpredictable daytime hours.

Although there is some flowering seasonality among ornithophilous plants of different families like Ericaceae and Rubiaceae, this Andean life zone between 12° north and south of the equator provides abundant nectar year-round, allowing the coexistence of over a dozen hummingbird species. The cloud forest trochilid community comprises a concentration of very small to medium-sized and large species from about 0.1 to 0.42 oz (3–12 g) with diverse bill shapes and sizes. Alongside a group of 14 core species another 10–15 hummingbird taxa—including lowland and high Andean species—may be found in the cloud forest during the peak of the flowering season, attracted by the nectar-rich ericad shrubs and *Inga* trees.

The tropical lowland forests of South America, in stark contrast, harbor a much impoverished hummingbird community. Dominant species of this life zone mostly belong to the subfamily Phaethornithinae (Androdon, Eutoxeres, Glaucis, Threnetes, and Phaethornis), whereas trochilines are normally represented by the genera Amazilia, Polyerata, and Agyrtria (Amazilia tzacatl, P. rosenbergi, west of the Andes; Agyrtria versicolor, P. fimbriata, Agyrtria leucogaster, east of the Andes), and Hylocharis (H. grayi, H. eliciae, west of the Andes; H. sapphirina, H. cyanus, mainly east of the Andes). Cis- and trans-Andean hummingbird taxa often constitute allospecies of a superspecies with almost identical ecological requirements. A fine example is provided by the two tropical lowland species of the genus Heliothryx, separated in their distribution by the Andes.

Hummingbirds occur in many other life zone including arid-scrub (Lucifer hummingbird, Calothorax lucifer; Peruvian sheartail, Thaumastura cora), desert oases (oasis hummingbird, Rhodopis vesper), Nearctic pine forests (many North American species: broad-tailed hummingbird, Selasphorus platycercus; magnificent hummingbird, Eugenes fulgens), mangrove swamps (mangrove hummingbird, Polyerata boucardi), and on remote islands in the Caribbean (Trochilus, Chlorostilbon, Eulampis, Mango, Orthorhynchus) and on the Juan Fernández Is. off Chile (green-backed firecrown, Sephanoides sephaniodes; Juan Fernandez firecrown, S. fernandensis). However, many of

these habitats are occupied only sporadically for a short period or seasonally during the breeding period, when foodplants are in flower. Birds leave these regions again when conditions become unfavorable. Many of the North American trochilids then disappear and migrate to their Central American winter quarters. The same is true for the greenbacked firecrown (*Sephanoides sephaniodes*) from Chile, which leaves its southernmost summer range on Tierra del Fuego to migrate northwards to western Chile and Argentina. On larger islands, hummingbirds show altitudinal migration or disperse to different lowland habitats.

Trochilid habitat requirements are still poorly understood. Many species exhibit a remarkable plasticity, easily adapting to man-made habitat changes, or even expanding their ranges if food conditions are favorable (Anna's hummingbird, *Calypte anna*). Others rapidly decline in numbers (hook-billed hermit, *Glaucis dohrnii*) and face extinction following environmental disturbance. Besides habitat changes, cases of competition for food from congeners must be thoroughly analyzed in the future to better understand hummingbird community structure and change, an important prerequisite for successful conservation programs.

Behavior

Physiological adaptations for nectar feeding, and energy regulation patterns resulting from limiting temporal and environmental conditions are fundamental factors for understanding of the general habits of hummingbirds. The utilization of energy-rich nectars most likely fostered strong individual competition for this food source, favoring the evolution of specific maintenance and survival strategies. As a general consequence, males and females of almost all hummingbird species so far studied are solitary, often aggressively defending nectar sources like flowering shrubs and trees against any potential food competitor. The sexes are polygamous and associate only briefly to fertilize the eggs.

Mainly the males of species with bright iridescent colors establish feeding territories at flowering bushes that allow them to cover their daily energy needs. In order to defend their nectar resources they often perch high on nearby exposed branches. These serve as a vantage point from which predators can be detected with ease or from which the area can be defended against possible intruders, including females, by vocal warning signals and agonistic flights. Often the territory holder first empties the nectar from peripheral flowers to remove or reduce the feeding reward for newly arriving competitors. Trespassers ignoring the threat calls of the territory owner are robustly attacked in flight, sometimes resulting in direct physical combat. An airborne fighting pair may then be locked in strong claw grips, tumbling to the ground like a falling stone. These fights are rarely harmful to the birds but occasionally small featherless dorsal parts can be seen as a result of such aggressive encounters.

Purple-throated carib (*Eulampis jugularis*) males react differently to territorial intruders and food competitors during the reproductive period. All but their mates are aggressively chased out of the defended feeding area. Incoming females,



A female Anna's hummingbird (*Calypte anna*) feeds her young in a nest made on a metal hanger (Los Osos, California). (Photo by George D. Lepp. Photo Researchers, Inc. Reproduced by permission.)

however, are guarded and allowed to feed prior to mating. A similar function of the feeding territory has been observed in the tiny dimorphic white-rumped green thorntail (Popelairia conversii) by K.-L. Schuchmann. In December to March, during the breeding period of the species, Inga trees begin to flower in southwestern Colombia. Then the males establish and defend feeding territories in these forest giants. Females entering these feeding grounds are allowed to feed on the nectar-rich brush-like white flowers of the trees. Frequently, males display to individual females and copulate with them while they are in their territory. Green thorntail males aggressively attack all possible territory intruders, even much larger trespassing birds like the numerous tropical kingbirds (Tyrannus melancholicus) gathered around flowering Inga trees. Besides females of the green thorntail, a small diurnal moth, the white-banded sphinxlet (Aellopos titan), similar in size, appearance, and flight behavior to the white-rumped hummingbird, visits the guarded territories. Being almost perfect female mimics to male hummingbirds, they are obviously considered as potential mates, as indicated by the displays directed at them. However, because of their fast and unpredictable flights within the densely packed Inga flowers, green thorntail males quickly lose interest in these female mimics but still continue with their mate-defense behavior. Hummingbird

males direct their agonistic flight maneuvers especially at tropical kingbirds, which prey on the white-banded sphinxlet. When hummingbird males were excluded from a flowering *Inga*, predation rate on the moths was over 80%, and individual moths spent only one to three seconds at each flower. When such an *Inga* tree was guarded by a green thorntail, male sphinxlet predation by kingbirds declined to 20% and most moths spent four to six seconds feeding at each flower visited. In the latter case, *Inga* seed production was significantly higher than in a territory without a hummingbird guard. This mimicry relationship between two different animals, a moth and a hummingbird, is an instructive example of the complex interrelated webs of adaptation in the tropics.

Females of a few hummingbird species may hold temporally and spatially limited territories around localized feeding sites during and after the reproductive period. Studies by J. Dorst, K. B. Armitage, and M. L. Cody looked at females defending a nest area or birds on migration defending a small area in a locally common food source. However, long-term feeding territories are known only for the brightly monomorphic fiery-throated hummingbird (Panterpe insignis) in southern Central America. This type of territoriality reflects the temporal and spatial decline of nectar resources and the resident status of the birds. L. L. Wolf, who has studied female territorial behavior of Panterpe insignis in Costa Rica, suggests that territoriality in hummingbirds is accompanied by strong selection for sexual monomorphism in plumage coloration (advantageous in aggressive encounters) and for sexual similarity in bill length (advantageous for efficient utilization of limited food resources).

Many species in tropical Central and South America do not establish feeding territories but are trapline feeders on flowers often too scattered to be defended. But between territoriality and trapline behavior many more intermediate feeding strategies can be found, depending on flower dispersion, morphology, and nectar reward.

Despite being under extreme pressure to gather energy quickly, and having developed many obvious behavioral traits for doing so, hummingbirds spend over 70% of their daily activity phase perched, apparently doing little else besides singing, self-preening, and sunbathing. Hummingbirds bathe several times a day. Some sit in shallow water and splash like sparrows, others cling to rocks beside waterfalls gathering moisture and spray from above, vibrating their wings and ruffling their body feathers. Hermits and many trochilines hover just above gently flowing forest streams then abruptly drop into the water, sometimes almost completely submerging their body. These dives are sometimes repeated over several minutes.

Hummingbirds do not show flocking behavior. Individual social contacts are rare but occasionally do occur around superabundant nectar sources and at cave roosting sites (Andean hillstars, *Oreotrochilus*). Nest aggregations within a few meters are known for the cave-breeding Ecuadorian hillstar (*Oreotrochilus chimborazo*) and within a 66–100-ft (20–30-m) radius for the Costa hummingbird (*Calypte costae*), Bahama woodstar (*Calliphlox evelynae*), rufous-tailed hummingbird (*Amazilia tzacatl*), and crimson topaz (*Topaza pella*).

Hummingbird foraging behavior is determined to a large extent by individual perception and memory capability. Field and laboratory studies by G. H. Pyke, conducted with North American broad-tailed hummingbirds (*Selasphorus platycercus*) and rufous hummingbirds (*S. rufus*), suggest that these hummingbirds may at least perceive and remember the number of flowers available on an inflorescence, the number of flowers already probed on the inflorescence, and the amount of nectar obtained at the present flower.

Many hummingbirds are already active before dawn and late after sunset. Remarkable examples are the incas and star-frontlets (*Coeligena*) which visit flowers in the early morning hours when it is still dark. Other species still continue to forage for nectar in the evening twilight before disappearing to their roosts. Although hummingbirds are not nocturnal, the night vision of some taxa seems to be excellent.

Ornithologists have discovered trochilids at their roosting sites on only a few occasions. Their sleeping places are sometimes well protected by leaves, as in the rufous-tailed hummingbird (*Amazilia tzacatl*), whereas the long-billed starthroat (*Heliomaster longirostris*) roosts on the thin exposed twigs of tree-tops. The sleeping position of perching trochilids is strikingly similar in all species observed: with both feet on the perch, head exposed, neck retracted, and the bill pointed forward and upward. By contrast, songbirds on their roosting sites cover their turned-back head with their shoulder feathers and often perch on one foot.

Hummingbirds are threatened by only a few predators among vertebrates. Camouflaged snakes on Heliconia flowers prey on them when they are foraging for nectar or when brooding. Forest-falcons occasionally capture hermits at their lek sites, pygmy-owls may attack them at dawn when still visiting flowers. Nest robbers like jays, toucans, and possibly some bats, however, seem to be the major predators. This information has been generated only by the occasional observation, and the impact of predation on hummingbird populations is almost completely unknown. Whenever a potential enemy is sighted by a hummingbird it is directly approached by rapid diving attacks accompanied by a series of high-pitched warning calls. These alarm signals regularly attract other bird species, which join in the aggressive flight encounters supported by continuous mobbing noises. Threat behavior like flight attacks are exhibited especially by hummingbird females against intruders near their nesting sites, even if they are not potential predators.

Feeding ecology and diet

Virtually thousands of New World plant species rely exclusively upon hummingbirds for pollination. As a consequence of the year-round high energy requirements of trochilids, plants that are pollinated by hummingbirds provide nectar at all times of the year, creating the opportunity of a phenological displacement of flowering times as a means of reducing interspecific pollen flow.

The evolutionary relationship between hummingbirds and their food plants is a good example of close mutualism, resulting in many adaptations between flower and pollen vector, called the syndrome of ornithophily. Plants that have converged upon the "hummingbird" syndrome bear relative large flowers, solitary or loosely clustered, often placed in a horizontal or pendant position. Typical hummingbird plants open their blossoms during the day, flowers are generally brightly colored—often red, orange, or yellow, sometimes in combination with contrasting white corolla parts. Exceptions can be found in the Gesneriaceae, where some ephiphytic species exhibit solitary inconspicuous whitish flowers. However, hummingbirds are attracted to these well-camouflaged flowers by ornamental red-edged or red-centered leaves, a little studied advertisement strategy in hummingbird pollinated plants, known as phylo-flagging.

Some of the more commonly known hummingbirdpollinated New World plant species belong to the genera Zauschneria (Onagraceae), Delphinium and Aquilegia (Ranunculaceae), Mimulus (Scrophulariaceae), Aphelandra (Acanthaceae), Centropogon (Lobeliaceae), Cavendishia (Ericaceae), Columnea (Gesneriaceae), Psitticanthus (Loranthaceae), and Heliconia (Heliconiaceae). Most ornithophilous plants are dicotyledons with perennial herbs and shrubs. Only a few New World trees are pollinated by hummingbird. Flowering trees with a very large nectar source, like many Erythrina species, are quickly occupied by territorial hummingbirds remaining in the tree tops for the whole flowering period until the nectar source declines. By doing so, pollen flow is extremely reduced. The corolla of a typical hummingbird flower is often long, thickened, tubular in shape, and scentless. It contains sucrose rich or sucrose dominat nectar which is exploited by trochilids in hovering or hover-clasping flight.

Hummingbird flowers supply their pollinators with large amounts of nectar per flower and day, but do not satisfy their nutritional requirements at one visit. However, P. Feinsinger discovered in a Costa Rican heliconia (Heliconia psittacorum) that only some flowers contain abundant nectar (bonanzas), some essentially none (blanks). Since hermits are the main pollinators of heliconias, Feinsinger suggested that these hummingbirds must visit many flowers in order to encounter one with high nectar content, thus the bonanza-blank pattern may support cross-pollination in *H. psittacorum*. In another field study on the pollination of successional plant species in the cloud forest at Monteverde, Costa Rica, Feinsinger observed that flowering was staggered among plant species, resulting in a constant nectar supply to trochilids. In five plant species that were closely investigated, measurements of nectar volume indicated that the bonanza pattern was evident. He concluded that plants may conserve energy by producing large numbers of nectarless flowers and a few bonanza flowers. By doing so hummingbirds are forced to visit many flowers to meet their energetic needs. By visiting many flowers, cross-pollination is promoted.

An obvious feature of most bird pollinators in relation to insects is their larger body mass. This, combined with endothermy increases the energy requirements of trochilids. Only a few species of large hawkmoths have higher energetic needs when active than hummingbirds, but reduce their metabolism like other insects when weather conditions are unfavorable. Hummingbirds use nocturnal torpor for short-term



A male green violet-ear hummingbird (*Colibri thalassinus*) dive-bombs a perched rival—a male of the same species—in Monteverde, Costa Rica. (Photo by Gregory G. Dimijian. Photo Researchers, Inc. Reproduced by permission.)

energy savings, remaining active even under inclement conditions during the day when insects are inactive. Trochilids are thus more reliable pollinators where cool or rainy conditions occur regularly. Hummingbirds, like other nectarivorous birds, forage throughout the day, with higher activities at dawn and dusk, although a small fraction of each hour may actually be spent feeding. Insects search for nectar only at certain periods during the day. Due to their high body mass, hummingbirds also have much higher potential mobility than most insects. A long-lived pollinator, such as a hummingbird, experiences several flowering seasons during its life span. These birds can easily remember flower stands of local or patchy distribution, and, thus, the floral environment for trochilids is much more differentiated in time and space than for insects.

There is a close fit between shape and length of the bill of some hummingbirds and the flowers on which they feed. Like the insect feeding apparatus, bird bills are evolutionary labile (readily undergoing change) structures. Selective forces have had a much stronger impact on morphological coadaptations between bird bills and flower shapes than between snout structures of bats and bat flowers. This may generally explain the higher species diversity of flower-visiting birds and insects compared to bats.

Bill structure and shape, which varies widely among trochilids, largely influences the efficiency with which they forage at each flower and determines the type they can successfully exploit. Hermit hummingbirds (Phaethornithinae) and certain species of trochilines (Trochilinae) have long straight or long and slightly decurved bills providing access to long-tubed flowers, rich in nectar. At the other extreme, many trochilines have short, straight bills allowing them to opportunistically exploit a variety of moderate to insect flowers. However, some short-billed species like *Heliothryx* are nectar robbers, taking nectar from flowers by piercing the corolla base.

In more complex tropical environments hummingbird communities may grouped, according to required power, into different foraging modes. "High-reward trapliners" with specialized long bills (almost all hermits, some non-hermits) visit widely scattered long-tubed and nectar-rich flowers following a repeated foraging circuit (trapline). "Low-reward trapliners" have smaller straight bills, visiting dispersed but less specialized flowers. "Territorialists" occupy "clumped moderate" (flowers with small to medium corollas and little nectar reward) and "clumped rich" (flowers with long corollas and high nectar production that occur in dense clumps) flowers. These are generally small hummingbirds with short bills and a moderate to high required power. They defend feeding territories against any potential hummingbird intruder. "Territory-parasites" frequently occur in "clumped moderate" flowering stands, parasitizing the territorial holder. These parasitizing trochilids may be large with medium-sized bills, high required power output, ignoring aggressive displacement displays by the territorial bird, or they may be very small, resembling large insects like *Lophornis* and *Atthis*, feeding at sections of a territory which are not directly visible or not regularly inspected by the resident bird. "Generalists" have short to moderate bills and small to medium body mass with moderate required power output. They behave opportunistically, switching feeding from dispersed moderate flowers to clumped flowers. Frequently these generalists are also called "faculative trapliners" since they may switch to lowreward traplining depending on the local nectar availability and competition for food.

A closer examination of the mutualistic relationship between hummingbirds and their food plants has shown that pairwise coevolution between a certain trochilid species and a certain plant species is non-existent. Plant-bird mutualisms are best described as having originated by "diffuse coevolution," in which hummingbird pollinated plants and trochilids are represented by an array of populations that generate a selective pressure as a group.

Hummingbirds in North America and Colombia have been observed to make use of sapsucker pits in living trees consuming the sugary sap and catching insects attracted to this food source. Especially *Archilochus colubris* from North America seems to benefit from these sugar sources during spring migration when plants just begin to flower.

Hummingbirds complement their nectar food with some pollen gathered when drinking nectar. Although nectar contains fragments of essential amino acids, the major protein supplement comes from arthropods. It has been noted that hermits differ from non-hermits with regard to higher insect consumption, but this idea is not supported from laboratory and field studies. F. G. Stiles concluded from his detailed field study in Costa Rica that there is no support for considering hermits to be more insectivorous than non-hermits. As a general approximation most hummingbirds consume a daily ratio of nectar to arthropods of roughly 9:1.

Hermits, which exclusively live in the understory are hover cleaners, specialized in collecting web spiders. *Threnetes ruckeri* forages for jumping spiders. The exception among the hermits seems to be *Eutoxeres aquila* which hawks for flying

insects. In most trochilines hawking for flying insects is a common foraging mode. Flies and wasps are the dominant prey, but spiders, ants, and small beetles also have been found in the stomachs of non-hermits.

There is no evidence that hummingbirds can extract arthropods from flowers with their bills. Insects do not stick to their tongue. It is more likely that selection for nectar drinking was the major evolutionary force in the developement of a hummingbird's feeding apparatus, and that bill morphologies in turn constrain arthropod foraging tactics.

Reproductive biology

Hummingbird males are polygynous, mating with several females during a reproductive period. In most species studied the male associates with the female only during a short period to fertilize her eggs. All remaining reproductive responsibilities like nest building, incubation, and rearing the young are carried out solely by the female. There are a few reports of males participating in incubation or feeding young, but whether these observations are accurate, random exceptions, or regular species-specific behavior still needs further investigation.

Interactions between hummingbird males and females are normally restricted to the short period of sexual synchronization. Males advertise themselves by song, iridescent plumage (Trochilinae), and aerial flights either at traditional display grounds, or leks, from dispersed singing posts, or at their feeding territories where they are visited by females when receptive to copulation. The male behavior for attracting females is similar to the defense display directed towards food competitors, predators, or any intruder to the feeding ground. By specific behavioral triggers, mainly perching motionless near an advertising male, the female switches the agonistically orientated display of the male into one which is sexually directed and leads to copulation. Thereafter both sexes separate again. Males of the fiery-throated hummingbird (Panterpe insignis) and purple-throated carib (Eulampis jugularis), among others, show a resource-based mating system, allowing conspecific females to enter their otherwise aggressively defended territories to feed on nectar-rich flowers. Females may copulate with males on these feeding grounds or may collect nectar for themselves or their offspring during the period of reproduction. In hillstars (*Oreotrochilus*) only females hold territories, on which they are visited by males in the breeding season.

The onset of breeding in hummingbirds is very variable from species to species and from region to region. As a general rule the peak reproduction in most trochilids is closely associated with the months of mass-flowering of many ornithophilous flowering plants. In the high Andes of Ecuador, violet-ears (Colibri), metaltails (Metallura), trainbearers (Lesbia), and pufflegs (Eriocnemis) begin to breed during most of the wet season often around mid-October and continue to March, sometimes to April. At similar altitudes further north or south the onset of reproduction starts about three months earlier or three months later than in the mountain regions near the equator, the breeding season often lasting only a few

weeks. At lower altitudes, seasonality of the reproductive cycle declines and nests of several species may be found throughout the year, with decreasing numbers during the peaks of the dry and wet season; these seasons differ greatly from region to region. North American trochilids (Selasphorus, Archilochus, Calypte costae, Calothorax, Stellula, Eugenes, and Lampornis) chiefly breed during spring to late summer, with the exception of Anna's hummingbird (Calypte anna), which generally nests during winter, probably as a strategy to avoid competition with other temperate trochilids that invade the coastal Californian scrub zone (chaparral) during the spring flowering peak of several nectar-rich food plants.

Females of many Trochilinae select nest-sites after a nearby rich nectar source has been located. Suitable branches for nesting are first inspected by hovering above the surface and touching down over the spot repeatedly. Nest-sites of hermits (Phaethornithinae) are not associated with nearby food sources. Females of this subfamily frequently cling with their feet to suitable green leaves of palms or *Heliconia* stands to which they later attach their cone-shaped nests. This behavior may serve to test the strength of the stratum for the purpose of nest construction.

Hummingbird nests are tiny and of various shapes, and are placed in a wide range of heights, locations, and substrates. Most nests are of a cup-like architecture, saddled on branches and large leaves (Anthracothorax, Florisuga), placed in forked twigs (Thalurania), glued to rocky walls (Oreotrochilus), hidden underneath a bulk of dense thickets overhanging a slope (Eriocnemis, Lesbia), attached to lianas (Heliothryx), or fastened beneath a pendular leaf which provides shelter from rain (Haplophaedia, most Phaethornithinae). Some genera like the sylphs (Aglaiocercus) construct completely domed nests, while others like the metaltails produce semi-domed nests.

Nests can be found at all heights, from a few inches above the ground (*Phaethornis*) to tree-top levels at 33–100 ft (10–30 m) (*Anthracothorax, Eulampis, Heliomaster, Eugenes*). Even within a species nest-sites may vary from low secondary vegetation to the canopy. Nests are commonly placed in locations giving some protection from direct sun and rain by overhanging leaves. For nest-site selection balanced microclimatic conditions, like temperature and humidity, seem to be a major prerequisite for ensuring the successful development of the embryos. Thus nests are often located near waterfalls, forest streams, or lake shores. The nest construction process lasts around five to ten days for most species studied.

Many hummingbirds decorate the outer wall of their nest with pieces of lichen, moss, dead leaves, rootlets, bark, and so on, making it almost indistinguishable from the immediate surroundings and thus difficult for predators to locate. Soft and fine plant materials, occasionally small feathers or animal hair, are used for the inner nest lining, providing optimal insulation during incubation. Among the exceptions are nests of high-altitude hummingbirds, like the sapphirevented puffleg (*Eriocnemis luciani*), in which the inner soft cup layer is absent.

Members of the genus *Phaethornis* construct compact pendent nests of soft plant fibers and spider web attached to the

inner side of elongated plant leaves. All other hermit genera build similar but loose nests with open walls of coarse material like stiff rootlets or dry pieces of leaves and liverworts. This nest structure is an adaptation to the wet lowland forests where most hermits occur, and the poor insulation provided by the coarse nest material is largely compensated for by the warm ambient lowland temperature.

Often nesting material is reused in a new nest or the old nest serves as a platform for a subsequent construction. Females repair nests regularly, especially during the incubation period. The clutch of all hummingbirds consists invariably of two eggs, which are white, non-glossy, and of elliptical oval shape. In hermits (Glaucis, Threnetes), nests with three or four eggs have been frequently observed, but these are apparently attributable to more than one female, so-called egg-dumping. Females of both genera regularly inspect active nests of conspecifics. Occasionally three eggs have also been found in the nest of a few trochilines (Colibri, Amazilia, Calypte), and again it is most likely that the additional egg was laid by another female. Eggs are usually laid in the early morning. Normally there is a two-day, rarely a one or three-day interval before the second egg is laid. Eggs are sometimes laid before the nest is completed; females then continue construction between incubation intervals. Incubation may begin when the first egg is laid but regular incubation starts with the second.

Hummingbird eggs are naturally very small. Eggs of the tiny bee hummingbird from Cuba (Mellisuga helenae) average 0.4×0.3 in $(11 \times 8$ mm), those of the much larger giant hummingbird (Patagona gigas) of the Andes have a size of 0.8×0.5 in $(20 \times 12$ mm). Two eggs of a small species—like the reddish hermit (Phaethornis ruber)—equal roughly 35% of female body mass, while for the giant hummingbird the figure is about 15%. The severe energy constraints on females of small species may explain why single annual broods are much more common in these species than in medium—to large-sized taxa.

The incubation period for the majority of trochilids lasts 16–19 days, about two to five days longer than in songbirds. The shortest periods are known for the white-eared hummingbird (*Basilinna leucotis*) from Central America with 14–16 days, whereas hillstars and other high Andean species can attend their clutch for 22–23 days.

For the few species studied in detail females incubated 75–90% of daylight hours. How do these birds, which normally consume nectar every 6–10 minutes, meet their energy requirements during this prolonged stationary period? A closer look at the thermoregulatory ability of incubating females reveals that they compensate for a reduced food intake during long attentive periods by reducing their body temperature from 105.8°F (41°C) to about 89.6°F (32°C), resulting in energy savings of almost 50% during the day.

Depending on the onset of incubation, eggs may hatch at intervals of 48 hours or almost synchronously. Hatchlings of all hummingbirds are altricial: nearly unfeathered, blind, and helpless. During their long nestling period of 23–26 days, in high Andean trochilids 30–40 days, the following three well-differentiated morphological stages of development can be observed.

During Stage One—from day one to about day five after hatching—the nestling is nearly naked and its eyes are still closed. The chicks are inactive in the nest and are fed regurgitated food by the female.

Stage Two extends from day six to day nine and is the period of major feather development on wings, tail, and back

Stage Three covers day 10 until fledging at around 17–19 days. By this time chicks are almost completely feathered and often sit on the edge of the nest facing outward.

Because hummingbirds forage while hovering they can no longer climb with their feet, which serve only for perching. Consequently, they build exposed but camouflaged nests easily accessible in flight. The often exposed nest-site and low reproductive output probably favored the development of a very specific gape-response behavior. Loud begging calls of the offspring, as well as uncontrolled begging and gaping movements through non-specific causes like vibration of nest by wind, are behaviors that could potentially betray the nestsite to predators such as tree lizards, snakes, and birds. Thus the highly specific stimuli (the female touches the chick behind the eye bulge with her bill) which elicit gaping by unfledged hummingbird chicks are most likely adaptations for reducing predation on exposed nest-sites. Also as part of a predator-avoidance strategy female hummingbirds never approach the nest directly. They often fly to the nest-site in fast semi-circles and/or zigzag maneuvers.

Hummingbird females feed their young throughout the day around twice per hour and brood them until an age of 7–12 days. Hummingbird nestlings grow quickly, reaching almost 80% of their adult mass within 10–12 days. At an age of 15–18 days, a few days before fledging, nestlings are much more active in the nest, preen their plumage for extended periods, and look around with interest when other birds or the parent is near the nest.

After leaving the nest the young are fed by the mother for 18-25 days, in some tropical genera like fairies and sylphs occasionally for up to a month. Juveniles do not follow their foraging parent but remain in a special place for several days, often high up in the tree-tops, where they are fed by the female. When flying well, often shortly after the fifth day of fledging, the female prolongs the feeding intervals, teaching the young by loud calls to come for food wherever she wants to feed them. By doing so the juveniles learn quickly to follow the parent bird to her feeding grounds in flowering shrubs, vines, or trees. Foraging for nectar is the next step for the young to learn, mainly achieved by observing the adult at close quarters when sampling nectar. However, this period of learning to choose the right food is often based on trial and error. Several days before juveniles achieve independence they show mutual agonistic behavior, often attacking each other with their feet, trying to prevent the brood-mate from being fed. Between feeding bouts, young hummingbirds are often seen to probe on twigs or red parts of leaves that resemble a flower in shape and color. This exploratory behavior is maintained throughout adolescence and leads them to new nectar sources.

Hummingbird females may successfully rear two broods in a season. In some North American species nest building and even incubation has been observed while the female was still attending nestlings in her first nest. For several tiny tropical species (*Chaetocercus, Lophornis*) one brood only seems likely for energetic reasons. Generally all species will attempt to nest a second or third time if their initial clutches or broods are lost at an early stage of reproduction.

Conservation status

Since 1987 all members of the Trochilidae have been placed in Appendix II of the Convention on International Trade in Endangered Species (CITES). This means that their conservation status gives sufficient cause for concern that trade in live birds is regulated and is not allowed without a permit. In any case, virtually all countries with populations of trochilids have prohibited the export of live birds so permit applications are rarely granted. Those birds most at risk are listed in Appendix I of the Convention, which forbids any trade in them, but at present the only hummingbird to receive this level of protection is the hook-billed hermit (*Glaucis dobrnii*).

Although hummingbirds are overwhelmingly breeding birds of the Neotropics, a part of the globe where habitat destruction is widespread and continuing-most particularly in lowland rainforests where the giant trees preferred by loggers are easiest to extract—their situation is not as dramatically bad as that of many other Central and South American bird families. There are various reasons for this. Their nesting sites are generally in the lowest forest strata, and their minute nests can be built in a wide variety of sites. Also, where forest is cleared flowering plants may appear, albeit perhaps briefly, supplying the birds with adequate food, and even crop plantations like banana or coffee are not entirely hostile environments for some species. Additionally, the relative paucity in lowland rainforests of those families of flowering plants preferred by trochilids, compared to montane forest, shrubby habitats, ravines, páramo, and other grasslands, means that these lowland forests, in contrast to the Andes, have never been a stronghold of hummingbird diversity.

The three classes (apart from Extinct) within "globally threatened" in the IUCN Red List Categories are: Critically Endangered—facing an extremely high risk of extinction (a probability of 50% in 10 years) in the wild in the immediate future; Endangered—facing a very high risk of extinction (a probability of 20% in 20 years) in the near future; and Vulnerable—facing a high risk of extinction (a probability of 10% in 100 years) in the medium-term future. Taxa categorized as Near Threatened are not considered to be conservation dependent though are close to qualifying as Vulnerable. Of the 27 globally threatened hummingbirds, 8 are Critically Endangered, 7 Endangered, and 12 Vulnerable. One of the Critically Endangered hummingbirds, the Bogotá sunangel (Heliangelus zusii), is not recognized here as a good species, and neither is the Táchira emerald (Amazilia distans) (Endangered), which is almost certainly a hybrid between the glittering-throated emerald (Polyerata fimbriata) and the white-chinned sapphire (Hylocharis cyanus). So for our purposes the numbers in these classes fall to seven and six respectively, and the total to 25.

If we look at the situation of several of the Critically Endangered hummingbirds more closely the various factors which, alone or especially in combination, can threaten the existence of a species become apparent.

The hook-billed hermit (Glaucis dohrnii) is now restricted to lowland Atlantic forests in eastern Brazil in the states of Bahia and Espírito Santo. There are estimated to be around 50-250 individuals remaining in highly fragmented and scattered remnants of the original habitat covering an area of perhaps less than 39 mi² (100 km²); its original range may once have been as large as 13,514 mi² (35,000 km²). It is the only trochilid in CITES Appendix I. This part of Brazil is densely populated and the influx of people continues unabated, so roads, settlements, and agriculture in the form of coffee, banana, and rubber plantations is eating into the forest. Other threats are logging and mining. Illegal squatters, deliberately started or poorly controlled fires, and road construction continue to degrade protected areas, including even national parks. However, the true status of the bird remains somewhat unclear, and additional hope for its future can be gained from the fact that five new bird species have been found in the wider region in the last ten years while others thought extinct have been rediscovered. Further exploration could conceivably reveal further populations of this hummingbird.

The sapphire-bellied hummingbird (Lepidopyga lilliae) is found only in and around small areas of mangrove forest on the north Colombian coast; all breeding individuals are apparently in a single population which could be less than 50 birds. Huge tracts of this rare habitat have been destroyed by urbanization and pollution which continue to threaten the remaining fragments. A new road and pipeline across the Isla de Salamanca National Park have altered tidal and river flows, leading to increased water salinity levels and extermination of large areas of mangrove. This species is severely threatened by a fatal combination of elements: a very small and probably declining population, a restricted habitat, and damaging human impact. Apart from the National Park 51,892 acres (21,000 ha) the hummingbird is protected within the Ciénaga Grande de Santa Marta Sanctuary 56,834 acres (23,000 ha), but mangrove there has also suffered damage.

The Juan Fernández firecrown (Sephanoides fernandensis) faces an even more complex series of threats. The species is restricted to the Juan Fernández archipelago in the Pacific, 423-493 mi (680-800 km) west of Chile, an important center of biodiversity; 98 of the 142 flowering plants recorded there are endemics. The nominate race is present on the 36 mi² (93 km²) Isla Robinson Crusoe (Más á Tierra), where there are thought to be around 250-400 individuals; it is estimated that the population of the archipelago in the nineteenth century could have been as high as 20,000. The main conservation problems are posed by introduced species, both plants and animals. Only about 10% of the area of Robinson Crusoe retains its native vegetation of evergreen trees, tree ferns, ferns, etc. The Juan Fernández firecrown also faces competition from a recently arrived congener, the greenbacked firecrown (S. sephaniodes), which copes much better

with the non-native vegetation since they are both of recent mainland origin. There are now estimated to be around 5,000 green-backed firecrowns on Robinson Crusoe. One of the principal threats from an introduced plant is posed by the bramble *Rubus ulmifolius*; apparently only the smaller female *S. fernandensis* and both *S. sephaniodes* sexes feed on its flowers. The islands have been a national park since 1935, a Biosphere Reserve since 1977, and have been nominated for World Heritage Site status. A \$2.5 million restoration program by the Chilean government is at present under way; the survival of the Juan Fernández firecrown depends on its success.

The black-breasted puffleg (Eriocnemis nigrivestis) is found only in stunted elfin forest with páramo on mountain crests in northwest Ecuador at altitudes of around 8,200-14,750 ft (2,500–4,500 m). Today it is possibly confined to a single peak, the volcano Pichincha, where three birds were seen in 1993, the first for 13 years. Its numbers in the past can be judged by the fact that over 100 skins can be found in museums. This puffleg is thought to be close to extinction, perhaps with a single population of below 50, because of habitat destruction for cattle grazing, potato growing, and charcoal making. However a concerted effort is being made by local and international conservationists to have its range protected. Eriocnemis nigrivestis occurs during the main part of the flowering season, in the rains between November and February, at elevations of 10,200-14,750 ft (3,100-4,500 m), when it most likely breeds in the humid elfin forest and páramo, spending the rest of the year in temperate forest around 7,875 ft (2,400 m). This critically endangered hummingbird has one advantage in that it is apparently more of a generalist feeder than some others, and although its movements are particularly dependent on the flowering of Fuchsia and Ericaceae it seems that it will accept a wider range of food plants than was once thought.

A crucial aspect of the threat facing the black-breasted puffleg is that it is an altitudinal migrant. This illustrates the important principle that it profits a montane species little to declare part of its range a reserve while another habitat, upor downslope of the protected area and equally important for its survival, continues to be destroyed. For such birds a small, protected area covering a large altitudinal range can be far more valuable than an extensive one spread over a single altitude. Ideally, similar considerations should also apply to long-distance migratory species to safeguard a food supply along the flyway between breeding and winter quarters.

If we briefly examine the reasons for placing some of the remaining 18 species in the IUCN categories Endangered and Vulnerable, the same overall pattern of threats emerges. All six of the species classed as Endangered occur in forest that is being cleared for cultivation, timber, or settlements. Three of them are Mexican endemics, the short-crested coquette (Lophornis brachylophus), Oaxaca hummingbird (E. cyanophrys), and white-tailed hummingbird (Eupherusa poliocerca), and all inhabit the deciduous, semi-deciduous, and montane evergreen forests and forest edges of the Sierra Madre del Sur in the states of Guerrero and Oaxaca. This area is undergoing rapid deforestation. The low-altitude zones are felled to make way for the cultivation of citrus fruits, maize, and coffee. The cloud forest is cleared for coffee plantations, while the oak,

fir, and pine trees above 5,900 ft (1,800 m) are cut for timber. Apparently only the white-tailed hummingbird enjoys any degree of protection since some of its range lies within Omiltemi State Ecological Park.

Another pair of endangered and sympatric (in western Ecuador) congeners are little woodstar (*Chaetocercus bombus*) and Esmeraldas woodstar (*C. berlepschi*). They are found in one of the most threatened forest types in the Neotropics, moist evergreen forest; *C. bombus* has a much greater range than *C. berlepschi*, extending into Peru, but there are few modern records of either species. The remaining hummingbird in this category, the chestnut-bellied hummingbird (*A. castaneiventris*) from the eastern Andes of Colombia, is threatened as much by its small numbers as by habitat destruction. Rapid and extensive deforestation is widespread throughout the area, even inside sanctuaries, compounded by the apparent rarity of the species; there has been one record of *A. castaneiventris* in the last 30 years.

The threats faced by the 12 Vulnerable species vary little from the preceding cases. Forest habitat destruction poses the greatest risk to the survival of the majority of them. Others are threatened by critically small populations and/or restricted ranges, usually as a result of past human interference.

Only two of the 25 globally threatened hummingbirds the purple-backed sunbeam (scrub) and Chilean woodstar (scrub, desert, and agricultural areas)—do not at least partly inhabit forest or woodland of one type or another. Many trochilids specializing in páramo grasslands, arid areas, scrubby thickets, and so on face threats from habitat destruction for cattle raising or other forms of cultivation, but they are possibly more adaptable, taking to secondary growth, plantations, and gardens more readily than true forest species. The few hummingbirds inhabiting high-altitude Andean páramo or puna and bordering stunted forest types, such as the hillstars (Oreotrochilus), the metaltails (Metallura), or the thornbills (*Chalcostigma*), face a lower risk because these rather inhospitable regions are in the main subject to little human interference. But, of course, the primary factor here is that montane humid tropical and subtropical forest, the home of the majority of trochilids, continues to be destroyed at a completely unsustainable rate.

Brace's emerald (Chlorostilbon bracei) from New Providence Island in the Bahamas is the only hummingbird species definitely known to be extinct. Although the taxon is known only from a single male specimen taken in July 1877, it has been shown to be a good species and not, as thought by many earlier this century, a possible race of the Cuban emerald (C. ricordii), also present on the islands though not on New Providence. Even when the holotype was taken the species must have been rare, and was probably restricted to scrubby thickets around the town of Nassau. No individual was ever seen again, but whether the cause of its extinction was primarily human interference or climate change remains obscure. Fossil remains appear to indicate that one further humming-bird no longer extant once inhabited New Providence Island.

The Bogotá sunangel has been described from a single specimen bought in Bogotá in 1909, though properly exam-

ined only in the late 1940s, and is thought to have come from the eastern or central Andes of Colombia, a region where much of the forest has been cleared for crops like potatoes, coffee, and maize. It may still exist in the cloud forest at around 4,600-7,200 ft (1,400-2,200 m) and would presumably be a relict species with a very restricted range. However, there is also the possibility that it could be a hybrid, just as many of the Bogotá trade skins have proved to be. On the basis of this uncertainty the form is not treated here as a good species, although the case for its being so has been well made. If it is a species and has disappeared it would be the first extinction of a trochilid in South America. Where the Colombian forests remain pristine there are still good hummingbird populations, showing that deforestation rather than nineteenth century collecting is responsible for the drastic reduction in range and numbers of many species

Now that killing for plumage is firmly in the past, hummingbirds face no special threats directed at or affecting them in particular. They are difficult birds to keep and only relatively few specialists are interested in them for the aviary trade. But their fate is tied to that of millions of other animal and plant species in the Neotropics if rampant deforestation is allowed to continue at its current rate. The world will be a poorer place if the tragic list of extinctions were to include more hummingbirds.

Significance to humans

Man's attitude to hummingbirds is a very unusual one in his relations with the rest of the animal kingdom: it is wholly characterized by positive emotions, such as aesthetic admiration, affection, and general amazement. As far as is known, hummingbirds have nowhere given cause for the kinds of persecution suffered by other bird families; they are not crop pests, they do not compete with or harm domestic animals, they are not noisy, and there is not much eating on them (although, surprisingly, there is a south Brazilian dish called passarinhos com polenta with hummingbird as the chief ingredient). Apart from adding to the sum of human pleasure they also carry out the important service of pollinating many of their food plants, some of which have coevolved with the birds; at least 58 plant families are pollinated by trochilids in Brazil alone, chief among them the Bromeliaceae.

The persecution to which they have been subjected is rooted in their virtues. Since the earliest times they have been killed for their wonderful plumage, and more recently captured in huge numbers so that people can appreciate them even more at close quarters. Mankind has always been astonished by their unearthly iridescent colors, their acrobatic flying skills, and their small size. They are among the most mysterious creatures on our planet.

Human's feelings towards these birds are well expressed in the names given to them. Their English names parallel both those in other languages and the normally unpoetic scientific nomenclature in attempting to capture some of the hummingbird magic: sapphire, emerald, goldenthroat, mountaingem, jewelfront, brilliant, hillstar, sunbeam, starfrontlet, sunangel, woodstar, sungem, sylph, woodnymph, and fairy. The Spanish name is *picaflor* (peck the flower), the Portuguese *beija flor* (kiss the flower).

Native peoples throughout South America use hummingbird plumage in their adornment, and it can be assumed that they always have. The esteem in which these minute glittering feathers were, and are, held is exemplified by the fact that the great ceremonial headdress of the Aztec king Moctezuma (Montezuma) II, the main element of which is the long green uppertail-coverts of the resplendent quetzal (Pharomachrus mocinno), the sacred bird of the Maya and Aztecs, also contains many hundreds of trochilid feathers, interspersed with tiny platelets of gold. The Aztecs kept hummingbirds and other species in special extensive zoos in order to have a supply of feathers and pelts for ceremonial purposes. In 1519 King Moctezuma presented this royal symbol to his eventual conqueror, Hernán Cortés, who in turn gave it to Emperor Charles V as part of a fabulous Aztec treasure of gold, silver, jade, pearl, and turquoise. After seeing this hoard in Brussels, the German artist Albrecht Dürer wrote "I have never seen anything in my entire life that filled my heart with greater delight." The treasure can be seen today in the Museum für Völkerkunde in Vienna.

Huitzilopochtli, hummingbird of the south, from "huitzilin" (hummingbird) and "pochtli" (southern), was actually one of the most powerful of the Aztec gods, associated with battle and human sacrifice, the bird being depicted actually feeding on the blood of sacrificial victims. Fallen warriors were metamorphosed into hummingbirds to accompany the sun on its daily journey for four years before returning to earth to feed on nectar for eternity. Huitzilopochtli had another special place in Aztec mythology as the bird which guided the people on their long trek southwards in search of a new homeland to the spot in present-day Mexico City where they built their capital Tenochtitlan.

The greatest of the gods, the feathered serpent Quetzalcoatl, wore a cape of trochilid feathers and a head adornment of flowers with hovering, feeding hummingbirds. The first ruler of the unified Aztec kingdom was called Huitzilihuite, or hummingbird feather, and during his reign in 1391-1415 he elevated Huitzilopochtli to the position of Sun God, the supreme power in the pantheon, a further member of which was the goddess of earthly pleasures, beauty, and birth Xochiquetzal, or flower bird, and she too was symbolized by a hummingbird. Hummingbird feathers were an integral part of a bride's wedding dress in Mexico into modern times. The bird was also an integral part of the Aztec calendar. This is more important than it might appear because this highly complex system lay at the very heart of Aztec culture and cosmology. Representations of hummingbirds in stone can be seen throughout the Aztec archaeological sites. The hummingbird is present too in the mythology and artifacts of the South American peoples, particularly the Inca and Nazca of the Andes, but to a much lesser degree than in Mesoamerica. Some of the gigantic figures inscribed by the Nazca on the surface of the dry plateaus of Peru probably represent hummingbirds.

A multitude of stories has arisen from the fact that hummingbirds often appear with the rains, since the flowers

bloom then, but of course they are credited in many legends, particularly in the dry southwest of the United States, with being rain bringers. Water vessels are commonly decorated with their image. The Hopi and Zuni peoples incorporate the hummingbird in their rain dances, and their inlaid jewellery of turquoise and silver features the birds as favourite motifs. In a Navajo legend, the first hummingbird was large, white, and very greedy, so much so that it killed many flowers in its search for ever more food. The Creator was displeased and made the bird smaller and smaller to reduce its appetite, but in the process it also lost its song, whereupon the other birds in their pity asked the Creator to compensate the hummingbird with the most beautiful plumage of all, which he duly did.

A belief in the special position of hummingbirds survives today in the form of superstition and folk medicine. On the whole they, and also their nests, are regarded as bringers of good luck. In Costa Rica, dried and perfumed nests are hung around the neck, on belts, or nowadays in cars as lucky talismans. In Mexico, amulets containing mummified or powdered hummingbirds can be bought in markets to bring good luck or success in love. The life-long fidelity of an unwitting partner can be secured by boiling up a dried hummingbird, including feathers, in a soup or stew, or by sprinkling the ashes of a hummingbird heart on the head of the object of desire; similar effects can be achieved by presenting him or her with soap containing trochilid extracts. Evil spirits can be pacified by constructing a little altar with candles before the body of a hummingbird wrapped in red twine.

It was not long before the breathtaking beauty of hummingbird plumage became a very desirable article on the European and North American fashion market. In the second half of the nineteenth century millions of hummingbird skins were exported from Central and South America, not only to decorate ladies' hats and clothes but also for the man-

ufacture of feather pictures, ornaments, and artificial flowers. The collection of mounted specimens was promoted by the naturalist Adolphe Boucard as an interesting and appropriate hobby for ladies. In London in 1888, 12,000 trochilid skins were sold in one month; at one sale there 37,603 hummingbird skins from South America and Trinidad were auctioned; a single delivery from a Brazilian port contained 3,000 skins of the ruby-topaz hummingbird (Chrysolampis mosquitus); 152,000 hummingbirds were sold by one auction house in London between 1904 and 1911, and in 1905, 8,000 were used to make a single shawl. Already in 1851 E. J. Silva Maia of the National Museum in Rio de Janeiro was warning that some species had disappeared in the area purely as a result of trapping for the fashion industry. Some species were probably hunted to extinction in this slaughter since a few were first described from such skins but never subsequently seen, although the hybridization between species, and even genera, frequently reported for trochilids is perhaps responsible for some of these forms.

Confronted with the task of describing hunmmingbirds, the ornithologist's first impulse on lifting the pen is often of a literary nature, if not always of the highest quality. Comte de Buffon, the great eighteenth century naturalist, thought them "of all animated beings . . . the most elegant in form and brilliant in color. The stones and metals polished by art are not comparable to this gem of nature. She has placed it in the order of birds, but among the tiniest of the race . . . she has loaded it with all the gifts of which she has only given other birds a share." A generation later John James Audubon described the hummingbird as a "glittering fragment of the rainbow . . . a lovely little creature moving on humming winglets through the air, suspended as if by magic in it, flitting from one flower to another, with motions as graceful as they are light and airy, pursuing its course and yielding new delights whenever it is seen."



1. Velvet-purple coronet (*Boissonneaua jardini*); 2. Red-billed streamertail (*Trochilus polytmus*); 3. Anna's hummingbird (*Calypte anna*); 4. Frilled coquette (*Lophornis magnificus*); 5. Ruby topaz (*Chrysolampis mosquitus*); 6. Sword-billed hummingbird (*Ensifera ensifera*); 7. Puerto Rican emerald (*Chlorostilbon maugaeus*); 8. Crimson topaz (*Topaza pella*); 9. Rufous-tailed hummingbird (*Amazilia tzacatl*). (Illustration by Patricia Ferrer)



1. Green hermit (*Phaethornis guy*); 2. Green-fronted lancebill (*Doryfera ludovicae*); 3. White-necked jacobin (*Florisuga mellivora*); 4. Hairy hermit (*Glaucis hirsuta*); 5. Sparkling violet-ear (*Colibri coruscans*); 6. White-tipped sicklebill (*Eutoxeres aquila*); 7. Saw-billed hermit (*Ramphodon naevius*); 8. Rufous sabrewing (*Campylopterus rufus*); 9. Band-tailed barbthroat (*Threnetes ruckeri*). (Illustration by Patricia Ferrer)

Species accounts

Saw-billed hermit

Ramphodon naevius

SUBFAMILY

Phaethornithinae

TAXONOMY

Trochilus naevius Dumont, 1818, Mount Corcovado, Rio de Janeiro, Brazil. Monotypic.

OTHER COMMON NAMES

French: Colibri tacheté; German: Sägeschnabel-Schattenkolibri; Spanish: Ermitaño Picosierra.

PHYSICAL CHARACTERISTICS

5.5–6.3 in (14–16 cm); female and male 0.19–0.3 oz (5.3–8.5 g). A large hummingbird and the only hermit with saw-like serration of the mandibles, and in the adult male, a hooked tip to the upper mandible. Bill straight. Male larger than female. Both sexes alike. Underneath rufous-ochraceous throat with dark gular stripe. Above copperish green. Immatures similar to adults, but upperparts with pale fringes.

DISTRIBUTION

Southeast Brazil (southern Minas Gerais and Espírito Santo to Santa Catarina, records from Rio Grande do Sul).

HABITAT

Understory of tropical rainforest up to 1,640 ft (500 m).



BEHAVIOR

Traplining plant visitor. Aggressively defends feeding routes over conspecifics and other hummingbirds. Males establish leks to attract females. Loud metallic flight call.

FEEDING ECOLOGY AND DIET

Collects nectar from long tubular-shaped flowers at forest understorey. Small arthropods are gleaned from vegetation.

REPRODUCTIVE BIOLOGY

Breeds from July to September. Cone shaped nest is loosely constructed and attached underneath a tip of a pendent leaf. Two elliptical eggs; incubation 16–17 days by female.

CONSERVATION STATUS

Restricted range species, considered Near Threatened. Locally common, but habitat destruction may be a threat in the future.

SIGNIFICANCE TO HUMANS

None known.

White-tipped sicklebill

Eutoxeres aquila

SUBFAMILY

Phaethornithinae

TAXONOMY

Trochilus aquila Bourcier, 1847, Bogotá, Colombia. Three subspecies are recognized.



OTHER COMMON NAMES

English: White/bronze/brown/-tailed sicklebill, common sicklebill; French: Bec-en-faucille aigle; German: Weisskehl-Sichelschnabel; Spanish: Picohoz Coliverde.

PHYSICAL CHARACTERISTICS

4.7–5.5 in (12–14 cm); female 0.3–0.35 oz (8–10 g), male 0.35–0.44 oz (10–12.5 g). Unmistakable hummingbird with strongly decurved bill. Underparts black and white streaked, upperparts dark green. Rectrices green and brown with contrasting white tips. Sexes are alike. Immatures resemble adults. Subspecies are alike.

DISTRIBUTION

E. a. salvini: Costa Rica to west Colombia; E. a. heterura: western Andes from southwestern Colombia to west Ecuador; E. a. aquila: east Andes from Colombia to northern Peru.

HABITAT

Understory of tropical rainforest, older second growth, forest edge near rivers. Often associated with *Heliconia* patches. Occurs from sea-level to 2,300 ft (700 m), but has also been observed at altitudes up to 6,900 ft (2,100 m) in Costa Rica and in Colombia.

BEHAVIOR

Sicklebills, unlike most other hummingbirds, perch while feeding on flowers. They establish feeding territories at *Heliconia* patches, but may also trapline for nectar along regular routes. Loud and melodious "wren-like" song. Sedentary.

FEEDING ECOLOGY AND DIET

Feeds mainly on *Heliconia* and *Centropogon* flowers with tubular corollas similar in curved shape to the bird's bill. Arthropods are caught in the air by hawking.

REPRODUCTIVE BIOLOGY

Establish leks during the reproductive period. Breeding takes place from January to June in Central America and from June to September in South America. Nest is a loosely woven cup of rootlets and plant fibers attached by cobweb underneath a long, hanging leaf. Two eggs, incubation 16–17 days by female. Chick is black with gray dorsal down; fledging 22–25 days.

CONSERVATION STATUS

Common throughout most of its range. Local densities of three to four pairs per km².

SIGNIFICANCE TO HUMANS

None known. ◆

Hairy hermit

Glaucis hirsuta

SUBFAMILY

Phaethornithinae

TAXONOMY

Trochilus birsutus J. F. Gmelin, 1788, northeastern Brazil. Two subspecies are recognized.

OTHER COMMON NAMES

English: Rufous-breasted hermit; French: Ermite hirsute; German: Rotschwanz-Schattenkolibri; Spanish: Ermitaño Hirsuto.



PHYSICAL CHARACTERISTICS

4–4.7 in (10–12 cm); female 0.19–0.26 oz (5.5–7.5 g), male 0.21–0.28 oz (6–8 g). A medium-sized hermit with green upperparts, brownish rufous underparts, slightly decurved bill. Four outer tail feathers rufous with broad black subterminal bands and contrasting white tips. Female has paler throat and upper breast; shorter wings and rectrices. Bill more decurved. Immatures similar to adults with upperparts ochraceous.

DISTRIBUTION

G. b. insularum: Grenada, Trinidad, and Tobago; G. b. birsuta: Panama, Colombia south to Bolivia, Venezuela to Guianas and almost all of Brazil.

HABITAT

Understory of various forest types and dense secondary growth, woodland clearings, riverine habitats, swamps, bamboo thickets, cerrado, and plantations. Mostly below 3,300 ft (1,000 m).

BEHAVIOR

Traplining species. Collects spiders from webs.

FEEDING ECOLOGY AND DIET

Nectar of various understory plants such as *Heliconia*, *Costus*, *Passiflora*, *Pachysstachys*, *Centropogon*, and *Trichantera* species and small arthropods.

REPRODUCTIVE BIOLOGY

Males establish leks during reproduction. Breeds from January to July on Trinidad, April to July in Panama, September to May in Brazil. Nest records in September in southeast Colombia, December and May in north Colombia, June in eastern Colombia, September to December in Surinam, February, March, July, August and December in French Guiana. Nest is

a cone-shaped cup, loosely constructed of plant fibers, built underneath pendent leaf. Eggs visible from the outside. Males sometimes visit nest area and defend nest. Normally two eggs, higher clutch sizes are due to conspecific females laying in the same nest. Incubation 17–19 days by female. Chick is black with gray dorsal down. Fledging 20–25 days. Young remain with female for three to four weeks.

CONSERVATION STATUS

Common throughout its extensive range.

SIGNIFICANCE TO HUMANS

None known. ◆

Band-tailed barbthroat

Threnetes ruckeri

SUBFAMILY

Phaethornithinae

TAXONOMY

Trochilus ruckeri Bourcier, 1847, Esmeraldas, Ecuador. Three subspecies currently recognized.

OTHER COMMON NAMES

English: Rucker's hermit; French: Ermite de Rucker; German: Weissbinden-Schattenkolibri; Spanish: Ermitão Barbudo Colibandeado.

PHYSICAL CHARACTERISTICS

4–4.3 in (10–11 cm); female 0.18–0.25 oz (5–7 g), male 0.19–0.25 oz (5.5–7 g). Medium-sized hummingbird with contrasting underpart coloration, almost straight bill, dark rectrices with white tips. Prominent white base to outer tail feathers, creating a subterminal black band. Immatures have ochraceous



feather fringes on upperparts and light tips to remiges, otherwise similar to adults.

DISTRIBUTION

T. r. ventosus: eastern Guatemala and Belize to Panama; T. r. ruckeri: northern and western Colombia, Ecuador; T. r. venezuelensis: northwestern Venezuela.

HARITAT

Understory of primary and disturbed forest, secondary growth, forest edge, plantations, and riverine vegetation from sea-level to 4,000 ft (1,200 m).

BEHAVIOR

Traplining-species. Soft flight call. Song, a series of whistles, can be heard from perching males throughout the day.

FEEDING ECOLOGY AND DIET

Nectar of *Heliconia*, *Costus*, and other tubular flowers; also small arthropods, especially spiders taken from webs or underneath leaves. Nectar robbery recorded by piercing corolla base of tubular flowers too long for its bill.

REPRODUCTIVE BIOLOGY

Males establish leks during reproduction. Breeds on the Caribbean slope of Costa Rica from February to May, on the Pacific slope from June to September; two nesting seasons in Colombia (January to April and in September). Nest is a loosely built cup of rootlets, plant fibers, vegetable hairs and spider web, similar, but more compact than that of *Glaucis*, and fixed to the underside tip of a long, pendent leaf. Two eggs; incubation 15–18 days by female. Fledging 23–25 days. Young remain with female for three to four weeks. Male observed in the vicinity of an incubating female.

CONSERVATION STATUS

Common throughout its range.

SIGNIFICANCE TO HUMANS

None known. ◆

Green hermit

Phaethornis guy

SUBFAMILY

Phaethornithinae

TAXONOMY

Trochilus guy Lesson, 1832, Trinidad. Four subspecies are recognized.

OTHER COMMON NAMES

English: Guy's hermit; French: Ermite vert; German: Grüner Schattenkolibri; Spanish: Ermitaño Verde.

PHYSICAL CHARACTERISTICS

5.1 in (13 cm); female 0.14–0.23 oz (4–6.5 g), male 0.14–0.25 oz (4–7 g). A medium-sized hermit with curved bill and an orange gular stripe. Male has nib-shaped central tail feathers, female has shorter and more decurved bill, shorter wings. Lighter underparts, ochraceous belly coloration, and longer rectrices. Immatures like adult female, but have ochraceous uppertail-coverts.

DISTRIBUTION

P. g. coruscus: Costa Rica to northwest Colombia; P. g. emiliae: Colombia (major river valleys); P. g. apicalis: eastern Andean



slopes from north Colombia and northwestern Venezuela to southeast Peru; P. g. guy: Trinidad and northeast Venezuela.

HABITAT

Understory of humid forest and adjacent forest edges, secondary growth, and plantations with dense vegetation. Recorded between 1,975 and 7,550 ft (600 and 2,300 m).

BEHAVIOR

Song consists of a series of squeaking notes, presented while perching at the lek. Sharp metallic flight call.

FEEDING ECOLOGY AND DIET

Nectar of *Heliconia*, *Costus*, *Razisea*, *Columnea*, *Pachystachys*, *Centropogon*, and of introduced plants like *Musa* and *Canna*; small arthropods. Casually searching for flowers in Polylepis forests. Traplining.

REPRODUCTIVE BIOLOGY

Males establish traditional leks throughout the year. Breeds in November to July, in particular January to April in Trinidad; February to September, December in Costa Rica and Panama; June to August in Colombia; July to November in Peru. Nest cone shaped, consisting of moss and fine plant material; placed at the tip of a long leaf, often near or above streams. Males sometimes defend nest, but do not participate in parental care. Two eggs; incubation 17–18 days by female with head towards the leaf. Fledging period 21–23, sometimes 27 days. Chicks have dark skin and sparse dorsal down. Well feathered when about two weeks old.

CONSERVATION STATUS

Uncommon to fairly common in most areas.

SIGNIFICANCE TO HUMANS

None known. ◆

Green-fronted lancebill

Doryfera ludovicae

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus Iudovicae Bourcier and Mulsant, 1847, Buena Vista, east Andes above Villavicencio, Meta, Colombia. Two subspecies are recognized.

OTHER COMMON NAMES

French: Porte-lance de Louise; German: Grünstirn-Lanzettschnabel; Spanish: Colibri Picolanza Mayor.

PHYSICAL CHARACTERISTICS

4.3–5.1 in (11–13 cm); female 0.19–0.21 oz (5.5–6.0 g), male 0.2–0.23 oz (5.9–6.4 g). Bill long, slightly upturned. Male with frontlet glittering green, crown and nape dark coppery-bronze, shading to bronzy-green on back; uppertail-coverts blue; tail black, narrowly tipped with dull grey; underparts dull, dark greenish bronze, darker and greener on throat. Female similar to male but frontlet smaller or absent. Immatures similar to adults.

DISTRIBUTION

D. l. veraguensis: north central Costa Rica to western Panama; D. l. ludovicae: extreme eastern Panama (Cerro Tacarcuna), Colombia and western Venezuela, south through Andes to northwestern Bolivia (east slope only from central Ecuador southwards).

HABITAT

Mid-strata and lower canopy of cloudforest and humid lower montane forest. Males often found along ridges while female prefers ravines and gorges particularly for nesting. Sometimes down at shrub-height. Mainly 2,450–7,550 ft (750–2,300 m).



BEHAVIOR

Territorial species, defending stands of flowers against other hummingbirds and conspecifics. High pitched melodious song.

FEEDING ECOLOGY AND DIET

Visits epiphytes with long, tubular, usually pendent corollas, including Ericaceae (*Psammisia*, *Cavendishia*, *Macleania*), Loranthaceae (*Psittacanthus*), Rubiaceae, and Gesneriaceae. Frequently flycatches, sallying from perch in canopy or along stream, or hover-hawks low over stream; also hover-gleans arthropods from vegetation.

REPRODUCTIVE BIOLOGY

Breeds in Costa Rica in the latter half of wet season to start of dry (August to January); in Colombia nesting recorded between July and late January. Nest a bulky cup of moss, treefern scales, fine fibers and cobwebs in dark, usually humid site; attached to hanging rootlet or vine rock overhang in ravine or gorge. Two eggs; incubation 19 days; fledging period 25 days.

CONSERVATION STATUS

Generally uncommon to locally fairly common in suitable habitat throughout range.

SIGNIFICANCE TO HUMANS

None known. ◆

Rufous sabrewing

Campylopterus rufus

SUBFAMILY

Trochilinae

TAXONOMY

Campylopterus rufus Lesson, 1840, no locality = Guatemala. Monotypic



OTHER COMMON NAMES

French: Campyloptére roux; German: Buntschwanz-Degenflügel; Spanish: Colibri Rojizo Mexicano.

PHYSICAL CHARACTERISTICS

4.9–5.5 in (12.5–14 cm); female 0.23–0.24 oz (6.6–6.9 g), male 0.32 oz (9 g). Male has medium-sized, slightly decurved black bill; upperparts metallic bronzy-green, postocular spot white; below uniform cinnamon; tail slightly rounded, central pair of rectrices golden-bronze, rest light cinnamon with black subterminal band, edged cinnamon, outermost tail feather cinnamon with lighter edges. Female similar to male, but smaller. Immatures like adults, but with head feathers fringed buffy.

DISTRIBUTION

Pacific slope of Mexico, southern Guatemala and El Salvador.

HARITAT

Rainforest and forest edge, canyons with pine-oak forests, plantations; occurs at 2,950–6,600 ft (900–2,000 m), occasionally at sea-level, most numerous above 3,300 ft (1,000 m).

BEHAVIOR

Behavior mostly unknown.

FEEDING ECOLOGY AND DIET

Nectar of flowering *Plantago*, *Erythrina*, *Salvia*, and *Castilleja*. Insects are caught in the air by hawking. Male occupies feeding territory at nectar-rich sources.

REPRODUCTIVE BIOLOGY

Males form small leks during reproduction. Breeds from April to May in Oaxaca, Mexico. Cup-shaped nest of moss lined with whitish thistle down, externally decorated with lichen, rather exposed on horizontal branch, 3.3–6.6 ft (1–2 m) above the ground. Two eggs; incubation 15–16 days by female. Chicks are blackish with two rows of buffy dorsal down; fledging 23–26 days.

CONSERVATION STATUS

Restricted-range species. Locally common. Readily accepts human-made habitats such as plantations or pastures with scattered shrubs.

SIGNIFICANCE TO HUMANS

None known. ◆

White-necked jacobin

Florisuga mellivora

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus mellivorus Linnaeus, 1758, India; error=Surinam. Two subspecies recognized.

OTHER COMMON NAMES

English: White-bellied hummingbird; French: Colibri jacobin; German: Weissnackenkolibri; Spanish: Colibrí Nuquiblanco.

PHYSICAL CHARACTERISTICS

4.3–4.7 in (11–12 cm); female 0.23 oz (6.5 g), male 0.26 oz (7.4 g). Bill and feet black. Adult male with head and chest blue, broad white crescent on nape, rest of upperparts bright green including elongated uppertail-coverts; belly and most of tail



white, narrowly edged and tipped black. Plumage of adult female notoriously variable, apparently individually; half to two-thirds show the typical female plumage with blue-green breast heavily scaled with whitish, belly dull white, upperparts entirely green and tail mostly green with dark blue tip, outer rectrix with white outer edge and tip; the remainder have plumage more or less male-like with a few only distinguishable from adult male by their longer bills and shorter wings and tails.

DISTRIBUTION

F. m. mellivora: southern Mexico to Panama and Colombia, south to west Ecuador, southeast Peru and northern Bolivia, and east to Venezuela, Trinidad, the Guianas and Amazonian Brazil. F. m. flabellifera: Tobago.

HABITAT

Humid forest canopy and borders, woodlands, plantations, tall second growth, and gallery forest. Usually high in trees, lower at edges and clearings. Occurs from sea-level up to 3,300 ft (1,000 m).

BEHAVIOR

Territorial. Mostly silent, at times lengthy hard utters. Sometimes 12–15 males gather at flowering trees.

FEEDING ECOLOGY AND DIET

Feeds high in flowering trees, including *Inga*, *Vochysia*, *Erythrina*, *Bauhinia*, and *Symphonia*, epiphytes, shrubs, and *Heliconia* along edges and in clearings. Hawks for insects for long periods, hovering and darting high above streams and clearings or sallying from tree-top perches.

REPRODUCTIVE BIOLOGY

Breeds during dry to early wet seasons between January and July in Costa Rica and Panama; between February and May in northwest Colombia, June and November in east Colombia. Nest is a rather shallow soft cup of light-colored plant down and cobweb on flat upper surface of broad leaf of understory

palm (*Geonoma*, *Asterogyne*), often sheltered from above by another such leaf, 3.3–10 ft (1–3 m) above ground, sometimes near a stream.

CONSERVATION STATUS

Uncommon to common. Adapts to human-made habitats such as tree plantations.

SIGNIFICANCE TO HUMANS

None known. ◆

Sparkling violet-ear

Colibri coruscans

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus [Petasophora] coruscans Gould, 1846, South America. Two subspecies recognized.

OTHER COMMON NAMES

English: Gould's violet-ear; French: Colibri anais; German: Grosser Veilcheohrkolibri; Spanish: Colibrí Rutilante.

PHYSICAL CHARACTERISTICS

5.1–5.5 in (13–14 cm); female 0.24–0.26 oz (6.7–7.5 g), Male 0.27–0.3 oz (7.7–8.5 g). Male has slightly decurved black bill; upperparts metallic bluish green, bluish violet ear plumes elongated and erect; chin bluish violet, rest of underparts green with blue belly; tail double-lobed, iridescent green with steely blue subterminal band. Female similar to



male. Immatures have no iridescent coloration, feathers fringed buff.

DISTRIBUTION

C. c. germanus: southern Venezuela, eastern Guyana and northern Brazil; C. c. coruscans: northwestern Venezuela and Colombia through Ecuador and Peru to Bolivia and northwestern Argentina; possibly also northern Chile.

HABITAT

Forest edges, open woodlands, flowering gardens, plantations, sub-páramo and páramo at 5,600–14,750 ft (1,700–4,500 m).

BEHAVIOR

Territorial. During display the male hovers close to the female in a semicircle and presents the violet ear plumes. A very vocal species with many local dialects.

FEEDING ECOLOGY AND DIET

Feeds on nectar of numerous flowers like *Castilleja*, *Centropogon*, *Clusia*, *Echeveria*, *Eleanthus*, *Erythrina*, *Eucalyptus*, *Guzmania*, *Inga*, *Salvia*, and *Puya*. Insects are caught in the air by hawking. Forages from ground level to canopy.

REPRODUCTIVE BIOLOGY

Males establish leks and sing throughout the day from treetops. Breeds in Venezuela from July to October. Cup-shaped nest built of various plant materials, decorated outside with lichens, twigs, or moss; placed on horizontal branch or attached to pendent twig in bush or placed in cleft in rocks. Two eggs; incubation 17–18 days by female. Chicks dark with two rows of dorsal down; fledging period 20–22 days.

CONSERVATION STATUS

Common to very common in many habitat types. Readily accepts human-made habitats. A typical hummingbird in many major Andean cities.

SIGNIFICANCE TO HUMANS

None known. ◆

Crimson topaz

Topaza pella

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus pella Linneaus 1758 Surinam. Four subspecies recognized.

OTHER COMMON NAMES

English: King hummingbird; French: Colibri topaze; German: Rotnacken-Topaskolibri; Spanish: Colibrí Topacio.

PHYSICAL CHARACTERISTICS

Female 5.1–5.5 in (13–14 cm), male 8.3–9.1 in (21–23 cm, including bill c. 1.6 in [4 cm] and tail 4.7–5.1 in [12–13 cm]); female c. 0.35 oz (10 g), male 0.35–0.49 oz (10–14 g). A large strikingly colored hummingbird. Male has straight black bill; top and sides of head and neck velvet black; back glittering crimson to purple, golden on uppertail-coverts; throat bright green with a golden sheen, surrounded by a black band, underparts bright red, undertail-coverts bronze; wings brown; central tail feathers bronzy golden-green, outer rectrices chestnut, submedian tail feathers elongated and crossed. Female bill similar to male's;



back dark green; throat green with crimson discs, underparts green with golden green discs, undertail-coverts iridescent green; central tail feathers bronzy, next pair violet, outermost pair chestnut. Immatures like adult female.

DISTRIBUTION

T. p. pyra: southeastern Colombia, eastern Ecuador, and northeastern Peru to northwestern Brazil (Rio Negro) and south Venezuela (Amazonas); T. p. pamprepta: eastern Ecuador (Suno, Rio Napo); T. p. pella: southern Venezuela (east Bolivar) and the Guianas to northern Brazil (Amapá); T. p. microrhyncha: northcentral Brazil, along south bank of lower Amazon in vicinity of Belém.

HABITAT

Occurs in lowland rainforests up to 1,640 ft (500 m), mainly inland. Frequently found in tree tops of forests around granite outcrops and along gallery forests near river banks and creeks.

BEHAVIOR

Territorial. Males announce their presence by shrill calls mainly given from tree tops. During display, male circles in slow-motion manner around perched female.

FEEDING ECOLOGY AND DIET

Mainly seen foraging for nectar in the upper story of flowering forest trees such as *Inga* and *Bombax*, but also visits flowers of vines and epiphytes. Occasionally found in much lower vegetation around inselbergs in Surinam where it forages for nectar near the ground at flowering stands of *Costus scaber* and in clumps of blooming *Pitcairnia nuda*. Insects are caught in the air, often high above tree tops.

REPRODUCTIVE BIOLOGY

Breeds from January to April and again in July to November in the Guianas; no nesting data from other areas. Nests found at

10–26 ft (3–8 m) often on vertical branches or in vines above or near water. The cup-shaped nest, consisting of soft grayish or brownish fibers of *Bombax* seeds and cobweb, is fairly small compared with the size of the bird. Two eggs; incubation time unknown; chicks black with some pale gray dorsal down; fledging period 21 days. Young remain with female for three weeks.

CONSERVATION STATUS

Locally common but frequently considered rare due to its secretive habits in the tree tops.

SIGNIFICANCE TO HUMANS

None known. ◆

Ruby topaz

Chrysolampis mosquitus

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus mosquitus Linnaeus, 1758, Surninam. Monotypic.

OTHER COMMON NAMES

English: Ruby-topaz hummingbird; French: Colibri rubistopaze; German: Mosquitokolibri; Spanish: Colibrí Rubí;.

PHYSICAL CHARACTERISTICS

3.1–3.5 in (8–9 cm); female and male 0.14–0.18 oz (4–5 g). Male has short straight black bill; crown and nape shining ruby red, back dark brown glossed dull olive; throat and breast



metallic golden; rest of underparts brown; rectrices rich chestnut tipped black. Female has copper-green back, below pale gray (on Trinidad and Tobago, some birds have greenish golden stripe from chin to breast); central tail feathers olive-green, the others rufous-chestnut with shining purple-black subterminal band, tipped white. Immature similar to adult female.

DISTRIBUTION

Eastern Panama and western north and central Colombia, east through Venezuela to the Guianas, then south through northeast and central Brazil to east Bolivia; also islands along north coast from Aruba, Curação and Bonaire east to Trinidad and Tobago.

HABITAT

Occurs in savanna-like vegetation from sea-level to shrubby arid hillsides at 5,600 ft (1,700 m); forages from low down to treetops in clearings, open country, parks, gardens, and plantations. Most numerous below 1,640 ft (500 m).

BEHAVIOR

Migratory. Arrives in the southern Cauca Valley, Colombia, in May and disappears in September; absent or rare on Trinidad and Tobago in August until November; appears in Paraná, Brazil, in October and leaves in April. Within Brazil north-south migration; along the coastal areas of the Guianas, Venezuela, and Colombia presumably an east-west migration with southward tendency towards Cauca and Magdalena Valleys, Colombia.

FEEDING ECOLOGY AND DIET

Nectar of flowering shrubs, cultivated crops, cacti, small and large trees. Tiny insects are caught in the air by hawking. Male defends feeding territories in flowering shrubs or trees.

REPRODUCTIVE BIOLOGY

Breeds from December to June on Trinidad and Tobago, Venezuela, Guianas; September to January in Brazil. Tiny cupshaped nest of fine plant fiber and cobweb, outside decorated with lichen and/or pieces of bark; built in fork of small branch, 3.3–13 ft (1–4 m) above ground, occasionally up to 26 ft (8 m). Two eggs; incubation 15–16 days by female. Chicks black with sparse brownish dorsal down; fledging in 19–22 days.

CONSERVATION STATUS

Common resident in the lowlands and coastal ranges.

SIGNIFICANCE TO HUMANS

None known. ◆

Frilled coquette

Lophornis magnificus

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus magnificus Viellot, 1817, Brazil. Monotypic.

OTHER COMMON NAMES

French: Coquette magnifique; German: Prachtelfe; Spanish: Coqueta Magnifica.

PHYSICAL CHARACTERISTICS

2.8–3 in (7.1–7.7 cm); female and male c. 0.11 oz (3 g). Male has short, straight bill, red tipped black; forehead metallic



green, crest rufous, rest of upperparts bronzy-green, white band across rump; throat shining emerald green, fan-shaped tufts white with iridescent green distal band, rufous at base; rest of underparts grayish green; tail squared, central tail feathers bronzy green, remaining rufous with bronzy green tips and edges. Female lacks tufts and crest, upperparts similar to male, throat with rufous discs and some white with dark crescents, below washed grayish green; tail squared, dark bronzy, distally rufous. Immatures similar to adult female.

DISTRIBUTION

Central eastern Brazil (Espírito Santo south to Santa Catarina), and west to Goiás and Mato Grosso.

HABITAT

Edges of humid forest, second growth, coffee plantations, and cerrado up to 3,300 ft (1,000 m).

BEHAVIOR

Disperses after reproductive period. Subordinate to other larger hummingbirds. During the display the male hovers in front of the perching female with fanned tufts.

FEEDING ECOLOGY AND DIET

Feeds on nectar of small flowering plants like *Duranta*, *Inga*, introduced *Eucalyptus*, *Lantana*, and *Psychotria*. Hawks for flying insects.

REPRODUCTIVE BIOLOGY

Breeds from August to March (Espírito Santo, Brazil). Cupshaped, tiny nest built of fine plant material, outside decorated with lichens; sited 6.6–16 ft (2–5 m) above ground, saddled on branches in bushes or small trees. Two eggs; incubation 12–13 days by female; fledging at 20 days.

CONSERVATION STATUS

Rare to locally common. Accepts human-made habitats like flowering gardens and plantations.

SIGNIFICANCE TO HUMANS

None known. ◆

Red-billed streamertail

Trochilus polytmus

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus polytmus Linnaeus, 1758, Jamaica. Monotypic.

OTHER COMMON NAMES

English: Jamaican doctor bird; French: Colibri à tête noire; German: Rotschnabel-Jamaikakolibri; Spanish: Colibrí Portacintas Piquirrojo.

PHYSICAL CHARACTERISTICS

Female c. 4.1 in (10.5 cm), male 8.7–11.8 in (22–30 cm including 0.9 in [2.3 cm] bill, 5.1–6.7 in [13–17 cm] tail); female c. 0.16 oz (4.4 g), male c. 0.18 oz (5.2 g). Male has straight bill, coral red, tipped in black; head black, lateral crown feathers and ear-coverts elongated beyond nape; body iridescent emerald green, darker on back; tail black, forked, second outermost tail feather very long (streamers), scalloped and fluted on the inside. Female's bill similar to male's, but duller red, with distal part black; above green; underparts white, lightly spotted on sides of breast and belly; tail centrally green, rest dark blue with contrasting broad white tips, no streamers.

DISTRIBUTION

Jamaica, except in extreme east.



HABITAT

Occurs from sea-level to elfin forest and found in all manmade habitats; forages mainly throughout mid-strata and at forest edge. Most numerous at c. 3,300 ft (1,000 m); most birds at higher altitudes are not currently breeding.

BEHAVIOR

Males are extremely territorial at flowering shrubs or trees. Song faint and complex. Individuals disperse to higher altitudes after main breeding season.

FEEDING ECOLOGY AND DIET

Forages for nectar at native and introduced flowers, including *Hohenbergia*, *Bauhinia*, *Meriania*, *Tecoma*, *Besleria*, *Psychotria*, *Erythrina*, *Eucalyptus*, *Spathodea*, and *Calliandra*, generally at height of 6.6–13 ft (2–4 m). Feeds on insects in the air, and takes them also from leaves, flowers, branches, or spider webs.

REPRODUCTIVE BIOLOGY

Breeds all year round, but chiefly from January to mid-May. Cup-shaped nest of fine plant fibers and cobweb, with lichen attached to outer wall, placed on thin twig 3.3–10 ft (1–3 m) above ground. Two eggs; incubation 17–19 days by female. Chicks black with two dorsal rows of pale gray down; fledging period 19–24 days. Young remain with female for three to four weeks; up to three broods per year.

CONSERVATION STATUS

Restricted range species. Common resident, particularly in the Blue Mountains.

SIGNIFICANCE TO HUMANS

None known. ◆

Puerto Rican emerald

Chlorostilbon maugaeus

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus maugaeus Audebert and Viellot, 1801, Puerto Rico. Monotypic.

OTHER COMMON NAMES

English: Antillian emerald; French: Émeraude de Porto Rico; German: Puerto-Rico-Smaragdkolibri; Spanish: Esmeralda Portorriqueña.

PHYSICAL CHARACTERISTICS

Female 3–3.3 in (7.5–8.5 cm), male 3.3–3.7 in (8.5–9.5 cm); female and male 0.12–0.13 oz (3.4–3.8 g). Male has short, straight bill, upper mandible black, lower red, tipped black; forehead and crown metallic green, dark shining green upperparts and uppertail-coverts; throat iridescent bluish green, rest of underparts and undertail-coverts glossy green; tail forked, shining steely blue. Female has bill black; forehead and crown dull dark green; upperparts and uppertail-coverts shining grass green; throat and breast are light gray becoming darker on belly; tail less forked, outer rectrices basally pale white, becoming brown in center and tipped with a large white spot, second outermost rectrices shing greenish white at base changing to steel blue, tipped with white spot, the next innermost two are



green from base to center, rest of feather dull brown, the inner rectrices are shining green. Immatures resemble adult females.

DISTRIBUTION

Puerto Rico, Virgin Islands.

HABITAT

Coastal mangroves to forested mountain summits. Open forest, woodland and coffee plantations, from sea-level to 2,625 ft (800 m).

BEHAVIOR

Forages in low to medium strata 3.3–20 ft (1–6 m). Song consists of rapid tic notes given at various speeds ending in a rapid trill with a high-pitched buzz at the end. Sedentary.

FEEDING ECOLOGY AND DIET

Feeds on nectar of a wide spectrum of flowers, including *Hohenbergia*, *Vriesea*, *Dilomilis*, *Epidendrum*, *Hedychium*, *Justicia*, *Ruellia*, *Clusia*, and *Erythrina*. Trap-liner. Insects are caught in the air and cleaned from leaves and branches of shrubs and trees.

REPRODUCTIVE BIOLOGY

Breeds from February to May, but irregular nesting all year round. The nest, a compact structure in the form of a small cup, is composed of dry plant fibers, such as tree fern scales, lined with wild cotton and other soft plant material, externally decorated with lichen. It is generally built in either low or medium-sized plants and trees. Two eggs, incubation 14–16 days by female. Chicks darkish gray with two rows of dark down on the upper side; fledging at 20–22 days.

CONSERVATION STATUS

Restricted-range species. Generally common throughout Puerto Rico. Readily accepts human-made habitats.

SIGNIFICANCE TO HUMANS

None known. ◆

Rufous-tailed hummingbird

Amazilia tzacatl

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus tzacatl De la Llave, 1833, Mexico. Five subspecies recognized.

OTHER COMMON NAMES

English: Rieffer's hummingbird; French: Ariane à ventre gris; German: Braunschwanzamazilie; Spanish: Amazilia Tzacatl.

PHYSICAL CHARACTERISTICS

3.1–4.3 in (8–11 cm); female c. 0.18 oz (5.2 g), male 0.19 oz (5.5 g); subspecies *A. t. handleyi* 0.25 oz (7.0 g). Male has straight, medium-sized bill, fleshy red with dark tip, or upper mandible blackish; upperparts, flanks, and belly golden green to bonzegreen; throat glittering golden green, sometimes with a turquoise gleam in certain lights; belly ashy gray to grayish brown; tail rufous, rectrices with bronze-green to copperish margins. Female similar to male, but has grayish subterminal bars on throat feathers and white belly. Immature darker grayish towards belly.

DISTRIBUTION

A. t. tzacatl: central-east, possibly northeast Mexico to central Panama; A. t. handleyi: Isla Escudo de Veraguas (off northwest Panama; A. t. fuscicaudata: north and west Colombia and west Venezuela; A. t. jucunda: southwest Colombia and west Ecuador; A. t. brebmi: Ricaurte, Nariño, Colombia; endemic to the upper Río Guiza valley.

HABITAT

Edges of humid evergreen forest, clearings, plantations, and man-made habitats. Often in second growth and semi-open,

Amazilia tzacatl

■ Resident

thicket-rich areas; in South America, partially in gallery forest and mangrove. Occurs from sea-level to 8,200 ft (2,500 m).

BEHAVIOR

Mainly territorial, also when associated in groups; intruders, even larger trochilids, butterflies, and euglossine bees are sometimes attacked in diving flight. More sedentary in humid regions than in arid areas. Northernmost population winters along Pacific and Caribbean coast of Mexico. Vagrants may occur farther north of the range limit and have been recorded from southern Texas in summer and autumn. Seasonal movements are known from Colombia and Ecuador due to altitudinal variation of flowering periods. Frequently gathers in some numbers with conspecific or congeners such as *A. amazilia* and *A. rutila*.

FEEDING ECOLOGY AND DIET

Nectar and arthropods. Forages in all strata from near the ground to the more open sides of tree crowns. Feeds on a wide range of plants, including *Antigonon, Callistrimon, Clitoria, Costus, Isertia, Hamelia, Heliconia, Stachytarpheta, Tabebuia,* and *Lantana*. Gleans insects and small spiders from leaves and branches.

REPRODUCTIVE BIOLOGY

Breeds all year round. Favorite nest-sites are horizontal branches in smaller trees or shrubs, mostly 6.6–16 ft (2–5 m) above ground; sometimes cup-shaped nest is placed in fork. Nest material varies, and includes plant down, yellowish brown to grayish brown fibers, cobweb, pieces of dead leaves, moss, and lichen. Two eggs; incubation 15–16 days by female. Chicks blackish, with buff dorsal down; fledging at 18–22 days.

CONSERVATION STATUS

Common to very common throughout range.

SIGNIFICANCE TO HUMANS

None known. ◆

Velvet-purple coronet

Boissonneaua jardini

SUBFAMILY

Trochilinae

TAXONOMY

Trochilus jardini Bourcier, 1851, Nanegal, Ecuador. Monotypic.

OTHER COMMON NAMES

English: Jardine's hummingbird; French: Colibri de Jardine; German: Hyazinthkolibri; Spanish: Colibrí Sietecolores.

PHYSICAL CHARACTERISTICS

4.3–4.7 in (11–12 cm); female and male 0.28–0.3 oz (8.0–8.5 g). Bill straight, black. Male shining bluish green above with head and throat velvety black; crown, breast, and belly glittering purplish blue; underwing-coverts cinnamon and conspicuous in flight; tail slightly forked, central feathers black, the rest white with black tips and edges; small leg puffs also white. Female similar but duller in coloration, with feathers of breast and belly fringed buff; wings are shorter and tail less deeply forked than in male. Immatures like females.

DISTRIBUTION

Pacific slope of western Andes in southwest Colombia and northwest Ecuador.



HABITAT

Prefers wet mossy forests and forest boders in tropical and subtropical zones, but can also be found at shrubby clearings in Pacific lowlands and on lower slopes. Records range from 1,150–7,200 ft (350–2,200 m), commonest above 4,000 ft (1,200 m).

BEHAVIOR

Defends nectar-rich food sources. Sedentary, but seasonal altitudinal dispersal known in Colombia.

FEEDING ECOLOGY AND DIET

Usually seen feeding at flowers from lower strata to tree tops. Insects are caught in the air by hawking.

REPRODUCTIVE BIOLOGY

Breeds from January to March. Nest cup-shaped, made of moss and lichen, placed on a horizontal branch or thin fork. Two eggs; incubation by female.

CONSERVATION STATUS

Restricted-range species. Uncommon and very local.

SIGNIFICANCE TO HUMANS

None known. ◆

Sword-billed hummingbird

Ensifera ensifera

SUBFAMILY

Trochilinae

TAXONOMY

Ornismya ensifera Boissonneau, 1840, Bogotá, Colombia. Monotypic.

OTHER COMMON NAMES

French: Colibri porte-épée; German: Schwertschnabelkolibri; Spanish: Colibrí Picoespada.

PHYSICAL CHARACTERISTICS

6.7–9 in (17–22.8 cm, including bill of 3.5–4.3 in [9–11 cm]); female and male 0.42–0.53 oz (12–15 g). Longest bill of any hummingbird; straight to slightly upturned, black. Male is dark green, head coppery, postocular spot white; throat blackish, underparts glittering emerald green, belly dark gray; tail forked, blackish. Female similar to male, has underparts lighter with throat and belly washed gray with green discs; tail less forked. Immatures resemble adult females.

DISTRIBUTION

Andes from west Venezuela through Colombia, Ecuador, and Peru to northeast Bolivia.

HABITAT

Humid to semi-humid upper montane forest and forest edges, sometimes at patches of shrubs in páramo, at 5,600–11,500 ft (1,700–3,500 m), commonest at 8,200–9,850 ft (2,500–3,000 m).

BEHAVIOR

Sedentary. A species little known to science.



FEEDING ECOLOGY AND DIET

Flowers visited for nectar have long, pendent corollas, and include *Fuchsia*, *Datura*, *Passiflora mixta*, and *Tacsonia*. Hawks for insects in swift-like manner with wide open bill. Trap-lines for flowers in mid- to upper strata; sometimes perches below flowers while feeding.

REPRODUCTIVE BIOLOGY

No reliable information. One unconfirmed observation of a female defending a possible nesting site high up in a tree in April (Ecuador); another doubtful description records several moss nests 50 ft (15 m) above ground in a tree.

CONSERVATION STATUS

Rare to locally common.

SIGNIFICANCE TO HUMANS

None known. ◆

Anna's hummingbird

Calypte anna

SUBFAMILY

Trochilinae

TAXONOMY

Ornismya anna Lesson, 1829, San Francisco, California. Monotypic.



OTHER COMMON NAMES

French: Colibri d'Anna; German: Annakolibri; Spanish: Colibrí de Ana.

PHYSICAL CHARACTERISTICS

3.9–4.3 in (10–11 cm); female 0.12–0.17 oz (3.3–4.7 g), male 0.12–0.2 oz (3.3–5.8 g). Male has short, straight black bill; upperparts golden green; head and elongated lateral throat feathers iridescent deep rose red, underparts gray washed with green, undertail-coverts green, edged gray; central rectrices golden green, lateral tail feathers dark greenish bronze. Female similar to male, head grayish, small white postocular spot, lacks iridescent rose red on head and throat, red discs on throat appear with age; median rectrices golden green, rest blackish, outermost feathers tipped white. Immatures similar to adult females.

DISTRIBUTION

Southwest Canada (British Columbia) through west United States (east to south Arizona) to northwest Mexico. Winter range highly unsettled, species occuring irregularly south to north Sonora, southeast to Gulf Coast of United States, and even north to southeastern Alaska; sporadically occurs much further east.

HARITAT

Chaparral, oak woodland, canyon bottoms, open woodland with evergreen broadleaf trees, riparian woodland, savanna-like vegetation, coastal shrub, and urban and suburban environments, at sea-level to 5,900 ft (1,800 m).

BEHAVIOR

Forages in low to high strata, usually at 6.6–26 ft (2–8 m). Male occupies feeding territories at nectar-rich sources. Extensive post-breeding wandering. In recent years the species has considerably expanded its range of winter occurence in the United States towards the southeast. Recently recorded for first time in San Luis Potosí (north-central Mexico).

FEEDING ECOLOGY AND DIET

Nectar of flowering native and introduced perennials, shrubs and trees including *Ribes*, *Diplacus*, *Salvia*, *Keckiella*, *Aquilegia*, *Mimulus*, *Tecomaria*, *Kniphofia*, *Agave*, and *Eucalyptus*. Insects are caught in the air by hawking or taken from foliage. Small flies constitute almost half of the arthropod consumption.

REPRODUCTIVE BIOLOGY

Breeding occurs from November to May, occasionally to July. Cup-shaped nest constructed of soft material such as plant down, feathers, and hair, held together by spider web and insect cocoon fibers and sometimes rodent hairs; decorated with lichen, moss, pieces of dead leaves and bark on external wall; placed on horizontal twigs, usually 6.6–20 ft (2–6 m), sometimes up to 65 ft (20 m) above ground. Two eggs; incubation 14–19 days by female. Chicks black with two dorsal rows of dull grayish down; fledging period 18–26 days.

CONSERVATION STATUS

Common throughout range and at present apparently in process of expansion.

SIGNIFICANCE TO HUMANS

None known. ◆

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Karl-L. Schuchmann, PhD, Prof

Coliiformes Mousebirds

(Coliidae)

Class Aves

Order Coliiformes

Suborder Coliidae

Family Collidae

Number of families 1

Thumbnail description

Small, long-tailed birds with elongated crestfeathers on the head

Size

10.2-15.7 in (26-39.8 cm); 1-2.9 oz (28-82 g)

Number of genera, species

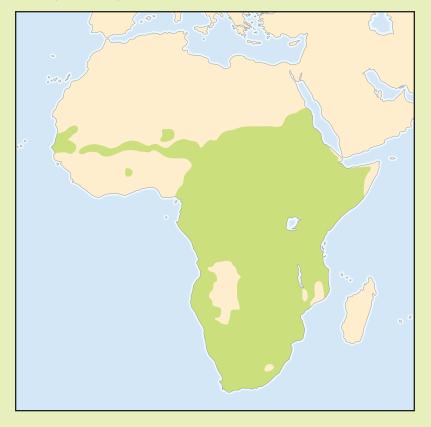
2 genera; 6 species

Habitat

Forest edge, woodland, and savanna

Conservation status

Not threatened



Distribution

Sub-Saharan Africa

Evolution and systematics

Mousebirds are not closely related to any other recent birds, but fossil remains of members of the closely related family Sandcoleidae have been discovered in Europe and northern America dating back to the Lower and Middle Eocene.

Physical characteristics

Soft, ragged plumage with fur-like gray and brown feathers give mousebirds a mouse-like appearance. They also have prominent crest feathers, long, stiff tails, short heavy bills, and heavy feet with first and fourth toes, called pamprodactylous, which can be turned forward and backward. The tail comprises about two-thirds of the bird's total body length. Between the lower jaw and the base of the skull is a supplementary joint that enables the birds to swallow large bits of food. Male and female mousebirds are alike.

Distribution

Mousebirds are now restricted to Africa south of the Sahara.

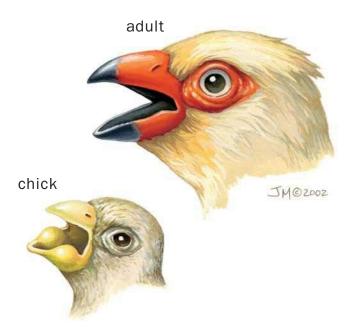
Habitat

Mousebirds inhabit forest edge, vegetation along rivers, woodland, and savanna with trees and brushwood.

Behavior

Mousebirds are very social birds most often seen in pairs or small family parties of five to seven, but occasionally in larger flights of 30 and more specimens, mostly during the dry seasons. Preening is very common behavior between pairs and members of a group. They cluster together during the day when they are resting and also during the night, holding on, much like bats, except with their heads up and their tails straight down. This clustering conserves body warmth and enables the birds to withstand low temperatures during the night. The body temperature may be lowered significantly as the birds fall into an energy-saving torpor, which is observed in only a few other bird groups such as hummingbirds. In torpor, the body temperature may be as low as 66.2–68°F (19–20°C).

Monotypic order: Colliformes Vol. 9: Birds II



Differing bill morphology showing bulbous swellings in a red-faced mousebird (*Urocolius indicus*) nestling's bill compared to adult. (Illustration by Jacqueline Mahannah)

Feeding ecology and diet

Almost exclusively vegetarians, mousebirds eat all sorts of fruit, buds, juicy leaves, and blossoms. They have been known to eat insects occasionally and captive specimens have used fresh pupae of ants to feed their young. They are rarely observed to eat meat, but are quite often seen to swallow earth, probably because of mineral contents.

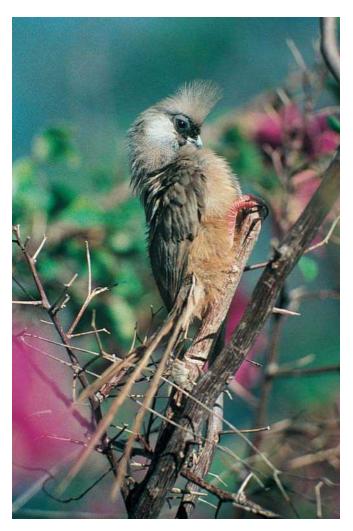
Reproductive biology

Mousebirds frequently nest close together in loose colonies, although nests may also be widely dispersed. Individual pairs maintain a strong bond that can last for years. During courtship, males hop on the same spot on a twig, but occasionally also on the ground. Courtship may last for several minutes and does not always attract females. Courting males do not sing but utter low, throaty, clicking sounds to attract females. The simple, bowl-shaped nests are built in dense brush or in thorny bushes or trees usually not more than 6 ft (2 m) above the ground. Nesting materials such as small sticks, grass, fibers, roots, and moss are mostly brought by the males and arranged by the females. Even during incubation, green leaves may be added to the nests. In some areas, mousebirds have been known to build their nests near those of a dangerous wasp species, Belonogaster rufipennis. Thus, the mousebirds have protection from nest robbers, particularly tree snakes, and the wasps do not molest the birds. Eggs are relatively small (0.75-0.87 in [19-22 mm] long and 0.6-0.7 in [15-18 mm] wide) and have a strangely rough, coarse-grained white shell. Clutches usually consist of two to five eggs. Both sexes share in incubation of the eggs, which lasts only 11-12 days, and they relieve each other several times

during those days. Newly hatched young weigh only 0.07 oz (2 g) or less, and their eyes are closed. They are almost naked or covered with only a sparse down coat, which grows quickly. Their eyes open and their first quills appear as early as the end of the first week. Towards the end of the second week, they are extensively feathered and, if threatened, they are able to leave the nest by climbing. Young mousebirds attempt their first flights when they are two and a half weeks old when they are still much smaller than their parents and have only a short tail. The young remain in close contact with their parents after leaving the nest and are still fed up to the age of four to six weeks. Birds from earlier broods may assist the parents in feeding the young and also assist in defending the nest and young.

Conservation status

Mousebirds are generally not threatened, but there are changes in distribution caused by human influence on vegetation.



A bar-breasted mousebird (*Colius striatus*) preens. (Photo by R. Cartmell/VIREO. Reproduced by permission.)

Vol. 9: Birds II Monotypic order: Coliiformes



Red-faced mousebirds (Colius indicus) drink in shallow water. (Photo by W. Tarboton/VIREO. Reproduced by permission.)

Significance to humans

Some species, especially the bar-breasted mousebird (*Colius striatus*), have adapted to live near humans and may even be found in gardens and parks in villages and cities. However, as they sometimes cause damage to crops and fruit, they are often not well liked by humans. Mousebirds were first brought live to Europe in the 1870s, but were quite fragile initially. Mousebirds are not well suited to being kept

in small cages, although life in aviaries in family groups agrees with them. While in natural surroundings they only reach an age of slightly more than 10 years, in captivity they may live for 12 years and more. Bar-breasted mousebirds were successfully bred in England as early as 1912, but have been regularly bred in more recent times. Young mousebirds removed from the nest and reared by hand can become very tame.



1. Bar-breasted mousebird (*Colius striatus*); 2. White-backed mousebird (*Colius colius*); 3. White-headed mousebird (*Colius leucocephalus*); 4. Bluenaped mousebird (*Urocolius macrourus*); 5. Red-faced mousebird (*Urocolius indicus*); 6. Chestnut-backed mousebird (*Colius castanotus*). (Illustration by Jacqueline Mahannah)

Species accounts

Bar-breasted mousebird

Colius striatus

TAXONOMY

Colius striatus Gmelin, 1789, Cape of Good Hope, South Africa. Nineteen subspecies.

OTHER COMMON NAMES

English: Speckled mousebird; French: Coliou strié, coliou rayé; German: Gestreifter Mausvogel, Braunflügel-Mausvogel; Spanish: Pájaro-ratón Común.

PHYSICAL CHARACTERISTICS

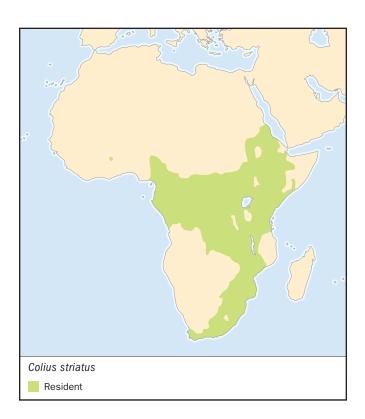
10.2–14.2 in (26–36 cm); 1.3–2.8 oz (36–80 g). Feathers are mostly gray-brown, but the transverse bands are not distinct in all subspecies. The more southerly subspecies have bills with an entirely black upper mandible and a silver-gray lower mandible; in the northerly subspecies, there is a white spot on top of the upper mandible. Eastern African subspecies are also characterized by white feathers at the sides of the head, which give them the name, white-eared mousebirds. Color of iris varies from white to brown and greenish; the color may also differ above or below the pupil.

DISTRIBUTION

Nigeria to Eritrea, Somalia, across the Congo to northern Angola, and from eastern Africa to the western Cape.

HABITAT

Forest edge, riverine forest, open woodland, and dense brush, as well as cultivated land, secondary growth, gardens, and parks.



BEHAVIOR

Live mostly in family groups, highly sedentary.

FEEDING ECOLOGY AND DIET

Fruits, buds, and leaves, and crops in cultivation and in human settlements.

REPRODUCTIVE BIOLOGY

Breeding throughout the year if conditions are good, and in areas with dry seasons when food is available.

CONSERVATION STATUS

Not threatened, even spreading in cultivated areas as observed in southern and eastern Africa.

SIGNIFICANCE TO HUMANS

Not liked by humans because they cause damage to orchards and gardens. ◆

Chestnut-backed mousebird

Colius castanotus

TAXONOMY

Colius castanotus Verreaux & Verreaux, 1855, Gabon, error = Angola. Monotypic.

OTHER COMMON NAMES

English: Red-backed mousebird; French: Coliou à dos marron; German: Rotrücken-Mausvogel; Spanish: Pájaro-ratón Dorsirrojo.



Monotypic order: Coliiformes Vol. 9: Birds II

PHYSICAL CHARACTERISTICS

11.4–15.0 in (29–38 cm); 1.4–2.9 oz (39–82 g). Upperparts are brown; underparts are grayish brown, buffy on belly. Has characteristic brown-red spot on the lower back rump. Face and forehead are black with whitish gray feather tips; sides of head and throat are grayish. Bill has black upper mandible with gray spot on culmen and whitish lower mandible. Feet are coral-red to scarlet. No barring on the feathers of the mantle, throat, or breast.

DISTRIBUTION

Western Angola from Congo mouth south to Namibia.

HABITAT

Forest edge, riverine growth, and cultivated land.

BEHAVIOR

Live in pairs and family groups, sedentary.

FEEDING ECOLOGY AND DIET

Fruits, buds, leaves, and crops in cultivation and in human settlements.

REPRODUCTIVE BIOLOGY

Breeding throughout the year when food supply is adequate.

CONSERVATION STATUS

Not threatened, though uncommon in parts of distribution area

SIGNIFICANCE TO HUMANS

Not liked by humans because they cause damage to orchards and gardens. $lack {f \Phi}$

White-headed mousebird

Colius leucocephalus

TAXONOMY

Colius leucocephalus Reichenow, 1879, Kinakomba, lower Tana River, Kenya. Two subspecies.

OTHER COMMON NAMES

French: Coliou à tête blanche; German: Weißkopf-Mausvogel; Spanish: Pájaro-ratón Cabeciblanco.

PHYSICAL CHARACTERISTICS

11.4–13.0 in (29–33 cm); 1.0–1.5 oz (28–42 g). Grayish upperparts with black-and-white barring on upper back; buff underparts with light barring on throat and breast. Creamy white crown, crest, and cheeks; blackish gray orbital skin. Bill has pale gray upper mandible with dark tip and paler lower mandible with yellowish tip. Feet are pinkish red to coral-red.

DISTRIBUTION

Southern Somalia through eastern Kenya to northern Tanzania.

HABITAT

Thorny woodland and savanna, but not far away from water supply.

BEHAVIOR

Live in pairs or family groups, more or less sedentary.

FEEDING ECOLOGY AND DIET

Fruits, leaves, and blossoms, especially observed to feed on *Salvadora* berries.



REPRODUCTIVE BIOLOGY

Mostly limited to breeding in seasons with best food supply, but will breed when enough food is available.

CONSERVATION STATUS

Not threatened, but change in distribution possible following change in vegetation; no longer found in some areas where noted in the past.

SIGNIFICANCE TO HUMANS

They do not interfere with humans. •

White-backed mousebird

Colius colius

TAXONOMY

Loxia colius Linnaeus, 1766, Cape of Good Hope, South Africa. Two subspecies.

OTHER COMMON NAMES

French: Coliou à dos blanc; German: Weißrücken-Mausvogel; Spanish: Pájaro-ratón Dorsiblanco.

PHYSICAL CHARACTERISTICS

11.4–13.0 in (29–33 cm); weight 1.3–2.3 oz (38–64 g). Has characteristic white back and dark red spot at the base of the tail; otherwise solid gray upperparts; buff underparts. Bill is bluish white with black tip. Legs and feet are coral-red.

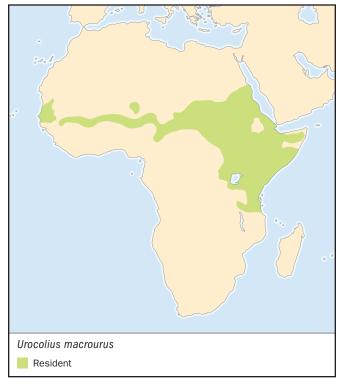
DISTRIBUTION

Namibia, southern Botswana, and southern Africa eastwards to Central Transvaal and eastern Cape.

HABITAT

Woodland areas, riverine growth, and cultivated areas.





BEHAVIOR

Live in family groups, sedentary.

FEEDING ECOLOGY AND DIET

Mostly fruits, some green matter, and nectar.

REPRODUCTIVE BIOLOGY

Breed throughout the year when conditions are favorable.

CONSERVATION STATUS

Not threatened, even spreading into cultivated areas.

SIGNIFICANCE TO HUMANS

Mostly none, but sometimes considered a pest. ◆

Blue-naped mousebird

Urocolius macrourus

TAXONOMY

Lanius macrourus Linnaeus, 1766, Senegal. Seven subspecies.

OTHER COMMON NAMES

French: Coliou huppé; German: Blaunacken-Mausvogel; Spanish: Pájaro-ratón Nuquiazul.

PHYSICAL CHARACTERISTICS

12.6–15.7 in (32–39.8 cm); 1.2–2.2 oz (34–62 g). Ash-gray plumage; upperparts darker than underparts; turquoise-blue patch on nape and hindneck. Long crest and very long, slender tail. Female's tail is shorter than male's.

DISTRIBUTION

Western Africa from south Mauritania to Somalia and Tanza-

HABITAT

Open woodland and savanna, often spreading in wetter seasons to breed, but moving to water-courses during the dry season.

BEHAVIOR

Pairs separated for breeding are afterwards observed in family parties, and sometimes in large concentrations near rivers in the dry season.

FEEDING ECOLOGY AND DIET

Fruits and other green matter, especially dependent on *Salvadora* berries; more recently observed feeding in human cultivations.

REPRODUCTIVE BIOLOGY

Fragile nests, eggs white with red-brown dots, streaks, and patches, clutches two to three eggs. Newly hatched young are naked with characteristic bulbous swellings at base of lower mandible. Grow quickly, flying after 16–18 days.

CONSERVATION STATUS

Not threatened and obviously expanding into western Africa, following the introduction of cultivated plants.

SIGNIFICANCE TO HUMANS

Not yet regarded as pests. ◆

Red-faced mousebird

Urocolius indicus

TAXONOMY

Colius indicus Latham, 1790, India, error = Gamtoos River, Cape Province, South Africa. Five subspecies.

Monotypic order: Coliiformes Vol. 9: Birds II

OTHER COMMON NAMES

French: Coliou quiriva; German: Rotzügel-Mausvogel, Brillen-Mausvogel; Spanish: Pájaro-ratón Carrirojo.

PHYSICAL CHARACTERISTICS

11.4–14.3 in (29–37 cm); 1.6–2.3 oz (45.1–65.9 g); in captivity to 2.5 oz (72 g). Upperparts gray with metallic greenish sheen; underparts buff. Tail is very long and slender. Bare skin around eyes and on lores is carmine-red. Most of upper mandible is red and the rest of the bill is black. Feet are purplish red. Subspecies differ primarily in intensity of plumage color.

DISTRIBUTION

Southern Africa from the Congo mouth, Angola, and southernmost Tanzania to the Cape.

HABITAT

Open woodland and savanna, moving widely for food supply; in recent times, more common in gardens and orchards in human settlements.

BEHAVIOR

Live in pairs or family parties, sometimes observed in larger groups.

FEEDING ECOLOGY AND DIET

Fruits and other green matter.

REPRODUCTIVE BIOLOGY

Eggs white with red-brown spots. Newly hatched young are naked with characteristic bulbous swellings at base of lower mandible. Grow quickly, flying after 16–18 days.

CONSERVATION STATUS

Not threatened, but changing numbers noted in some areas following changes in vegetation.



SIGNIFICANCE TO HUMANS

Mostly none, but sometimes considered pests in gardens and other human cultivations. ◆

Resources

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Herbert K. Schifter, PhD

Trogoniformes Trogons

(Trogonidae)

Class Aves

Order Trogoniformes

Family Trogonidae

Number of families 1

Thumbnail description

Compact, brightly colored arboreal birds with short, broad bills, long tails, and very small legs

Size

9.1-15.7 in (23-40 cm), 1.2-7.3 oz (35-210 g)

Number of genera, species

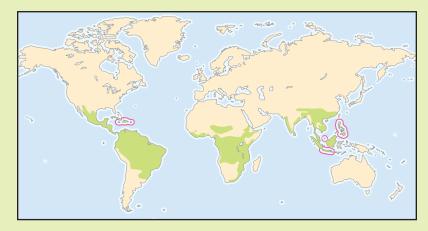
8 genera, 37 species

Habitat

Woodlands from rainforest to savannas

Conservation status

Near Threatened: 10 species



Distribution

Tropics of Africa, Asia, and New World

Evolution and systematics

Generally considered distinct enough to form their own order, trogons have traditionally been placed within the Coraciiformes near the toucans, parrots, puffbirds, cuckoos, rollers, and
jacamars. The closest living relative, the mousebird, supports
molecular evidence that Africa is the trogons' ancestral home,
despite only three of 37 trogon species being found there today.
The oldest trogoniform fossils, found in Europe, date to the Tertiary period, and it is thought that the other surviving groups
split from their African relatives between 20–36 million years ago.

Divisions within the trogons remain somewhat unclear. Many authorities divide the family into African and non-African subfamilies and six genera. This system, however, groups together the New World and the Asian trogons, which are separated not only by a great geographic distance, but also by the other subfamily. An alternative solution, which seems more intuitive, proposes three subfamilies based on geography (African, Asian, and American trogons) and eight genera.

Physical characteristics

Trogons are brightly colored, compact birds with short, rounded wings, broad squared tails, and small legs and feet. Bills are short, stout, and decurved, with serrated tomia (cutting edges) and a wide gape that allows trogons to grasp and swallow prey that is large, squirming, or both.

Trogon feet are notable not only in their small size and relative weakness—the birds are unable to rotate on a perch without using their wings—but for their morphology. On each foot, two toes point forward and two point back, but un-

like other zygodactyls, trogons have their first and second toes, rather than the first and fourth, directed backwards. This distinctive adaptation may help trogons cling to the sides of trees like woodpeckers, which have a similar toe arrangement.

Adult male trogons are among the most brilliantly colored of all tropical birds. Their notably soft, dense plumage is a brilliant green, blue, or violet on the upper body and chest, with yellow, orange, pink, or red underparts providing kaleidoscopic contrast. In American and African trogons, and one Asian species, the upper colors are iridescent, changing hue dramatically depending on the angle of light. Many trogons have distinctive barred or vermiculated wing panels, colored white on black in males and buff on black in females. The family's dazzling plumage is carried to an extreme in the resplendent quetzal (*Pharomachrus mocinno*), whose spectacular uppertail coverts are up to 25.6 in (65 cm) long.

Females are plainer, with browns and grays replacing the greens and blues of males. Female underparts, however, are often as brightly colored as those of males. Juveniles are mottled brown with white and buff spotting.

Distribution

Trogons are found in Africa, Asia, and the Americas. Most species occur in the tropics, and species richness is greatest in the Neotropics, where 25 species range from southern Arizona to Brazil. Colombia and Ecuador each have a dozen or more breeding species. This pan-tropical distribution, rare among avian families, spreads across almost 70 degrees of latitude and 11,500 ft (3,500 m) of elevation.

Monotypic order: Trogoniformes Vol. 9: Birds II



Resplendent quetzal (*Pharomachrus mocinno*) in flight in Costa Rica. (Photo by Gregory G. Dimijian. Photo Researchers, Inc. Reproduced by permission.)

Habitat

Trogons are fundamentally forest birds, occasionally spreading from humid woodlands into more open habitats. Most inhabit the shady middle strata of tropical and subtropical forests. Trogons also inhabit drier habitats including thorn forests, bamboo thickets, and savanna, particularly toward the northern and southern limits of their ranges.

An ecological analysis of 25 New World species found over half utilized tropical evergreen forests, and 14 occur in at least two forest types (some use as many as four). Four or five trogon species may overlap in the tall rainforests of Asia, while the trogons of Africa range from primary forests to habitats altered by human or natural disturbances.

Behavior

Generally sedate, trogons spend most of their time perched immobile and silent. This may be in part an antipredator strategy balancing the birds' bright coloration. The main activity periods in early morning and late afternoon are punctuated with short undulatory flights after food or in defense of small territories. There is little evidence of migratory behavior among trogons, although some montane species have been noted to move to lower elevations during the summer non-breeding season to follow fruiting events. Trogons are most often found alone or in pairs.

Accounts of visual displays are rare, but male resplendent quetzals (*P. mocinno*) and golden-headed quetzals (*P. auriceps*) both perform aerial display flights. Details on territoriality are also sparse, although strong territorial defense seems to be the norm.

Trogons' calls are typically melodious, loud, and simple. Males may repeat a monosyllabic, plaintive hoot over 100 times and give a hoarse chatter when disturbed. The calls of the quetzals and Caribbean species are slightly more complex. Songs appear to be used in territoriality and possibly mating

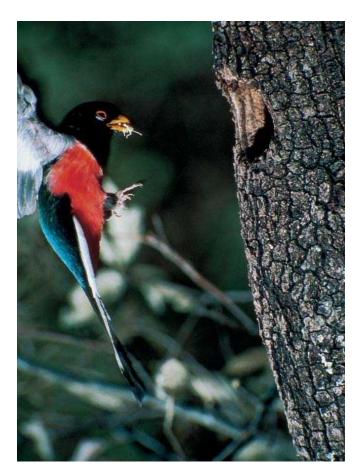
bonding. Pair duetting has been observed in the bar-tailed trogon (*Apaloderma vittatum*).

Feeding ecology and diet

Fruits and insects are trogons' two main foods, although diets vary. While African species are either exclusively insectivorous or carnivorous, species in Asia and the New World eat both types of food. The quetzals, almost entirely frugivorous for most of the year, are an exception. Among the omnivores, larger species tend to eat a higher proportion of fruit. In Asia and the Americas, trogons often join mixed-species feeding flocks, and rarely follow monkey troops or army ant columns to capture disturbed insects.

Smooth-skinned caterpillars are a trogon favorite, but hairy ones are also taken infrequently, along with adult butterflies and moths. The ingestion of noxious insects may account for the unpleasant smell reported for trogon excrement and flesh. Stick insects, beetles, and other large, slow insects are also on the menu, as are the occasional small lizard, snail, or frog. Trogons eat enough fruits to be important seed dispersers: in Panama, the slaty-tailed trogon (*T. massena*) was found to account for 11% of all the dispersed seeds of *Virola surinamensis*.

Insects and fruits are obtained on the wing using a technique known alternately as "hawking," for insects, or "hover-



An elegant trogon (*Trogon elegans*) returns to its nest with an insect in Arizona. (Photo by S. & S. Rucker/VIREO. Reproduced by permission.)

gleaning." Trogons' deeply slotted wings allow them to stall momentarily, without losing flight control, to pluck a food item from the air or protruding stem.

Reproductive biology

Trogons pair monogamously, probably for life. Among tropical species, breeding occurs around the dry season when food items are more abundant. Spring and summer breeding is typical among species in temperate and arid areas. Pairformation, pair-maintenance, and copulatory behavior are little understood. All trogons are cavity nesters.

Mating generally begins with a male finding a suitable nesting spot, beginning excavation, and then advertising for a mate by singing. Both members of the pair help with the construction, which may take several months. Nests are most often built in decaying tree trunks, but epiphyte root masses and occupied termitaries are also used. The violaceous trogon (*T. violaceus*) has alone been observed to co-occupy the nests of arboreal wasps or ants. Excavation is done mostly with the bill, and the nest cavities are either enclosed chambers accessed by an ascending tunnel, or shallow depressions that leave most of the occupying bird exposed.

Two to four eggs are laid in the unlined nest cavities. The eggs range from white to greenish or bluish in quetzals. Incubation is 16–21 days and is shared by both sexes, with the female typically taking the night shift. Chicks are fed and brooded by both parents. They are fed mostly on insects, either whole or regurgitated, and must cope with a lack of nest sanitation so pronounced that it may help discourage predators—refuse can accumulate 3.9 in (10 cm) deep in the nests of the resplendent quetzal (*P. mocinno*).

Conservation status

Trogons are considered relatively common, although estimating the family's overall welfare is difficult. They are especially sensitive to habitat destruction, in part because of their choosiness when it comes to selecting nesting trees. As forests are cut around the globe, it is inevitable that forest-dwelling species will decline. This is a particular concern in peninsular Malaysia, but in South America the white-tailed (*T. viridis*) and violaceous trogons (*T. violaceus*) have actually been shown to benefit from selective logging. Trogon numbers have declined near human settlements, an important consideration in ecotourism destinations such as Costa Rica, where resplendent quetzals (*P. mocinno*) almost single-handedly draw millions of tourist dollars every year.

Ten trogons were recognized as Lower Risk: Near Threatened on the IUCN Red List in 2002: Diard's trogon (Harpactes diardii), Whitehead's trogon (H. whiteheadi), Ward's trogon (H. wardi), Baird's trogon (T. bairdii), the Hispaniolan trogon (Temnotrogon roseigaster), the eared trogon (Euptilotis neoxenus), the scarlet-rumped trogon (H. duvaucelii), the cinnamon-rumped trogon (H. orrhophaeus), the red-naped trogon (H. kasumba), and the resplendent quetzal (P. mocinno).

Chiefly because of its great beauty, the resplendent quetzal (*P. mocinno*) may be the most threatened trogon of all. For



An elegant trogon (*Trogon elegans*) with an insect at its nest. (Photo by S. & S. Rucker/VIREO. Reproduced by permission.)

centuries, the birds' spectacular tail feathers have made them the target of hunters and collectors. Well into the twentieth century, hundreds of quetzals were exported annually from Central America for zoos, aviaries, and the decorative appeal of their tail feathers. This destructive practice likely continues to the present.

Significance to humans

Humans have long considered trogons to be special birds. Quetzalcoatl, chief god of sea, land, and air to the Aztecs and Maya of Central America, combined the body of a snake with the wings of a resplendent quetzal (*P. mocinno*). This bird was highly revered by both cultures, who forbade anyone but priests and royalty from possessing the tail feathers, on punishment of death—the same sentence decreed for anyone found killing a quetzal.

"Quetzal" itself comes from the Aztec word quetzalli, meaning "tail feather" but also "beautiful" or "precious." Today, the quetzal gives its name to the currency of Guatemala and its image to countless brochures and photos advertising the tropical wonders of Central and South America. The elusive quetzal remains one of the top targets for nature-oriented tourism in the region.



1. Cuban trogon (*Priotelus temnurus*); 2. Resplendent quetzal (*Pharomachrus mocinno*); 3. Eared quetzal (*Euptilotis neoxenus*); 4. Collared trogon (*Trogon collaris*); 5. Orange-breasted trogon (*Harpactes oreskios*); 6. Javan trogon (*Apalharpactes reinwardtii*); 7. Hispaniolan trogon (*Temnotrogon roseigaster*); 8. Narina trogon (*Apaloderma narina*). (Illustration by Bruce Worden)

Species accounts

Narina trogon

Apaloderma narina

SUBFAMILY

Apalodermatinae

TAXONOMY

Trogon narina Stephens, 1815, Cape Province. Six subspecies.

OTHER COMMON NAMES

French; Couroucou narina; German: Narinatrogon; Spanish: Trogón de Narina.

PHYSICAL CHARACTERISTICS

11.8–12.6 in (30–32 cm); 1.8–3.3 oz (51–95 g). Upperparts and underparts iridescent green to midbreast, abdomen and flanks crimson, undertail whitish, white bar on underwing, yellow bill.

DISTRIBUTION

Sub-Saharan Africa, from Sierra Leone through Congo Basin and Rift Valley to Ethiopia and eastern South Africa.

HARITAT

Mid-altitude rainforests, gallery forests, savanna, and woodlands.

BEHAVIOR

Territorial, with non-lek male singing groups congregating during breeding season.

FEEDING ECOLOGY AND DIET

Sally-gleaning insectivore, feeding on caterpillars, orthopterans, beetles, spiders, and small reptiles.



REPRODUCTIVE BIOLOGY

Monogamous. Breeds year-round continent-wide, but primarily in spring and summer; nests in unlined natural cavities; lays one to four eggs (most often two or three); incubates 16–21 days; fledges in 25–28 days.

CONSERVATION STATUS

The most widespread trogon in Africa, albeit uncommon; densities up to 1.25 individuals per hectare reported.

SIGNIFICANCE TO HUMANS

None known.

Javan trogon

Apalharpactes reinwardtii

SUBFAMILY

Harpactinae

TAXONOMY

Trogon reinwardtii Temminck, 1822, Java. Occasionally considered conspecific with Sumatran trogon (A. mackloti), although range and appearance differ. Monotypic.

OTHER COMMON NAMES

English: Blue-tailed trogon, Macklot's trogon, Reinwardt's trogon; French: Trogon de Reinwardt; German: Reinwardttrogon; Spanish: Trogón de Java.



PHYSICAL CHARACTERISTICS

13.4 in (34 cm), weight unknown. Olive-brown head and shoulders, blue-green upperparts, yellow throat and lower breast, metallic blue tail, with three outer retrices tipped and edged in white, red bill.

DISTRIBUTION

West Java.

HABITAT

Montane evergreen forests.

BEHAVIOR

Little known; probably sedentary.

FEEDING ECOLOGY AND DIET

Eats insects, including beetles, cicadas, caterpillars, grasshoppers, as well as fruit, including figs.

REPRODUCTIVE BIOLOGY

Little known; breeding reported April through December; lays one to three eggs.

CONSERVATION STATUS

Uncommon within restricted range.

SIGNIFICANCE TO HUMANS

None known. ◆

Orange-breasted trogon

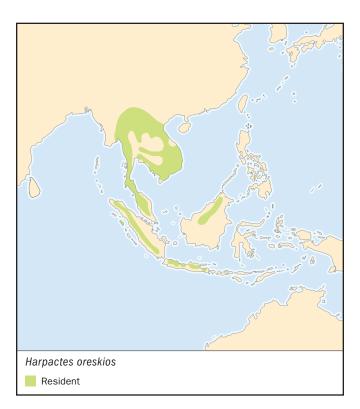
Harpactes oreskios

SUBFAMILY

Harpactinae

TAXONOMY

Harpactes oreskios Temminck, 1823, Java. Four subspecies.



OTHER COMMON NAMES

English: Malayan orange-breasted trogon, mountain trogon, Stella's orange-breasted trogon, yellow-breasted trogon; French: Trogon à poitrine jaune; German: Orangebrusttrogon; Spanish; Trogón Pechinaranja.

PHYSICAL CHARACTERISTICS

Olive-yellow head, rich chestnut upperparts, orange breast fading to bright yellow on upper and lower breast, white and black undertail, white wingpanel bars, blue orbital ring and bill.

DISTRIBUTION

Southern China, Malaysian Peninsula, Java, Sumatra, and northern Borneo.

HABITAT

Humid, lower elevation evergreen forests, open dry forest, and bamboo forest.

BEHAVIOR

Perches on shorter trees in middle and upper canopy, alone and in pairs.

FEEDING ECOLOGY AND DIET

Fruits and insects including crickets, grasshoppers, beetles, ants, lizards, and various vegetable material. Occasionally feeds on ground or in mixed-species foraging flocks.

REPRODUCTIVE BIOLOGY

Breeds January to June over range, primarily in February and March; nests in hollow stumps, often low to ground; lays one to four eggs, most often two or three. No information on brood rearing.

CONSERVATION STATUS

Most common trogon on Malaysian Peninsula; not threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Collared trogon

Trogon collaris

SUBFAMILY

Trogoninae

TAXONOMY

Trogon collaris Viellot, 1817, Cayenne. Eight subspecies.

OTHER COMMON NAMES

English: Bar-tailed trogon, ray-tailed trogon, red-bellied trogon; French: Trogon rosalba; German: Jungferntrogon; Spanish: Trogón Acollarado, Sorocua Acollarado.

PHYSICAL CHARACTERISTICS

9.8–11.4 in (25–29 cm), 1.4–2.4 oz (40–70 g). Upperparts greenish bronze, white breast band, red lower breast, blackish face and throat, yellow bill, barred black and white undertail and wingpanel.

DISTRIBUTION

South Mexico through Central America, Amazonian and northeast coastal South America to southeast Brazil.

HABITAT

Lowland tropical evergreen forest, including cloud forest, rainforest, gallery forest, and open woodlands, especially edges.



BEHAVIOR

Solitary, retiring.

FEEDING ECOLOGY AND DIET

Fruits and insects, including stick insects, beetles, and caterpillars. Often found in mixed-species flocks.

REPRODUCTIVE BIOLOGY

Breeds January through June over range, as well as November through December, in French Guiana; nests in shallow unlined niche or cavity, occasionally termitaria; lays two or three eggs; brood rearing little known.

CONSERVATION STATUS

Not threatened; most abundant and one of the broadest ranging of trogons.

SIGNIFICANCE TO HUMANS

None known. ◆

Cuban trogon

Priotelus temnurus

SUBFAMILY

Trogoninae

TAXONOMY

Trogon temnurus Temminck, 1825, Cuba. Two subspecies.

OTHER COMMON NAMES

English: Isle of Pines trogon; French: Trogon de Cuba; German: Kubatrogon; Spanish: Trogón Tocororo, Guatini.

PHYSICAL CHARACTERISTICS

9.1–9.8 in (23–25 cm), 1.8–2.1 oz (53–60 g). Blue crown and nape, blackish face, grayish white chin, throat, and breast, red



belly, upperparts iridescent bronze-green with white spots on coverts and primaries, green-blue uppertail, distinctive scalloped retrices.

DISTRIBUTION

Cuba, including offshore islands.

HARITAT

Wet and dry tropical forests, both evergreen and deciduous, as well as pine forests and secondary forests.

BEHAVIOR

Sedentary, tame.

FEEDING ECOLOGY AND DIET

Hovers to feed on flowers with tongue split at tip, also insects, fruits.

REPRODUCTIVE BIOLOGY

Breeds May through August; nests in natural cavity or abandoned woodpecker hole; lays three or four eggs. No information on brood rearing.

CONSERVATION STATUS

Common over range.

SIGNIFICANCE TO HUMANS

None known. ◆

Hispaniolan trogon

Temnotrogon roseigaster

SUBFAMILY

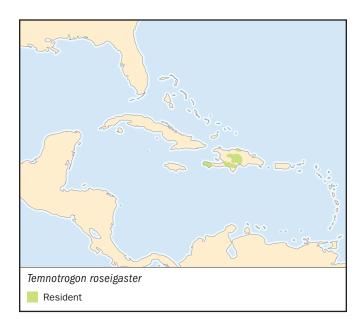
Trogoninae

TAXONOMY

Trogon roseigaster Viellot, 1817, Santo Domingo. Monotypic.

OTHER COMMON NAMES

English: Santo Domingo trogon; French: Trogon damoiseau; German: Rosentrogon; Spanish; Trogón de la Española, Cotorrita de Sierra, Papagayo.



PHYSICAL CHARACTERISTICS

10.6–11.8 in (27–30) cm, 2.5 oz (74 g). Bronze-green crown and upperparts, throat, breast and upper belly gray, lower belly and undertail-coverts red, uppertail bluish green with white tips, white wingpanel bars, yellow bill.

DISTRIBUTION

Hispaniola.

HABITAT

Montane evergreen, pine, and deciduous forests, occasionally mangroves.

BEHAVIOR

Little known; gather for vocal-visual mating displays.

FEEDING ECOLOGY AND DIET

Eats fruits, insects, and small lizards.

REPRODUCTIVE BIOLOGY

Breeds March through July, nests in tree cavity or stubs, lays two eggs.

CONSERVATION STATUS

IUCN Near Threatened species with restricted range.

SIGNIFICANCE TO HUMANS

None known. ◆

Eared quetzal

Euptilotis neoxenus

SUBFAMILY

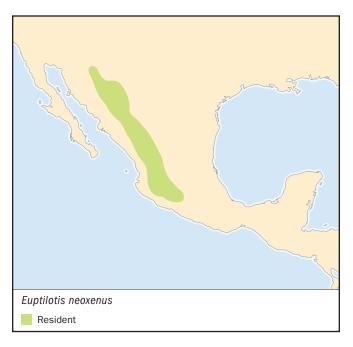
Trogoninae

TAXONOMY

Trogon neoxenus Gould, 1838, Mexico. Monotypic.

OTHER COMMON NAMES

English: Eared trogon, welcome trogon; French: Trogon oreillard; German: Haabüscheltrogon; Spanish: Trogón Orejón, Quetzal Mexicano.



PHYSICAL CHARACTERISTICS

13–14.2 in (33–36 cm), 3.6–5.2 oz (103–149 g). Upperparts and breast dark bronze-green, lower breast to undertail-coverts red, uppertail dark blue-green, wings green to slaty, primaries and three outer retrices edged in white, black head with filamentous ear-coverts and small bill.

DISTRIBUTION

Southern Arizona to western Mexico.

HABITAT

Pine woodlands, also pine-oak and pine-evergreen forests, especially canyons.

BEHAVIOR

Particularly mobile for a trogon; possible seasonal altitude displacement.

FEEDING ECOLOGY AND DIET

Eats insects and fruits, favoring madroña (Arbutus arizonica).

REPRODUCTIVE BIOLOGY

Breeds June through October, nests in live or dead tree cavities. No information on egg-laying or brood rearing.

CONSERVATION STATUS

IUCN Near Threatened. Occurs in low densities, possibly sensitive to logging.

SIGNIFICANCE TO HUMANS

None known. ◆

Resplendent quetzal

Pharomachrus mocinno

SUBFAMILY

Trogoninae

TAXONOMY

Pharomachrus mocinno de la Lave, 1832, Guatemala and Chiapas. Two subspecies.

OTHER COMMON NAMES

English: Coasta Rican quetzal, northern quetzal, magnificent quetzal; French: Quetzal resplendissant; German: Quetzal; Spanish: Quetzal Guatemalteco, Quetzal Centroamericano

PHYSICAL CHARACTERISTICS

14.2–15.7 in (36–40 cm), with 25.6–in (65 cm) tail-streamers, 6.2–7.3 oz (180–210 g). Head, chest upperparts, and elongate greater coverts brilliant gold-green iridescing to bluish, flight feathers blackish, lower breast and undertail-coverts red, undertail white, yellow bill. Filamentous feathers give head bristling appearance.

DISTRIBUTION

Discontinuous through Central America, from southern Mexico to western Panama.

HABITAT

Cloud forests, forest edges.

BEHAVIOR

Territorial. Males engage in flight displays during breeding season.

FEEDING ECOLOGY AND DIET

Sally-gleans fruit, insects, small reptiles and amphibians. Primarily frugivorous.

REPRODUCTIVE BIOLOGY

Breeds March through June over range; nests in deep cavity in decaying tree stumps often high above ground; lays one to two eggs, incubates 17–19 days, fledges in 23–31 days. High chick mortality.



CONSERVATION STATUS

IUCN Near Threatened species. Threatened locally by poaching and habitat disturbance.

SIGNIFICANCE TO HUMANS

Revered by Maya and Aztecs of Central America; plumes used for decoration well into the twentieth century; very popular birdwatching target. •

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Glossary

The following glossary is not intended to be exhaustive, but rather includes primarily terms that (1) have some specific importance to our understanding of birds, (2) have been used in these volumes, (3) might have varying definitions relative to birds as opposed to common usage, or (4) are often misunderstood.

- Accipiter—This is the genus name for a group of birdeating hawks (Accipitridae; e.g., sharp-shinned hawk, Cooper's hawk). These birds show similar behavior and appearance and extreme sexual dimorphism. Females are much larger than males and the female of the sharp-shinned hawk often seems as large as the male of the Cooper's hawk, leading to some confusion on the part of birders. In the face of uncertainty, these birds are often just referred to as "Accipiters" and the name is now firmly ensconced in "birding" terminology.
- **Adaptive radiation**—Diversification of a species or single ancestral type into several forms that are each adaptively specialized to a specific niche.
- Aftershaft—A second rachis (= shaft) arising near the base of a contour feather, creating a feather that "branches." Aftershafts can be found in many birds (e.g., pheasants) but in most the aftershaft is much smaller than the main shaft of the feather. In ratites (ostrich-like birds), the aftershaft is about the same size as the main shaft. Sometimes the term "aftershaft" is restricted to the rachis that extends from the main rachis and the whole secondary structure is referred to as the "afterfeather."
- Agonistic—Behavioral patterns that are aggressive in context. Most aggressive behavior in birds is expressed as song (in songbirds) or other vocal or mechanical sound (e.g. see Drumming). The next level of intensity is display, and only in extreme circumstances do birds resort to physical aggression.
- Air sac—Thin-walled, extensions of the lungs, lying in the abdomen and thorax, and extending even into some bones of birds. Air sacs allow an increased respiratory capacity of birds and the removal of oxygen both as air passes in through the lungs and also as it passes back through the lungs as the bird exhales. The flow of air through the air sacs also helps dissipate the heat produced through muscle activity and increases a bird's volume while only minimally increasing weight—thus effectively making birds lighter relative to their size and more efficient in flying. Air sacs are best developed in

- the strongest flying birds and least developed in some groups that are flightless.
- **Alcid**—Referring to a member of the family Alcidae; including puffins, auks, auklets, murres, razorbills, and guillemots.
- **Allopatric**—Occurring in separate, nonoverlapping geographic areas.
- **Allopreening**—Mutual preening; preening of the feathers of one bird by another; often a part of courtship or pair bond maintenance.
- **Alpha breeder**—The reproductively dominant member of a social unit.
- **Alternate plumage**—The breeding plumage of passerines, ducks, and many other groups; typically acquired through a partial molt prior to the beginning of courtship.
- **Altricial**—An adjective referring to a bird that hatches with little, if any, down, is unable to feed itself, and initially has poor sensory and thermoregulatory abilities.
- Alula—Small feathers at the leading edge of the wing and attached to the thumb; also called bastard wing; functions in controlling air flow over the surface of the wing, thus allowing a bird to land at a relatively slow speed.
- **Anatid**—A collective term referring to members of the family Anatidae; ducks, geese, and swans.
- **Anisodactyl** An adjective that describes a bird's foot in which three toes point forward and one points backwards, a characteristic of songbirds.
- Anserine—Goose-like.
- **Anting**—A behavior of birds that involves rubbing live ants on the feathers, presumably to kill skin parasites.

Antiphonal duet—Vocalizations by two birds delivered alternately in response to one another; also known as responsive singing.

AOU—American Ornithologists' Union; the premier professional ornithological organization in North America; the organizational arbiter of scientific and standardized common names of North American birds as given in the periodically revised Check-list of North American Birds.

Arena—See Lek.

Aspect ratio—Length of a wing divided by width of the wing; High aspect wings are long and narrow. These are characteristic of dynamic soaring seabirds such as albatrosses. These birds have tremendous abilities to soar over the open ocean, but poor ability to maneuver in a small area. In contrast, low aspect ratio wings are short and broad, characteristic of many forest birds, and provide great ability to quickly maneuver in a small space.

Asynchronous—Not simultaneous; in ornithology often used with respect to the hatching of eggs in a clutch in which hatching occurs over two or more days, typically a result of initiation of incubation prior to laying of the last egg.

Auricular—An adjective referring to the region of the ear in birds, often to a particular plumage pattern over the ear.

Austral—May refer to "southern regions," typically meaning Southern Hemisphere. May also refer to the geographical region included within the Transition, Upper Austral, and Lower Austral Life Zones as defined by C. Hart Merriam in 1892–1898. These zones are often characterized by specific plant and animal communities and were originally defined by temperature gradients especially in the mountains of southwestern North America.

Autochthonous—An adjective that indicates that a species originated in the region where it now resides.

Barb—One of the hair-like extensions from the rachis of a feather. Barbs with barbules and other microstructures can adhere to one another, forming the strong, yet flexible vane needed for flight and protection and streamlining of body surfaces.

Barbules—A structural component of the barbs of many feathers; minute often interlocking filaments in a row at each side of a barb. As a result of their microstructure, barbules adhere to one another much like "Velcro®" thus assuring that feathers provide a stiff, yet flexible vane.

Basic plumage—The plumage an adult bird acquires as a result of its complete (or near complete) annual molt.

Bergmann's rule—Within a species or among closely related species of mammals and birds, those individuals in colder environments often are larger in body size.

Bergmann's rule is a generalization that reflects the ability of warm-blooded animals to more easily retain body heat (in cold climates) if they have a high body surface to body volume ratio, and to more easily dissipate excess body heat (in hot environments) if they have a low body surface to body volume ratio.

Bioacoustics—The study of biological sounds such as the sounds produced by birds.

Biogeographic region—One of several major divisions of the earth defined by a distinctive assemblage of animals and plants. Sometimes referred to as "zoogeographic regions or realms" (for animals) or "phytogeographic regions or realms" (for plants). Such terminology dates from the late nineteenth century and varies considerably. Major biogeographic regions each have a somewhat distinctive flora and fauna. Those generally recognized include Nearctic, Neotropical, Palearctic, Ethiopian, Oriental, and Australian.

Biomagnification—Sometimes referred to as "bioaccumulation." Some toxic elements and chemical compounds are not readily excreted by animals and instead are stored in fatty tissues, removing them from active metabolic pathways. Birds that are low in a food chain (e.g., sparrows that eat seeds) accumulate these chemicals in their fatty tissues. When a bird that is higher in the food chain (e.g., a predator like a falcon) eats its prey (e.g., sparrows), it accumulates these chemicals from the fatty tissue of each prey individual, thus magnifying the level of the chemical in its own tissues. When the predator then comes under stress and all of these chemicals are released from its fat into its system, the effect can be lethal. Chemicals capable of such biomagnification include heavy metals such as lead and mercury, and such manmade compounds as organochlorine pesticides and polychlorinated biphenyls (PCBs).

Booming ground—See Lek.

Booted—An adjective describing a bird tarsus (leg) that has a smooth, generally undivided, rather than scaly (= scutellate) appearance. The extent of the smooth or scaly appearance of a bird tarsus varies among taxonomic groups and there are many different, more specific, patterns of tarsal appearance that are recognized.

Boreal—Often used as an adjective meaning "northern"; also may refer to the northern climatic zone immediately south of the Arctic; may also include the Arctic, Hudsonian, and Canadian Life Zones described by C. Hart Merriam.

Bristle—In ornithology, a feather with a thick, tapered rachis and no vane except for a remnant sometimes found near the bristle base.

- **Brood**—As a noun: the young produced by a pair of birds during one reproductive effort. As a verb: to provide warmth and shelter to chicks by gathering them under the protection of breast and/or wings.
- **Brood parasitism**—Reproductive strategy where one species of bird (the parasite) lays its eggs in the nests of another species (the host). An acceptable host will incubate the eggs and rear the chicks of the brood parasite, often to the detriment or loss of the host's own offspring.
- Brood patch—A bare area of skin on the belly of a bird, the brood patch is enlarged beyond the normal apterium (bare area) as a result of loss of feathers. It becomes highly vascularized (many blood vessels just under the surface). The brood patch is very warm to the touch and the bird uses it to cover and warm its chicks. In terms of structure, the brood patch is the same as the incubation patch and the two terms are often used synonymously. Technically the brood patch and incubation patch differ in function: the incubation patch is used in incubating eggs, the brood patch is used to brood the young after the eggs hatch.
- Brood reduction—Reduction in the number of young in the nest. Viewed from an evolutionary perspective, mechanisms that allow for brood reduction may assure that at least some offspring survive during stressful times and that during times of abundant resources all young may survive. Asynchronous hatching results in young of different ages and sizes in a nest and is a mechanism that facilitates brood reduction: the smallest chick often dies if there is a shortage of food. The barn owl (*Tyto alba*; Tytonidae) depends on food resources that vary greatly in availability from year to year and it often experiences brood reduction.
- **Buteo**—This is the genus name for a group of hawks that have broad wings and soar. These hawks are often seen at a distance and are easily recognized as "Buteos" although they may not be identifiable as species. Hence the genus name has come into common English usage.
- Caecum (pl. caeca)—Blindly-ending branch extending from the junction of the small and large intestine. Most birds have two caeca, but the number and their development in birds is highly variable. Caeca seem to be most highly developed and functional in facilitating microbial digestion of food in those birds that eat primarily plant materials.
- **Caruncle**—An exposed, often brightly colored, fleshy protuberance or wrinkled facial skin of some birds.
- Casque—An enlargement at the front of the head (e.g., on cassowaries, Casuaridae) or sometimes of the bill (e.g., on hornbills, Bucerotidae) of a bird. A casque may be bony, cartilaginous, or composed of feathers (e.g., Pri-

- onopidae). A casque is often sexual ornamentation, but may protect the head of a cassowary crashing through underbrush, may be used for vocal amplification, or may serve a physiological function.
- Cavity nester—A species that nests in some sort of a cavity. Primary cavity nesters (e.g., woodpeckers, Picidae; kingfishers, Alcedinidae; some swallows, Hirundinidae) are capable of excavating their own cavities; secondary cavity nesters (e.g., starlings, Sturnidae; House Sparrows, Passeridae; bluebirds, Turdidae) are not capable of excavating their own cavities.
- Cere—The soft, sometimes enlarged, and often differently colored basal covering of the upper bill (maxilla) of many hawks (Falconiformes), parrots (Psitaciformes), and owls (Strigiformes). The nostrils are often within or at the edge of the cere. In parrots the cere is sometimes feathered.
- **Cladistic**—Evolutionary relationships suggested as "tree" branches to indicate lines of common ancestry.
- Cleidoic eggs—Cleidoic eggs are simply ones that are contained, hence protected, inside of a somewhat impervious shell—such as the eggs of birds. The presence of a shell around an egg freed the amphibian ancestors of reptiles from the need to return to the water to lay eggs and provided greater protection from dying.
- Cline—A gradient in a measurable character, such as size and color, showing geographic differentiation. Various patterns of geographic variation are reflected as clines or clinal variation, and have been described as "ecogeographic rules."
- Clutch—The set of eggs laid by a female bird during one reproductive effort. In most species, a female will lay one egg per day until the clutch is complete; in some species, particularly larger ones (e.g., New World vultures, Cathartidae), the interval between eggs may be more than one day.
- **Colony**—A group of birds nesting in close proximity, interacting, and usually aiding in early warning of the presence of predators and in group defense.
- **Commensal**—A relationship between species in which one benefits and the other is neither benefited nor harmed.
- **Congeneric**—Descriptive of two or more species that belong to the same genus.
- **Conspecific**—Descriptive of two or more individuals or populations that belong to the same species.
- **Conspecific colony**—A colony of birds that includes only members of one species.
- **Contact call**—Simple vocalization used to maintain communication or physical proximity among members of a social unit.

- **Contour feather**—One of those feathers covering the body, head, neck, and limbs of a bird and giving rise to the shape (contours) of the bird.
- Convergent evolution—When two evolutionarily unrelated groups of organisms develop similar characteristics due to adaptation to similar aspects of their environment or niche. The sharply pointed and curved talons of hawks and owls are convergent adaptations for their predatory lifestyle.
- Cooperative breeding—A breeding system in which birds other than the genetic parents share in the care of eggs and young. There are many variants of cooperative breeding. The birds that assist with the care are usually referred to as "helpers" and these are often offspring of the same breeding pair, thus genetically related to the chicks they are tending. Cooperative breeding is most common among tropical birds and seems most common in situations where nest sites or breeding territories are very limited. Several studies have demonstrated that "helping" increases reproductive success. By helping a helper is often assuring survival of genes shared with the related offspring. The helper also may gain important experience and ultimately gain access to a breeding site.
- Coracoid—A bone in birds and some other vertebrates extending from the scapula and clavicle to the sternum; the coracoid serves as a strut supporting the chest of the bird during powerful muscle movements associated with flapping flight.
- Cosmopolitan—Adjective describing the distribution pattern of a bird found around the world in suitable habitats.
- Countershading—A color pattern in which a bird or other animal is darker above and lighter below. The adaptive value of the pattern is its ability to help conceal the animal: a predator looking down from above sees the darker back against the dark ground; a predator looking up from below sees the lighter breast against the light sky; a predator looking from the side sees the dark back made lighter by the light from above and the light breast made darker by shading.
- **Covert**—A feather that covers the gap at the base between flight feathers of the wing and tail; coverts help create smooth wing and tail contours that make flight more efficient.
- Covey—A group of birds, often comprised of family members that remain together for periods of time; usually applied to game birds such as quail (Odontophorinae).
- **Crepuscular**—Active at dawn and at dusk.
- Crèche—An aggregation of young of many coloniallynesting birds (e.g., penguins, Spheniscidae; terns, Laridae). There is greater safety from predators in a crèche.

- **Crissum**—The undertail coverts of a bird; often distinctively colored.
- Critically Endangered—A technical category used by IUCN for a species that is at an extremely high risk of extinction in the wild in the immediate future.
- Cryptic—Hidden or concealed; i.e., well-camouflaged patterning.
- **Dichromic**—Occurring in two distinct color patterns (e.g., the bright red of male and dull red-brown of female northern cardinals, Cardinalis cardinalis)
- **Diurnal**—Active during the day.
- **Dimorphic**—Occurring in two distinct forms (e.g., in reference to the differences in tail length of male and female boat-tailed grackles, Cassidix major).
- **Disjunct**—A distribution pattern characterized by populations that are geographically separated from one another.
- Dispersal—Broadly defined: movement from an area; narrowly defined: movement from place of hatching to
- Dispersion—The pattern of spatial arrangement of individuals, populations, or other groups; no movement is implied.
- **Disruptive color**—A color pattern such as the breast bands on a killdeer (Charadrius vociferus) that breaks up the outline of the bird, making it less visible to a potential predator, when viewed from a distance
- DNA-DNA hybridization—A technique whereby the genetic similarity of different bird groups is determined based on the extent to which short stretches of their DNA, when mixed together in solution in the laboratory, are able to join with each other.
- Dominance hierarchy—"Peck order"; the social status of individuals in a group; each animal can usually dominate those animals below it in a hierarchy.
- **Dummy nest**—Sometimes called a "cock nest." An "extra" nest, often incomplete, sometimes used for roosting, built by aggressive males of polygynous birds. Dummy nests may aid in the attraction of additional mates, help define a male's territory, or confuse potential predators.
- **Dump nest**—A nest in which more than one female lays eggs. Dump nesting is a phenomenon often linked to young, inexperienced females or habitats in which nest sites are scarce. The eggs in dump nest are usually not incubated. Dump nesting may occur within a species or between species.

- **Dynamic soaring**—A type of soaring characteristic of oceanic birds such as albatrosses (Diomedeidae) in which the bird takes advantage of adjacent wind currents that are of different speeds in order to gain altitude and effortlessly stay aloft.
- **Echolocation**—A method of navigation used by some swifts (Apodidae) and oilbirds (Steatornithidae) to move in darkness, such as through caves to nesting sites. The birds emit audible "clicks" and determine pathways by using the echo of the sound from structures in the area.
- Eclipse plumage—A dull, female-like plumage of males of Northern Hemisphere ducks (Anatidae) and other birds such as house sparrows (*Passer domesticus*) typically attained in late summer prior to the annual fall molt. Ducks are flightless at this time and the eclipse plumage aids in their concealment at a time when they would be especially vulnerable to predators.
- **Ecotourism**—Travel for the primary purpose of viewing nature. Ecotourism is now "big business" and is used as a non-consumptive but financially rewarding way to protect important areas for conservation.
- **Ectoparasites**—Relative to birds, these are parasites such as feather lice and ticks that typically make their home on the skin or feathers.
- Emarginate—Adjective referring to the tail of a bird that it notched or forked or otherwise has an irregular margin as a result of tail feathers (rectrices) being of different lengths. Sometimes refers to individual flight feather that is particularly narrowed at the tip.
- **Endangered**—A term used by IUCN and also under the Endangered Species Act of 1973 in the United States in reference to a species that is threatened with imminent extinction or extirpation over all or a significant portion of its range.
- Endemic—Native to only one specific area.
- **Eocene**—Geological time period; subdivision of the Tertiary, from about 55.5 to 33.7 million years ago.
- Erythrocytes—Red blood cells; in birds, unlike mammals, these retain a nucleus and are longer lived. Songbirds tend to have smaller, more numerous (per volume) erythrocytes that are richer in hemoglobin than are the erythrocytes of more primitive birds.
- Ethology—The study of animal behavior.
- Exotic—Not native.
- Extant—Still in existence; not destroyed, lost, or extinct.
- Extinct—Refers to a species that no longer survives anywhere.

- **Extirpated**—Referring to a local extinction of a species that can still be found elsewhere.
- Extra-pair copulation—In a monogamous species, refers to any mating that occurs between unpaired males and females.
- **Facial disc**—Concave arrangement of feathers on the face of an owl. The facial discs on an owl serve as sound parabolas, focusing sound into the ears around which the facial discs are centered, thus enhancing their hearing.
- **Fecal sac**—Nestling songbirds (Passeriformes) and closely related groups void their excrement in "packages"—enclosed in thin membranes—allowing parents to remove the material from the nest. Removal of fecal material likely reduces the potential for attraction of predators.
- **Feminization**—A process, often resulting from exposure to environmental contaminants, in which males produce a higher levels of female hormones (or lower male hormone levels), and exhibit female behavioral or physiological traits.
- **Feral**—Gone wild; i.e., human-aided establishment of nonnative species.
- **Fledge**—The act of a juvenile making its first flight; sometimes generally used to refer to a juvenile becoming independent.
- Fledgling—A juvenile that has recently fledged. An emphasis should be placed on "recently." A fledgling generally lacks in motor skills and knowledge of its habitat and fledglings are very vulnerable, hence under considerable parental care. Within a matter of a few days, however, they gain skills and knowledge and less parental care is needed.
- Flight feathers—The major feathers of the wing and tail that are crucial to flight. (See Primary, Secondary, Tertial, Alula, Remex, Rectrix)
- Flyway—A major pathway used by a group of birds during migration. The flyway concept was developed primarily with regard to North American waterfowl (Anatidae) and has been used by government agencies in waterfowl management. Major flyways described include the Atlantic, Mississippi, Central, and Pacific flyways. While the flyway concept is often used in discussions of other groups of birds, even for waterfowl the concept is an oversimplification. The patterns of movements of migrant waterfowl and other birds vary greatly among species.
- Frugivorous—Feeds on fruit.
- Galliform—Chicken-like, a member of the Galliformes.

Gape—The opening of the mouth of a bird; the act of opening the mouth, as in begging.

Gizzard—The conspicuous, muscular portion of the stomach of a bird. Birds may swallow grit or retain bits of bone or hard parts of arthropods in the gizzard and these function in a manner analogous to teeth as the strong muscles of the gizzard contract, thus breaking food into smaller particles. The gizzard is best developed in birds that eat seeds and other plant parts; in some fruit-eating birds the gizzard is very poorly developed.

Glareolid—A member of the family Glareolidae.

Gloger's rule—Gloger's rule is an ecogeographic generalization that suggests that within a species or closely related group of birds there is more melanin (a dark pigment) in feathers in warm humid parts of the species' or groups' range, and less melanin in feathers in dry or cooler parts of the range.

Gorget—Colorful throat patch or bib (e.g., of many hummingbirds, Trochilidae).

Graduated—An adjective used to describe the tail of a bird in which the central rectrices are longest and those to the outside are increasingly shorter.

Granivorous—Feeding on seeds.

Gregarious—Occurring in large groups.

Gular—The throat region.

Hallux—The innermost digit of a hind or lower limb.

Hawk—Noun: a member of the family Accipitridae. Verb: catching insects by flying around with the mouth open (e.g. swallows, Hirundinidae; nightjars, Caprimulgidae).

Heterospecific colony—A colony of birds with two or more species.

Heterothermy—In birds, the ability to go into a state of torpor or even hibernation, lowering body temperature through reduced metabolic activity and thus conserving energy resources during periods of inclement weather or low food.

Hibernation—A deep state of reduced metabolic activity and lowered body temperature that may last for weeks; attained by few birds, resulting from reduced food supplies and cool or cold weather.

Holarctic—The Palearctic and Nearctic bigeographic regions combined.

Homeothermy—In birds the metabolic ability to maintain a constant body temperature. The lack of development of homeothermy in new-hatched chicks is the underlying need for brooding behavior.

Hover-dip—A method of foraging involving hovering low over the water, and then dipping forward to pick up prey from the surface (e.g., many herons, Ardeidae).

Hybrid—The offspring resulting from a cross between two different species (or sometimes between distinctive subspecies).

Imprinting—A process that begins with an innate response of a chick to its parent or some other animal (or object!) that displays the appropriate stimulus to elicit the chick's response. The process continues with the chick rapidly learning to recognize its parents. Imprinting typically occurs within a few hours (often 13–16 hours) after hatching. Imprinting then leads to learning behavioral characteristics that facilitate its survival, including such things as choice of foraging sites and foods, shelter, recognition of danger, and identification of a potential mate. The most elaborate (and best studied) imprinting is associated with precocial chicks such as waterfowl (Anatidae).

Incubation patch—See Brood patch.

Indigenous—See Endemic.

Innate—An inherited characteristic; e.g., see Imprinting.

Insectivorous—In ornithology technically refers to a bird that eats insects; generally refers to in birds that feed primarily on insects and other arthropods.

Introduced species—An animal or plant that has been introduced to an area where it normally does not occur.

Iridescent—Showing a rainbow-like play of color caused by differential refraction of light waves that change as the angle of view changes. The iridescence of bird feathers is a result of a thinly laminated structure in the barbules of those feathers. Iridescent feathers are made more brilliant by pigments that underlie this structure, but the pigments do not cause the iridescence.

Irruptive—A species of bird that is characterized by irregular long-distance movements, often in response to a fluctuating food supply (e.g., red crossbill, *Loxia curvirostra*, Fringillidae; snowy owl, *Nyctea scandiaca*, Strigidae).

IUCN—The World Conservation Union; formerly the International Union for the Conservation of Nature, hence IUCN. It is the largest consortium of governmental and nongovernmental organizations focused on conservation issues.

- **Juvenal**—In ornithology (contrary to most dictionaries), restricted to use as an adjective referring to a characteristic (usually the plumage) of a juvenile bird.
- Juvenile—A young bird, typically one that has left the nest.
- **Kleptoparasitism**—Behavior in which one individual takes ("steals") food, nest materials, or a nest site from another.
- **Lachrymal**—Part of the skull cranium, near the orbit; lachrymal and Harderian glands in this region lubricate and protect the surface of the eye.
- Lamellae—Transverse tooth-like or comb-like ridges inside the cutting edge of the bill of birds such as ducks (Anatidae) and flamingos (Phoenicopteridae). Lamellae serve as a sieve during feeding: the bird takes material into its mouth, then uses its tongue to force water out through the lamellae, while retaining food particles.
- **Lek**—A loose to tight association of several males vying for females through elaborate display; lek also refers to the specific site where these males gather to display. Lek species include such birds as prairie chickens (Phasianidae) and manakins (Pipridae).
- **Lobed feet**—Feet that have toes with stiff scale-covered flaps that extend to provide a surface analogous to webbing on a duck as an aid in swimming.
- Lore—The space between the eye and bill in a bird. The loral region often differs in color from adjacent areas of a bird's face. In some species the area is darker, thus helping to reduce glare, serving the same function as the dark pigment some football players apply beneath each eye. In predatory birds, a dark line may extend from the eye to the bill, perhaps decreasing glare, but also serving as a sight to better aim its bill. The color and pattern of plumage and skin in the loral region is species-specific and often of use in helping birders identify a bird.
- Malar—Referring to the region of the face extending from near the bill to below the eye; markings in the region are often referred to as "moustache" stripes.
- Mandible—Technically the lower half of a bird's bill. The plural, mandibles, is used to refer to both the upper and lower bill. The upper half of a bird's bill is technically the maxilla, but often called the "upper mandible."
- Mantle—Noun: The plumage of the back of the bird, including wing coverts evident in the back region on top of the folded wing (especially used in describing hawks (Accipitridae) and gulls (Laridae). Verb: The behavior in which a raptor (typically on the ground) shields its acquired prey to protect it from other predators.

- **Mesoptile**—On chicks, the second down feathers; these grow attached to the initial down, or protoptile.
- Metabolic rate—The rate of chemical processes in living organisms, resulting in energy expenditure and growth. Hummingbirds (Trochilidae), for example, have a very high metabolic rate. Metabolic rate decreases when a bird is resting and increases during activity.
- **Miocene**—The geological time period that lasted from about 23.8 to 5.6 million years ago.
- **Migration**—A two-way movement in birds, often dramatically seasonal. Typically latitudinal, though in some species is altitudinal or longitudinal. May be short-distance or long-distance. (See Dispersal)
- Mitochondrial DNA—Genetic material located in the mitochondria (a cellular organelle outside of the nucleus). During fertilization of an egg, only the DNA from the nucleus of a sperm combines with the DNA from the nucleus of an egg. The mitochondrial DNA of each offspring is inherited only from its mother. Changes in mitochondrial DNA occur quickly through mutation and studying differences in mitochondrial DNA helps scientists better understand relationships among groups.
- Mobbing—A defensive behavior in which one or more birds of the same or different species fly toward a potential predator, such as a hawk, owl, snake, or a mammal, swooping toward it repeatedly in a threatening manner, usually without actually striking the predator. Most predators depend on the element of surprise in capturing their prey and avoid the expenditure of energy associated with a chase. Mobbing alerts all in the neighborhood that a potential predator is at hand and the predator often moves on. Rarely, a predator will capture a bird that is mobbing it.
- **Molecular phylogenetics**—The use of molecular (usually genetic) techniques to study evolutionary relationships between or among different groups of organisms.
- Molt—The systematic and periodic loss and replacement of feathers. Once grown, feathers are dead structures that continually wear. Birds typically undergo a complete or near-complete molt each year and during this molt feathers are usually lost and replaced with synchrony between right and left sides of the body, and gradually, so that the bird retains the ability to fly. Some species, such as northern hemisphere ducks, molt all of their flight feathers at once, thus become flightless for a short time. Partial molts, typically involving only contour feathers, may occur prior to the breeding season.
- **Monophyletic**—A group (or clade) that shares a common ancestor.

- **Monotypic**—A taxonomic category that includes only one form (e.g., a genus that includes only one species; a species that includes no subspecies).
- **Montane**—Of or inhabiting the biogeographic zone of relatively moist, cool upland slopes below timberline dominated by large coniferous trees.
- Morphology—The form and structure of animals and plants.
- Mutualism—Ecological relationship between two species in which both gain benefit.
- Nail—The horny tip on the leathery bill of ducks, geese, and swans (Anatidae).
- Nectarivore—A nectar-eater (e.g., hummingbirds, Trochilidae; Hawaiian honeycreepers, Drepaniidae).
- **Near Threatened**—A category defined by the IUCN suggesting possible risk of extinction in the medium term future.
- **Nearctic**—The biogeographic region that includes temperate North America faunal region.
- **Neotropical**—The biogeographic region that includes South and Central America, the West Indies, and tropical Mexico.
- **Nestling**—A young bird that stays in the nest and needs care from parents.
- **New World**—A general descriptive term encompassing the Nearctic and Neotropical biogeographic regions.
- Niche—The role of an organism in its environment; multidimensional, with habitat and behavioral components.
- Nictitating membrane—The third eyelid of birds; may be transparent or opaque; lies under the upper and lower eyelids. When not in use, the nictitating membrane is held at the corner of the eye closest to the bill; in use it moves horizontally or diagonally across the eye. In flight it keeps the bird's eyes from drying out; some aquatic birds have a lens-like window in the nictitating membrane, facilitating vision underwater.
- **Nidicolous**—An adjective describing young that remain in the nest after hatching until grown or nearly grown.
- **Nidifugous**—An adjective describing young birds that leave the nest soon after hatching.
- **Nocturnal**—Active at night.
- **Nominate subspecies**—The subspecies described to represent its species, the first described, bearing the specific name.

- **Nuclear DNA**—Genetic material from the nucleus of a cell from any part of a bird's body other than its reproductive cells (eggs or sperm).
- **Nuptial displays**—Behavioral displays associated with courtship.
- **Oligocene**—The geologic time period occurring from about 33.7 to 23.8 million years ago.
- Old World—A general term that usually describes a species or group as being from Eurasia or Africa.
- Omnivorous—Feeding on a broad range of foods, both plant and animal matter.
- Oscine—A songbird that is in the suborder Passeri, order Passeriformes; their several distinct pairs of muscles within the syrinx allow these birds to produce the diversity of sounds that give meaning to the term "songbird."
- **Osteological**—Pertaining to the bony skeleton.
- Palearctic—A biogeographic region that includes temperate Eurasia and Africa north of the Sahara.
- **Paleocene**—Geological period, subdivision of the Tertiary, from 65 to 55.5 million years ago.
- **Pamprodactyl**—The arrangement of toes on a bird's foot in which all four toes are pointed forward; characteristic of swifts (Apodidae).
- **Parallaxis**—Comparing the difference in timing and intensity of sounds reaching each ear (in owls).
- Passerine—A songbird; a member of the order Passeriformes.
- **Pecten**—A comb-like structure in the eye of birds and reptiles, consisting of a network of blood vessels projecting inwards from the retina. The main function of the pecten seems to be to provide oxygen to the tissues of the eye.
- **Pectinate**—Having a toothed edge like that of a comb. A pectinate claw on the middle toe is a characteristic of nightjars, herons, and barn owls. Also known as a "feather comb" since the pectinate claw is used in preening.
- **Pelagic**—An adjective used to indicate a relationship to the open sea.
- **Phalloid organ**—Penis-like structure on the belly of buffalo weavers; a solid rod, not connected to reproductive or excretory system.

Philopatry—Literally "love of homeland"; a bird that is philopatric is one that typically returns to nest in the same area in which it was hatched. Strongly philopatric species (e.g., hairy woodpecker, *Picoides borealis*) tend to accumulate genetic characteristics that adapt them to local conditions, hence come to show considerable geographic variation; those species that show little philopatry tend to show little geographic variation.

Phylogenetics—The study of racial evolution.

Phylogeny—A grouping of taxa based on evolutionary history.

Picid—A member of the family Picide (woodpeckers, wrynecks, piculets).

Piscivorous—Fish-eating.

Pleistocene—In general, the time of the great ice ages; geological period variously considered to include the last 1 to 1.8 million years.

Pliocene—The geological period preceding the Pleistocence; the last subdivision of what is known as the Tertiary; lasted from 5.5 to 1.8 million years ago.

Plumage—The complete set of feathers that a bird has.

Plunge-diving—A method of foraging whereby the bird plunges from at least several feet up, head-first into the water, seizes its prey, and quickly takes to the wing (e.g., terns, Laridae; gannets, Sulidae).

Polygamy—A breeding system in which either or both male and female may have two or more mates.

Polyandry—A breeding system in which one female bird mates with two or more males. Polyandry is relatively rare among birds.

Polygyny—A breeding system in which one male bird mates with two or more females.

Polyphyletic—A taxonomic group that is believed to have originated from more than one group of ancestors.

Powder down—Specialized feathers that grow continuously and break down into a fine powder. In some groups (e.g., herons, Ardeidae) powder downs occur in discrete patches (on the breast and flanks); in others (e.g., parrots, Psitacidae) they are scattered throughout the plumage. Usually used to waterproof the other feathers (especially in birds with few or no oil glands).

Precocial—An adjective used to describe chicks that hatch in an advanced state of development such that they generally can leave the nest quickly and obtain their own food, although they are often led to food, guarded, and brooded by a parent (e.g., plovers, Charadriidae; chicken-like birds, Galliformes).

Preen—A verb used to describe the behavior of a bird when it cleans and straightens its feathers, generally with the bill.

Primaries—Unusually strong feathers, usually numbering nine or ten, attached to the fused bones of the hand at the tip of a bird's wing.

Protoptile—The initial down on chicks.

Pterylosis—The arrangement of feathers on a bird.

Quaternary—The geological period, from 1.8 million years ago to the present, usually including two subdivisions: the Pleistocene, and the Holocene.

Quill—An old term that generally refers to a primary feather.

Rachis—The shaft of a feather.

Radiation—The diversification of an ancestral species into many distinct species as they adapt to different environments.

Ratite—Any of the ostrich-like birds; characteristically lack a keel on the sternum (breastbone).

Rectrix (pl. rectrices)—A tail feather of a bird; the rectrices are attached to the fused vertebrae that form a bird's bony tail.

Remex (pl. remiges)—A flight feather of the wing; remiges include the primaries, secondaries, tertials, and alula).

Reproductive longevity—The length of a bird's life over which it is capable of reproduction.

Resident—Nonmigratory.

Rhampotheca—The horny covering of a bird's bill.

Rictal bristle— A specialized tactile, stiff, hairlike feather with elongated, tapering shaft, sometimes with short barbs at the base. Rictal bristles prominently surround the mouth of birds such as many nightjars (Caprimulgidae), New World flycatchers (Tyrannidae), swallows (Hirundinidae), hawks (Accipitridae) and owls (Strigidae). They are occasionally, but less precisely referred to as "vibrissae," a term more appropriate to the "whiskers" on a mammal.

Rookery—Originally a place where rooks nest; now a term often used to refer to a breeding colony of gregarious birds.

- **Sally**—A feeding technique that involves a short flight from a perch or from the ground to catch a prey item before returning to a perch.
- **Salt gland**—Also nasal gland because of their association with the nostrils; a gland capable of concentrating and excreting salt, thus allowing birds to drink saltwater. These glands are best developed in marine birds.
- **Scapulars**—Feathers at sides of shoulders.
- **Schemochrome**—A structural color such as blue or iridescence; such colors result from the structure of the feather rather than from the presence of a pigment.
- **Scutellation**—An arrangement or a covering of scales, as that on a bird's leg.
- **Secondaries**—Major flight feathers of the wing that are attached to the ulna.
- **Sexual dichromatism**—Male and female differ in color pattern (e.g., male hairy woodpecker [*Picoides villosus*, Picidae] has a red band on the back of the head, female has no red).
- **Sexual dimorphism**—Male and female differ in morphology, such as size, feather size or shape, or bill size or shape.
- Sibling species—Two or more species that are very closely related, presumably having differentiated from a common ancestor in the recent past; often difficult to distinguish, often interspecifically territorial.
- **Skimming**—A method of foraging whereby the skimmers (Rhynchopidae) fly low over the water with the bottom bill slicing through the water and the tip of the bill above. When the bird hits a fish, the top bill snaps shut.
- **Slotting**—Abrupt narrowing of the inner vane at the tip of some outer primaries on birds that soar; slotting breaks up wing-tip turbulence, thus facilitating soaring.
- **Sonagram**—A graphic representation of sound.
- **Speciation**—The evolution of new species.
- **Speculum**—Colored patch on the wing, typically the secondaries, of many ducks (Anatidae).
- **Spur**—A horny projection with a bony core found on the tarsometatarsus.
- Sternum—Breastbone.
- Structural color—See Schemochrome.

- **Suboscine** A songbird in the suborder Passeri, order Passeriformes, whose songs are thought to be innate, rather than learned.
- **Sympatric**—Inhabiting the same range.
- **Syndactyl**—Describes a condition of the foot of birds in which two toes are fused near the base for part of their length (e.g., kingfishers, Alcedinidae; hornbills, Bucerotidae.
- **Synsacrum**—The expanded and elongated pelvis of birds that is fused with the lower vertebrae.
- Syrinx (pl. syringes)—The "voice box" of a bird; a structure of cartilage and muscle located at the junction of the trachea and bronchi, lower on the trachea than the larynx of mammals. The number and complexity of muscles in the syrinx vary among groups of birds and have been of value in determining relationships among groups.
- **Systematist**—A specialist in the classification of organisms; systematists strive to classify organisms on the basis of their evolutionary relationships.
- Tarsus—In ornithology also sometimes called Tarsometatarsus or Metatarsus; the straight part of a bird's foot immediately above its toes. To the non-biologist, this seems to be the "leg" bone—leading to the notion that a bird's "knee" bends backwards. It does not. The joint at the top of the Tarsometatarsus is the "heel" joint, where the Tarsometarsus meets the Tibiotarsus. The "knee" joint is between the Tibiotarsus and Femur.
- **Taxon (pl. taxa)**—Any unit of scientific classification (e.g., species, genus, family, order).
- Taxonomist— A specialist in the naming and classification of organisms. (See also Systematist. Taxonomy is the older science of naming things; identification of evolutionary relationships has not always been the goal of taxonomists. The modern science of Systematics generally incorporates taxonomy with the search for evolutionary relationships.)
- **Taxonomy**—The science of identifying, naming, and classifying organisms into groups.
- **Teleoptiles**—Juvenal feathers.
- Territory—Any defended area. Typically birds defend a territory with sound such as song or drumming. Territorial defense is typically male against male, female against female, and within a species or between sibling species. Area defended varies greatly among taxa, seasons, and habitats. A territory may include the entire home range, only the area immediately around a nest, or only a feeding or roosting area.

- **Tertiary**—The geological period including most of the Cenozoic; from about 65 to 1.8 million years ago.
- **Tertial**—A flight feather of the wing that is loosely associated with the humerus; tertials fill the gap between the secondary feathers and the body.
- Thermoregulation—The ability to regulate body temperature; can be either behavioral or physiological. Birds can regulate body temperature by sunning or moving to shade or water, but also generally regulate their body temperature through metabolic processes. Baby birds initially have poor thermoregulatory abilities and thus must be brooded.
- **Threatened**—A category defined by IUCN and by the Endangered Species Act of 1973 in the United States to refer to a species that is at risk of becoming endangered.
- **Tomium (pl. tomia)**—The cutting edges of a bird's bill.
- **Torpor**—A period of reduced metabolic activity and lowered body temperature; often results from reduced availability of food or inclement weather; generally lasts for only a few hours (e.g., hummingbirds, Trochilidae; swifts, Apodidae).
- **Totipalmate**—All toes joined by webs, a characteristic that identifies members of the order Pelecaniformes.
- **Tribe**—A unit of classification below the subfamily and above the genus.
- Tubercle—A knob- or wart-like projection.
- Urohydrosis—A behavior characteristic of storks and New World vultures (Ciconiiformes) wherein these birds excrete on their legs and make use of the evaporation of the water from the excrement as an evaporative cooling mechanism.

- **Uropygial gland**—A large gland resting atop the last fused vertebrae of birds at the base of a bird's tail; also known as oil gland or preen gland; secretes an oil used in preening.
- **Vane**—The combined barbs that form a strong, yet flexible surface extending from the rachis of a feather.
- Vaned feather—Any feather with vanes.
- Viable population—A population that is capable of maintaining itself over a period of time. One of the major conservation issues of the twenty-first century is determining what is a minimum viable population size. Population geneticists have generally come up with estimates of about 500 breeding pairs.
- Vibrissae—See Rictal bristle.
- **Vulnerable**—A category defined by IUCN as a species that is not Critically Endangered or Endangered, but is still facing a threat of extinction.
- Wallacea—The area of Indonesia transition between the Oriental and Australian biogeographical realms, named after Alfred Russell Wallace, who intensively studied this area.
- **Wattles**—Sexual ornamentation that usually consists of flaps of skin on or near the base of the bill.
- Zoogeographic region—See Biogeographic region.
- **Zygodactyl**—Adjective referring to the arrangement of toes on a bird in which two toes project forward and two to the back.

Compiled by Jerome A. Jackson, PhD

Aves species list

Struthioniformes [Order]	C. strigulosus	D. melanophrys
Struthionidae [Family]	C. duidae	D. cauta
Struthio [Genus]	C. erythropus	D. chrysostoma
S. camelus [Species]	C. noctivagus	D. chlororhynchos
-	C. atrocapillus	D. bulleri
Rheidae [Family]	C. cinnamomeus	Phoebetria [Genus]
Rhea [Genus]	C. boucardi	P. fusca [Species]
R. Americana [Species]	C. kerriae	P. palpebrata
Pterocnemia [Genus]	C. variegatus	Macronectes [Genus]
P. pennata [Species]	C. brevirostris	M. giganteus [Species]
C	C. bartletti	M. halli
Casuaridae [Family]	C. parvirostris	Fulmarus [Genus]
Casuarius [Genus]	C. casiquiare	F. glacialoides [Species]
C. bennetti [Species]	C. tataupa	F. glacialis
C. casuarius	Rhynchotus [Genus]	Thalassoica [Genus]
C. unappendiculatus	R. rufescens [Species]	T. antarctica [Species]
Dromaiidae [Family]	Nothoprocta [Genus]	Daption [Genus]
Dromaius [Genus]	N. taczanowski [Species]	D. capense [Species]
D. novaehollandiae [Species]	N. kalinowskii	Pagodroma [Genus]
D. diemenianus	N. omata	P. nivea [Species]
D. atementanus		Pterodroma [Genus]
Apterygidae [Family]	N. perdicaria	P. macroptera [Species]
Apteryx [Genus]	N. cinerascens	P. lessonii
A. australis [Species]	N. pentlandii	P. incerta
A. owenii	N. curvirostris	P. solandri
A. haastii	Nothura [Genus]	P. magentae
11. 150005000	N. boraquira [Species]	P. rostrata
Tinamiiformes [Order]	N. minor	P. macgillivrayi
Tinamidae [Family]	N. darwinii	P. neglecta
Tinamus [Genus]	N. maculosa	P. arminjoniana
T. tao [Species]	Taoniscus [Genus]	P. alba
T. solitarius	T. nanus [Species]	P. ultima
T. $osgoodi$	Eudromia [Genus]	P. brevirostris
T. major	E. elegans [Species]	P. mollis
T. guttatus	E. formosa	P. inexpectata
Nothocercus [Genus]	Tinamotis [Genus]	P. cahow
N. bonapartei [Species]	T. pentlandii [Species]	P. hasitata
N. julius	T. ingoufi	P. externa
N. nigrocapillus	D 11 'C (O.1.1	P. baraui
Crypturellus [Genus]	Procellariformes [Order]	
C. berlepschi [Species]	Diomedidae [Family]	P. phaeopygia
	Diomedea [Genus]	P. hypoleuca
C. cinereus	D. exulans [Species]	P. nigripennis
C. soui	D. epomophora	P. axillaris
C. ptaritepui	D. irrorata	P. cookii
C. obsoletus	D. albatrus	P. defilippiana
C. undulatus	D. nigripes	P. longirostris
C. transfasciatus	D. immutabilis	P. leucoptera

Halobaena [Genus]	O. hornbyi	P. auritus
H. caerulea	O. furcata	P. grisegena
Pachyptila [Genus]	Pelecanoides [Genus]	P. cristatus
P. vittata [Species]	P. garnotii [Species]	P. nigricollis
P. desolata	P. magellani	P. occipitalis
P. belcheri	P. georgicus	P. taczanowskii
P. turtur	P. urinator	P. gallardoi
	1. urmutor	
P. crassirostris	Sphenisciformes [Order]	Aechmophorus [Genus]
Bulweria [Genus]	Spheniscidae [Family]	A. occidentalis [Species]
B. bulwerii [Species]	Aptenodytes [Genus]	Pelecaniformes [Order]
B. fallax	A. patagonicus [Species]	Phaethontidae [Family]
Procellaria [Genus]	A. forsteri	Phaethon [Genus]
P. aequinoctialis [Species]	·	P. aethereus [Species]
P. westlandica	Pygoscelis [Genus]	P. rubricauda
P. parkinsoni	P. papua [Species]	
P. cinerea	P. adeliae	P. lepturus
Calonectris [Genus]	P. antarctica	Fregatidae [Family]
C. diomedea [Species]	Eudyptes [Genus]	Fregata [Genus]
C. leucomelas	E. chrysocome [Species]	F. magnificens [Species]
Puffinus [Genus]	E. pachyrhynchus	F. minor
P. pacificus [Species]	E. robustus	F. ariel
P. bulleri	E. sclateri	
	E. chryoslophus	F. andrewsi
P. carneipes	Megadyptes [Genus]	Phalacrocoracidae [Family]
P. creatopus	M. antipodes [Species]	Phalacrocorax [Genus]
P. gravis	Eudyptula [Genus]	P. carbo [Species]
P. griseus	E. minor [Species]	P. capillatus
P. tenuirostris	Spheniscus [Genus]	
P. nativitatis	S. demersus [Species]	P. nigrogularis P. varius
P. puffinus	S. humboldti	
P. gavia		P. harrisi
P. huttoni	S. magellanicus S. mendiculus	P. auritus
P. lherminieri	S. menawuus	P. olivaceous
P. assimilis	Gaviiformes [Order]	P. fuscicollis
Oceanites [Genus]		P. sulcirostris
O. oceanicus [Species]	Gaviidae [Family]	P. penicillatus
O. gracilis	Gavia [Genus]	P. capensis
Garrodia [Genus]	G. stellata [Species]	P. neglectus
G. nereis [Species]	G. arctica	P. punctatus
Pelagodroma [Genus]	G. immer	P. aristotelis
P. marina [Species]	G. adamsii	P. perspicillatus
Fregetta [Genus]		P. urile
	Podicipediformes [Order]	P. pelagicus
F. tropica [Species]	D. 11.1 11.1 IE 11.1	P. gaimardi
F. grallaria	Podicipedidae [Family]	P. magellanicus
Nesofregetta [Genus]	Rollandia [Genus]	P. bouganvillii
N. fuliginosa [Species]	R. rolland [Species]	P. atriceps
Hydrobates [Genus]	R. microptera	P. albiventer
H. pelagicus [Species]	Tachybaptus [Genus]	P. carunculatus
Halocyptena [Genus]	T. novaehollandiae [Species]	P. campbelli
H. microsoma [Species]	T. ruficollis	P. fuscescens
Oceanodroma [Genus]	T. rufolavatus	P. melanoleucos
O. tethys [Species]	T. pelzelnii	P. niger
O. castro	T. dominicus	
O. monorhis	Podilymbus [Genus]	P. pygmaeus P. africanus
O. leucorhoa	P. podiceps [Species]	
O. macrodactyla	P. gigas	Anhinga [Genus]
O. markhami	Poliocephalus [Genus]	A. anhinga [Species]
O. tristami	P. poliocephalus [Species]	A. melanogaster
O. melania	P. rufopectus	Sulidae [Family]
O. matsudairae	Podiceps [Genus]	Sula [Genus]
O. homochroa	P. major [Species]	S. bassana [Species]
J. DUILDOWI ON	1. major [opecies]	o. viissiiiii [opecies]

	4	
S. capensis	Agamia [Genus]	Leptoptilos [Genus]
S. serrator	A. agami [Species]	L. javanicus [Species]
S. nebouxii	Nyctanassa [Genus]	L. dubius
S. variegata	N. violacea [Species]	L. crumeniferus
S. dactylatra	Nycticorax [Genus]	Balaenicipitidae [Family]
S. sula	N. nycticorax [Species] N. caledonicus	Balaeniceps [Genus]
S. leucogaster	N. leuconotus	B. rex [Species]
S. abbotti	N. magnificus	•
Pelecanidae [Family]	N. goisagi	Threskiornithidae [Family]
Pelecanus [Genus]	N. melanolophus	Eudocimus [Genus]
P. onocrotalus [Species]	Cochlearius [Genus]	E. albus [Species]
P. rufescens	C. cochlearius [Species]	E. ruber
P. philippensis	Tigrisoma [Genus]	Phimosus [Genus]
P. conspicillatus	T. mexicanum [Species]	P. infuscatus [Species]
P. erythrorhynchos	T. fasciatum	Plegadis [Genus]
P. occidentalis	T. lineatum	P. falcinellus [Species] P. chihi
	Zonerdius [Genus]	P. ridgwayi
Ciconiiformes [Order]	Z. heliosylus [Species]	Cercibis [Genus]
Ardeidae [Family]	Tigriornis [Genus]	C. oxycerca [Species]
Syrigma [Genus]	T. leucolophus [Species]	Theristicus [Genus]
S. sibilatrix [Species]	Zebrilus [Genus]	T. caerulescens [Species]
Pilherodius [Genus]	Z. undulatus [Species]	T. caudatus
P. pileatus [Species]	Ixobrychus [Genus]	T. melanopsis
Ardea [Genus]	I. involucris [Species]	Mesembrinibis [Genus]
A. cinerea [Species]	I. exilis	M. cayennensis [Species]
A. herodias	I. minutus	Bostrychia [Genus]
A. cocoi	1. sinensis	B. hagedash [Species]
A. pacifica	I. eurhythmus	B. carunculata
A. melanocephala	1. cinnamomeus	B. olivacea
A. hombloti	I. sturmii	B. rara
A. imperialis	I. flavicollis	Lophotibis [Genus]
A. sumatrana	Botaurus [Genus]	L. cristata [Species]
A. goliath	B. pinnatus [Species]	Threskiornis [Genus]
A. purpurea	B. lentiginosus B. stellaris	T. aethiopicus [Species]
A. alba	B. poiciloptilus	T. spinicollis
Egretta [Genus]	B. poictiopitius	Geronticus [Genus]
E. rufescens [Species]	Scopidae [Family]	G. eremita [Species]
E. picata	Scopus [Genus]	G. calvus
E. vinaceigula	S. umbretta [Species]	Pseudibis [Genus]
E. ardesiaca	Ciconiidoo [Family]	P. papillosa [Species]
E. tricolor	Ciconiidae [Family] <i>Mycteria</i> [Genus]	P. gigantea
E. intermedia	M. americana [Species]	Nipponia [Genus]
E. ibis	M. cinerea	N. nippon [Species]
E. novaehollandiae	M. ibis	Platalea [Genus]
E. caerulea	M. leucocephala	P. leucocorodia [Species]
E. thula	Anastomus [Genus]	P. minor
E. garzetta	A. oscitans [Species]	P. alba
E. gularis	A. lamelligerus	P. flavipes
E. dimorpha	Ciconia [Genus]	P. ajaja
E. eulophotes	C. nigra [Species]	Phoenicopteriformes [Order]
E. sacra	C. abdimii	Phoenicopteridae [Family]
Ardeola [Genus]	C. episcopus	Phoenicopterus [Genus]
A. ralloides [Species]	C. maguari	P. ruber [Species]
A. grayii	C. ciconia	P. chilensis
A. bacchus	Ephippiorhynchus [Genus]	Phoeniconaias [Genus]
A. speciosa	E. asiaticus [Species]	P. minor [Species]
A. idae	E. senegalensis	Phoenicoparrus [Genus]
A. rufiventris	Jabiru [Genus]	P. andinus [Species]
A. striata	J. mycteria [Species]	P. jamesii

Falconiformes [Order] Milvus [Genus] C. macrourus Cathartidae [Family] M. milvus [Species] C. melanoleucos Coragyps [Genus] M. migrans C. pygargus C. atratus [Species] Haliastur [Genus] C. ranivorus H. sphenurus [Species] C. aeruginosus Cathartes [Genus] C. burrovianus [Species] H. indus C. spilonotus Haliaeetus [Genus] C. approximans C. melambrotus Gymnogyps [Genus] H. leucogaster [Species] C. maillardi H. sanfordi C. buffoni G. californianus [Species] H. vocifer Melierax [Genus] Vultur [Genus] V. gryphus [Species] H. vociferoides M. gabar [Species] Sarcoramphus [Genus] H. leucoryphus M. metabates S. papa [Species] H. albicilla M. canorus H. leucocephalus Accipiter [Genus] Accipitridae [Family] H. pelagicus A. poliogaster [Species] Pandion [Genus] Ichthyophaga [Genus] A. trivirgatus P. haliaetus [Species] I. humilis [Species] A. griseiceps Aviceda [Genus] I. ichthyaetus A. tachiro A. cuculoides [Species] Gypohierax [Genus] A. castanilius A. madagascariensis G. angolensis [Species] A. badius A. ierdoni Gypaetus [Genus] A. brevipes A. subcristata G. barbatus [Species] A. butleri A. leuphotes A. soloensis Neophron [Genus] Leptodon [Genus] N. percnopterus [Species] A. francesii L. cayanensis [Species] Necrosyrtes [Genus] A. trinotatus Chondrobierax [Genus] N. monachus [Species] A. fasciatus C. uncinatus [Species] Gyps [Genus] A. novaehollandiae *Henicopernis* [Genus] G. bengalensis [Species] A. melanochlamys H. longicauda [Species] G. africanus A. albogularis H. infuscata G. indicus A. rufitorques Pernis [Genus] G. rueppellii A. haplochrous P. aviporus [Species] A. henicogrammus G. himalayensis P. ptilorhynchus G. fulvus A. luteoschistaceus P. celebensis Aegypius [Genus] A. imitator Elanoides [Genus] A. monachus [Species] A. poliocephalus E. forficatus [Species] A. tracheliotus A. princeps Macheiramphus [Genus] A. occipitalis A. superciliosus M. alcinus [Species] A. calvus A. collaris Gampsonyx [Genus] Circaetus [Genus] A. erythropus G. swainsonii [Species] C. gallicus [Species] A. minullus Elanus [Genus] C. cinereus A. gularis E. leucurus [Species] C. fasciolatus A. virgatus E. caeruleus C. cinerascens A. nanus E. notatus Terathopius [Genus] A. cirrhocephalus E. scriptus T. ecaudatus [Species] A. brachyurus Chelictinia [Genus] Spilornis [Genus] A. erythrauchen C. riocourii [Species] A. rhodogaster S. cheela [Species] Rostrhamus [Genus] S. elgini A. ovampensis A. madagascariensis R. sociabilis [Species] Dryotriorchis [Genus] R. hamatus D. spectabilis [Species] A. nisus Harpagus [Genus] Eutriorchis [Genus] A. rufiventris H. bidentatus [Species] A. striatus E. astur [Species] H. diodon Polyboroides [Genus] A. bicolor Ictinia [Genus] P. typus [Species] A. cooperii I. plumbea [Species] P. radiatus A. gundlachi I. misisippiensis Circus [Genus] A. melanoleucus C. assimilis [Species] Lophoictinia [Genus] A. henstii L. isura [Species] C. maurus A. gentilis C. cyaneus Hamirostra [Genus] A. meyerianus H. melanosternon [Species] C. cinereus A. buergersi

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A. radiatus	B. hemilasius	Phalcoboenus [Genus]
A. doriae	B. regalis	P. megalopterus [Species]
Urotriorchis [Genus]	B. lagopus	P. australis
U. macrourus [Species]	B. auguralis	Polyborus [Genus]
Butastur [Genus]	B. rufofuscus	P. plancus [Species]
B. rufipennis [Species]	Morphnus [Genus]	Milvago [Genus]
B. liventer	M. guianensis [Species]	M. chimachima [Species]
B. teesa	Harpia [Genus]	M. chimango
B. indicus	H. harpyja [Species]	Herpetotheres [Genus]
Kaupifalco [Genus]	Pithecophaga [Genus]	H. cachinnans [Species]
K. monogrammicus [Species]	P. jeffreyi [Species]	Micrastur [Genus]
Geranospiza [Genus]	Ictinaetus [Genus]	M. ruficollis [Species]
G. caerulescens [Species]	I. malayensis [Species]	M. gilvicollis
Leucopternis [Genus]	Aquila [Genus]	M. mirandollei
L. schistacea [Species]	A. pomarina [Species]	M. semitorquatus
L. plumbea	A. clanga	M. buckleyî
L. princeps	A. rapax	Spiziapteryx [Genus]
L. melanops	A. heliaca	S. circumcinctus [Species]
L. kuhli	A. wahlbergi	Polihierax [Genus]
L. lacernulata	A. gurneyi	P. semitorquatus [Species]
L. semiplumbea	A. chrysaetos	P. insignis
L. albicollis	A. audax	Microhierax [Genus]
L. polionota	A. verreauxii	M. caerulescens [Species]
Asturina [Genus]	Hieraaetus [Genus]	M fringillarius
A. nitida [Species]	H. fasciatus [Species]	M. latifrons
Buteogallus [Genus]	H. spilogaster	M. erythrogerys
B. aequinoctialis [Species]	H. pennatus	M. melanoleucus
B. subtilis	H. morphnoides	Falco [Genus]
B. anthracinus	H. dubius	F. berigora [Species]
B. urubitinga	11. auvius H. kienerii	F. naumanni
B. meridionalis		F. sparverius
Parabuteo [Genus]	Spizastur [Genus]	F. tinnunculus
P. unicinctus [Species]	S. melanoleucus [Species]	F. newtoni
Busarellus [Genus]	Lophaetus [Genus]	F. punctatus
B. nigricollis [Species]	L. occipitalis [Species]	F. araea
Geranoaetus [Genus]	Spizaetus [Genus]	F. moluccensis
G. melanoleucus [Species]	S. africanus [Species]	F. cenchroides
Harpyhaliaetus [Genus]	S. cirrhatus	F. rupicoloides
H. solitarius [Species]	S. nipalensis	F. alopex
H. coronatus	S. bertelsi	F. ardosiaceus
Buteo [Genus]	S. lanceolatus	F. dickinsoni
B. magnirostris [Species]	S. philippensis	F. zoniventris
B. leucorrhous	S. alboniger	F. chicquera
B. ridgwayi	S. nanus	F. vespertinus
B. lineatus	S. tyrannus	F. amurensis
B. platypterus	S. ornatus	F. eleonorae
B. brachyurus	Stephanoaetus [Genus]	F. concolor
B. swainsoni	S. coronatus [Species]	F. femoralis
B. galapagoensis	Oroaetus [Genus]	F. columbarius
B. albicaudatus	O. isidori [Species]	F. rufigularis
B. polyosoma	Polemaetus [Genus]	F. subbuteo
B. poecilochrous	P. bellicosus [Species]	F. cuvieri
B. albonotatus	Sagittariidae [Family]	F. severus
B. solitarius	Sagittarius [Genus]	F. longipennis
B. ventralis	S. serpentarius [Species]	F. novaeseelandiae
B. jamaicensis	o. serpenum um [opecies]	F. hypoleucos
B. buteo	Falconidae [Family]	F. subniger
B. oreophilus	Daptrius [Genus]	F. mexicanus
B. brachypterus	D. ater [Species]	F. jugger
B. rufinus	D. americanus	F. biarmicus

Neochen [Genus] A. melleri F. cherrug F. rusticolus N. jubata [Species] A. poecilorbyncha F. kreyenborgi Alopochen [Genus] A. superciliosa F. peregrinus A. aegyptiaca [Species] A. luzonica F. deiroleucus Tadorna [Genus] A. sparsa F. fasciinucha T. ferruginea [Species] A. specularioides T. cana A. specularis Anseriformes [Order] T. variegata A. acuta Anatidae [Family] T. cristata A. georgica Anseranas [Genus] T. tadornoides A. bahamensis A. semipalmata [Species] T. tadorna A. erythrorhyncha Dendrocygna [Genus] T. radjah A. versicolor D. guttata [Species] Tachyeres [Genus] A. hottentota D. eytoni T. pteneres [Species] A. querquedula D. bicolor T. brachypterus A. discors D. arcuata T. patachonicus A. cyanoptera D. javanica Plectropterus [Genus] A. platalea D. viduata P. gambensis [Species] A. smithii D. arborea Cairina [Genus] A. rhynchotis D. autumnalis C. moschata [Species] A. clypeata Thalassornis [Genus] C. scutulata Malacorhynchus [Genus] T. leuconotus [Species] Pteronetta [Genus] M. membranaceus [Species] Cygnus [Genus] P. hartlaubii Marmaronetta [Genus] C. olor [Species] Sarkidiornis [Genus] M. angustirostris [Species] C. atratus S. melanotos [Species] Rhodonessa [Genus] C. melanocoryphus Nettapus [Genus] R. caryophyllacea [Species] C. buccinator N. pulchellus [Species] Netta [Genus] C. cygnus N. coromandelianus N. rufina [Species] C. bewickii N. auritus N. peposaca C. columbianus Callonetta [Genus] N. erythrophthalma Coscoroba [Genus] C. leucophrys [Species] Aythya [Genus] C. coscoroba [Species] Aix [Genus] A. valisineria [Species] Anser [Genus] A. sponsa [Species] A. ferina A. cygnoides [Species] A. galericulata A. americana A. fabalis Chenonetta [Genus] A. collaris A. albifrons C. jubata [Species] A. australis A. erythropus Amazonetta [Genus] A. baeri A. anser A. brasiliensis [Species] A. nyroca A. indicus Merganetta [Genus] A. innotata A. caerulescens M. armata [Species] A. novaeseelandiae A. rossii Hymenolaimus [Genus] A. fuligula A. canagicus H. malacorhynchos [Species] A. marila Branta [Genus] Anas [Genus] A. affinis B. sandvicensis [Species] A. waigiuensis [Species] Somateria [Genus] B. canadensis A. penelope S. mollissima [Species] B. leucopsis A. americana S. spectabilis B. bernicla A. sibilatrix S. fischeri B. ruficollis A. falcata Polysticta [Genus] Cereopsis [Genus] A. strepera P. stelleri [Species] C. novaehollandiae [Species] A. formosa Camptorhynchus [Genus] Stictonetta [Genus] A. crecca C. labradorius [Species] S. naevosa [Species] A. flavirostris Histrionicus [Genus] Cyanochen [Genus] A. capensis A. gibberifrons H. histrionicus [Species] C. cyanopterus [Species] Clangula [Genus] Chloephaga [Genus] A. bernieri C. hyemalis [Species] C. melanoptera [Species] A. castanea C. picta A. aucklandica Melanitta [Genus] C. hybrida A. platyrhynchos M. nigra [Species] C. poliocephala A. rubripes M. perspicillata C. rubidiceps A. undulata M. fusca

Bucephala [Genus]	Mitu [Genus]	Dendragapus [Genus]
B. clangula [Species]	M. tomentosa [Species]	D. obscurus [Species]
B. islandica	M. salvini	Lagopus [Genus]
B. albeola	M. mitu	L. scoticus [Species]
Mergus [Genus]	Pauxi [Genus]	L. lagopus
M. albellus [Species]	P. pauxi [Species]	L. mutus
M. cucullatus	Crax [Genus]	L. leucurus
M. octosetaceous	C. nigra [Species]	Canachites [Genus]
M. serrator	C. alberti	C. canadensis [Species]
M. squamatus	C. fasciolata	C. franklinii
M. merganser	C. pinima	
M. australis		Falcipennis [Genus]
	C. globulosa	F. falcipennis [Species]
Heteronetta [Genus]	C. blumenbachii	Tetrastes [Genus]
H. atricapilla [Species]	C. rubra	T. bonasia [Species]
Oxyura [Genus]	Penelope [Genus]	T. sewerzowi
O. dominica [Species]	P. purpurascens [Species]	Bonasa [Genus]
O. jamaicensis	P. ortoni	B. umbellus [Species]
O. leucocephala	P. albipennis	Pedioecetes [Genus]
О. тассоа	P. marail	P. phasianellus [Species]
O. vittata	P. montagnii	Tympanuchus [Genus]
O. australis	P. obscura	T. cupido [Species]
Biziura [Genus]	P. superciliaris	T. palladicinctus
B. lobata [Species]	P. jacu-caca	Centrocercus [Genus]
•	P. ochrogaster	C. urophasianus [Species]
Anhimidae [Family]	e e	G. uropiiusumus [Species]
Anhima [Genus]	P. pileata	Phasianidae [Family]
A. cornuta [Species]	P. argyrotis	Dendrortyx [Genus]
Chauna [Genus]	Ortalis [Genus]	D. barbatus [Species]
C. chavaria [Species]	O. motmot [Species]	D. macroura
C. torquata	O. spixi	D. leucophrys
2	O. araucuan	D. hypospodius
Galliformes [Order]	O. superciliaris	Oreortyx [Genus]
Megapodiidae [Family]	O. guttata	
Megapodius [Genus]	O. columbiana	O. picta [Species]
M. nicobariens [Species]	O. wagleri	Callipepla [Genus]
M. tenimberens	O. vetula	C. squamota [Species]
M. reinwardt	O. ruficrissa	Lophortyx [Genus]
M. affinis	O. ruficauda	L. californica [Species]
M. eremita	O. garrula	L. gambelli
M. freycinet	O. canicollis	L. leucoprosopon
M. laperouse	O. erythroptera	L. douglasii
M. layardi	Penelopina [Genus]	Philortyx [Genus]
M. pritchardii	P. nigra [Species]	P. fasciatus [Species]
	Chamaepetes [Genus]	Colinus [Genus]
Eulipoa [Genus]		C. virginianus [Species]
E. wallacei [Species]	C. goudotii [Species] C. unicolor	C. nigrogularis
Leipoa [Genus]		C. leucopogon
L. ocellata [Species]	Pipile [Genus]	C. cristatus
Alectura [Genus]	P. pipile [Species]	Odontophorus [Genus]
A. lathami [Species]	P. cumanensis	O. gujanensis [Species]
Talegalla [Genus]	P. jacutinga	O. capueira
T. cuvieri [Species]	Aburria [Genus]	1
T. fuscirostris	A. aburri [Species]	O. erythrops
T. jobiensis	Oreophasis [Genus]	O. hyperythrus
Aepypodius [Genus]	O. derbianus [Species]	O. melanonotus
A. arfakianus [Species]	77	O. speciosus
A. bruijnii	Tetraonidae [Family]	O. loricatus
Macrocephalon [Genus]	Tetrao [Genus]	O. parambae
M. maleo [Species]	T. urogallus [Species]	O. strophium
*	T. parvirostris	O. atrifrons
Cracidae [Family]	Lyrurus [Genus]	O. leucolaemus
Nothocrax [Genus]	L. tetrix [Species]	O. columbianus
N. urumutum [Species]	L. mlokosiewiczi	O. soderstromii

O. balliviani F. ahantensis Haematortyx [Genus] O. stellatus F. griseostriatus H. sanguiniceps [Species] F. camerunensis Rollulus [Genus] O. guttatus Dactylortyx [Genus] F. nobilis R. roulroul [Species] F. jacksoni Ptilopachus [Genus] D. thoracicus [Species] F. castaneicollis P. petrosus [Species] Cyrtonyx [Genus] F. atrifrons C. montezumae [Species] Bambusicola [Genus] F. erckelii B. fytchii [Species] C. sallei Pternistis [Genus] B. thoracica C. ocellatus Galloperdix [Genus] *P. rufopictus* [Species] *Rhynchortyx* [Genus] P. afer G. spadicea [Species] R. cinctus [Species] P. swainsonii G. lunulata Lerwa [Genus] P. leucoscepus G. bicalcarata L. lerwa [Species] Perdix [Genus] Ophrysia [Genus] Ammoperdix [Genus] P. perdix [Species] O. superciliosa [Species] A. griseogularis [Species] P. barbata Ithaginis [Genus] A. heyi P. hodgsoniae *I. cruentus* [Species] Tetraogallus [Genus] Rhizothera [Genus] Tragopan [Genus] T. caucasicus [Species] R. longirostris [Species] T. melanocephalus [Species] T. caspius Margaroperdix [Genus] T. satyra T. tibetanus T. blythii M. madagarensis [Species] T. altaicus Melanoperdix [Genus] T. temminckii T. himalayensis M. nigra [Species] T. caboti Tetraophasis [Genus] Coternix [Genus] Lophophorus [Genus] T. obscurus [Species] *C. coturnix* [Species] L. impejanus [Species] T. szechenyii C. coromandelica L. sclateri Alectoris [Genus] L. lhuysii C. delegorguei A. graeca [Species] C. pectoralis Crossoptilon [Genus] A. rufa C. novaezelandiae C. mantchuricum [Species] A. barbara Synoicus [Genus] C. auritum A. melanocephala S. ypsilophorus [Species] C. crossoptilon Anurophasis [Genus] Excalfactoria [Genus] Gennaeus [Genus] A. monorthonyx [Species] E. adansonii [Species] G. leucomelanos [Species] Francolinus [Genus] E. chinensis G. horsfieldii F. francolinus [Species] Perdicula [Genus] G. lineatus F. pictus P. asiatica [Species] G. nycthemerus F. pintadeanus Cryptoplectron [Genus] Hierophasis [Genus] F. pondicerianus C. erythrorhynchum [Species] H. swinhoii [Species] F. gularis C. manipurensis H. imperialis F. lathami Arborophila [Genus] H. edwardsi F. nahani A. torqueola [Species] Houppifer [Genus] F. streptophorus A. rufogularis H. erythrophthalmus [Species] F. coqui A. atrogularis H. inornatus F. albogularis A. crudigularis Lophura [Genus] F. sephaena A. mandellii L. rufa [Species] F. africanus A. brunneopectus L. ignita F. shelleyi A. rufipectus Diardigallus [Genus] F. levaillantii A. gingica D. diardi [Species] F. finschi A. davidi Lobiophasis [Genus] F. gariepensis A. cambodiana L. bulweri [Species] F. adspersus A. orientalis Gallus [Genus] F. capensis A. javanica G. gallus [Species] F. natalensis A. rubrirostris G. lafayetii F. harwoodi A. hyperythra G. sonneratii F. bicalcaratus G. varius A. ardens *F. icterorhynchus* Tropicoperdix [Genus] Pucrasia [Genus] F. clappertoni T. charltonii [Species] P. macrolopha [Species] F. hartlaubi T. chloropus Catreus [Genus] F. swierstrai T. merlini C. wallichii [Species] F. hildebrandti Caloperdix [Genus] Phasianus [Genus] C. oculea [Species] F. squamatus P. colchicus [Species]

Syrmaticus [Genus]	T. nana	Nesolimnas [Genus]
S. reevesii [Species]	T. hottentotta	N. dieffenbachii [Species]
S. soemmerringii	T. tanki	Cabalus [Genus]
S. humiae	T. suscitator	C. modestus [Species]
S. ellioti	T. nigricollis	Atlantisia [Genus]
S. mikado	T. ocellata	A. rogersi [Species]
Chrysolophus [Genus]	T. melanogaster	Tricholimnas [Genus]
	T. varia	T. conditicius [Species]
C. pictus [Species]	T. castanota	T. lafresnayanus
C. amherstiae	T. pyrrhothorax	T. sylvestris
Chalcurus [Genus]	T. velox	
C. inopinatus [Species]	Ortyxelos [Genus]	Ortygonax [Genus]
C. chalcurus	O. meiffrenii [Species]	O. rytirhynchos [Species]
Polyplecton [Genus]	Pedionomus [Genus]	O. nigricans
P. bicalcaratum [Species]	P. torquatus [Species]	Pardirallus [Genus]
P. germaini	1. torquitus [Species]	P. maculatus [Species]
P. malacensis	Gruidae [Family]	Dryolimnas [Genus]
P. schleiermacheri	Grus [Genus]	D. cuvieri [Species]
P. emphanum	G. grus [Species]	Rougetius [Genus]
Rheinardia [Genus]	G. nigricollis	R. rougetii [Species]
R. ocellata [Species]	G. monacha	Amaurolimnas [Genus]
Argusianus [Genus]	G. canadensis	A. concolor [Species]
A. argus [Species]	G. japonensis	Rallina [Genus]
Pavo [Genus]	G. americana	R. fasciata [Species]
P. cristatus [Species]	G. vipio	R. eurizonoides
P. muticus	G. antigone	R. canningi
	G. rubicunda	R. tricolor
Numididae [Family]	G. leucogeranus	Rallicula [Genus]
Phasidus [Genus]	Bugeranus [Genus]	R. rubra [Species]
P. niger [Species]	B. carunculatus [Species]	R. leucospila
Agelastes [Genus]	Anthropoides [Genus]	Cyanolimnas [Genus]
A. meleagrides [Species]	A. virgo [Species]	C. cerverai [Species]
Numida [Genus]	A. paradisea	Aramides [Genus]
N. meleagris [Species]	Balearica [Genus]	A. mangle [Species]
Guttera [Genus]	B. pavonina [Species]	A. cajanea
G. plumifera [Species]	D. paconina [Species]	A. wolfi
G. edouardi	Aramidae [Family]	A. gutturalis
G. pucherani	Aramus [Genus]	A. ypecaha
Acryllium [Genus]	A. scolopaceus [Species]	A. axillaris
A. vulturinum [Species]		A. calopterus
11. vaitai mam [opecies]	Psophiidae [Family]	A. saracura
Meleagridae [Family]	Psophia [Genus]	Aramidopsis [Genus]
Meleagris [Genus]	P. crepitans [Species]	A. plateni [Species]
M. gallopavo [Species]	P. leucoptera	Nesoclopeus [Genus]
Agriocharis [Genus]	P. viridis	N. poeciloptera [Species]
A. ocellata [Species]	Dallidaa [Family]	N. woodfordi
in occurre [epecies]	Rallidae [Family]	Gymnocrex [Genus]
Opisthocomidae [Family]	Rallus [Genus]	G. rosenbergii [Species]
Opisthocomus [Genus]	R. longirostris [Species]	G. plumbeiventris
O. hoazin [Species]	R. elegans	G. pumoeiventris Gallirallus [Genus]
	R. limicola	
Gruiformes [Order]	R. semiplumbeus	G. australis [Species]
Mesoenatidae [Family]	R. aquaticus	G. troglodytes
Mesoenas [Genus]	R. caerulescens	Habropteryx [Genus]
M. variegata [Species]	R. madagascariensis	H. insignis [Species]
M. unicolor	R. pectoralis	Habroptila [Genus]
Monias [Genus]	R. muelleri	H. wallacii [Species]
M. benschi [Species]	R. striatus	Megacrex [Genus]
- 	R. philippensis	M. inepta [Species]
Turnicidae [Family]	R. ecaudata	Eulabeornis [Genus]
Turnix [Genus]	R. torquatus	E. castaneoventris [Species]
T. sylvatica [Species]	R. owstoni	Himantornis [Genus]
T. worcesteri	R. wakensis	H. haematopus [Species]

Canirallus [Genus] S. bohmi Rhynochetidae [Family] C. oculeus [Species] S. antonii Rhynochetos [Genus] Mentocrex [Genus] S. lineata R. jubatus [Species] M. kioloides [Species] S. insularis Eurypygidae [Family] S. watersi Crecopsis [Genus] Eurypyga [Genus] Aenigmatolimnas [Genus] C. egregria [Species] E. helias [Species] Crex [Genus] A. marginalis [Species] C. crex [Species] Poliolimnas [Genus] Cariamidae [Family] P. cinereus [Species] Anurolimnas [Genus] Cariama [Genus] Porphyriops [Genus] A. castaneiceps [Species] C. cristata [Species] P. melanops [Species] Limnocorax [Genus] Chunga [Genus] *Tribonyx* [Genus] L. flavirostra [Species] C. burmeisteri [Species] T. ventralis [Species] Porzana [Genus] Otidae [Family] T. mortierii P. parva [Species] Tetrax [Genus] Amaurornis [Genus] P. pusilla T. tetrax [Species] A. akool [Species] P. porzana Otis [Genus] A. olivacea P. fluminea O. tarda [Species] A. isabellina P. carolina Neotis [Genus] A. phoenicurus P. spiloptera Gallicrex [Genus] N. cafra [Species] P. flaviventer G. cinerea [Species] N. ludwigii P. albicollis N. burchellii Gallinula [Genus] P. fusca N. Nuba G. tenebrosa [Species] P. paykullii N. heuglinii G. chloropus P. olivieri Choriotius [Genus] G. angulata P. bicolor C. arabs [Species] Porphyriornis [Genus] P. tabuensis P. nesiotis [Species] C. kori Porzanula [Genus] C. nigriceps P. comeri P. palmeri [Species] C. australis Pareudiastes [Genus] Pennula [Genus] Chlamydotis [Genus] P. pacificus [Species] P. millsi [Species] C. undulata [Species] Porphyrula [Genus] P. sandwichensis P. alleni [Species] Lophotis [Genus] Nesophylax [Genus] L. savilei [Species] P. martinica N. ater [Species] P. parva L. ruficrista Aphanolimnas [Genus] Porphyrio [Genus] Afrotis [Genus] A. monasa [Species] P. porphyrio [Species] A. atra [Species] Laterallus [Genus] P. madagascariensis Eupodotis [Genus] L. jamaicensis [Species] P. poliocephalus E. vigorsii [Species] L. spilonotus E. ruppellii P. albus L. exilis P. pulverulentus E. humilis L. albigularis Notornis [Genus] E. senegalensis L. melanophaius N. mantelli [Species] E. caerulescens L. ruber Fulica [Genus] Lissotis [Genus] L. levraudi L. melanogaster [Species] F. atra [Species] L. viridis L. hartlaubii F. cristata L. hauxwelli Houbaropsis [Genus] F. americana L. leucopyrrhus H. bengalensis [Species] F. ardesiaca Micropygia [Genus] F. armillata Sypheotides [Genus] M. schomburgkii [Species] F. caribaea S. indica [Species] Coturnicops [Genus] F. leucoptera C. exquisita [Species] Charadriiformes [Order] F. rufrifrons C. noveboracensis Jacanidae [Family] F. gigantea C. notata Microparra [Genus] F. cornuta C. ayresi M. capensis [Species] Neocrex [Genus] Heliornithidae [Family] Actophilornis [Genus] *N. erythrops* [Species] Podica [Genus] A. africana [Species] P. senegalensis [Species] Sarothura [Genus] A. albinucha S. rufa [Species] Heliopais [Genus] Irediparra [Genus] S. lugeus H. personata [Species] I. gallinacea [Species] S. pulchra Heliornis [Genus] Hydrophasianus [Genus] S. elegans H. fulica [Species] H. chirurgus [Species]

Numenius [Genus] Metopidius [Genus] Sarciophorus [Genus] M. indicus [Species] S. tectus [Species] N. minutus [Species] Facana [Genus] Squatarola [Genus] N. borealis S. squatarola [Species] J. spinosa [Species] N. phaeopus Pluvialis [Genus] N. tahitiensis Rostratulidae [Family] P. apricaria [Species] N. tenuirostris Rostratula [Genus] P. dominica N. arquata R. benghalensis [Species] Pluviorbynchus [Genus] N. madagascariensis Nycticryphes [Genus] P. obscurus [Species] N. americanus N. semicollaris [Species] Charadrius [Genus] Limosa [Genus] *C. rubricollis* [Species] L. limosa [Species] Haematopodidae [Family] C. hiaticula L. haemastica Haematopus [Genus] C. melodus L. lapponica H. ostralegus [Species] C. dubius L. fedoa H. leucopodus C. alexandrinus Tringa [Genus] H. fuliginosus C. venustus T. erythropus [Species] H. ater C. falklandicus T. totanus Chettusia [Genus] C. alticola T. flavipes C. leucura [Species] C. bicinctus T. stagnatilis C. gregaria C. peronii T. nebularia C. collaris Charadriidae [Family] T. melanoleuca C. pecuarius Vanellus [Genus] T. ocrophus C. sanctaehelenae V. vanellus [Species] T. solitaria C. thoracicus Belonopterus [Genus] T. glareola C. placidus B. chilensis [Species] Pseudototanus [Genus] C. vociferus Hemiparra [Genus] P. guttifer [Species] C. tricollaris H. crassirostris [Species] Xenus [Genus] C. mongolus Tylibyx [Genus] X. cinereus [Species] C. wilsonia T. melanocephalus [Species] Actitis [Genus] C. leschenaultii Microsarcops [Genus] A. hypoleucos [Species] Elsevornis [Genus] M. cinereus [Species] A. macularia E. melanops [Species] Lobivanellus [Genus] Catoptrophorus [Genus] Eupoda [Genus] L. indicus [Species] C. semipalmatus [Species] E. asiatica [Species] Xiphidiopterus [Genus] Heteroscelus [Genus] E. veredus X. albiceps [Species] H. brevipes [Species] E. montana Rogibyx [Genus] H. incanus Oreopholus [Genus] R. tricolor [Species] Aphriza [Genus] O. ruficollis [Species] Lobibyx [Genus] A. virgata [Species] Erythrogonys [Genus] L. novaehollandiae [Species] Arenaria [Genus] E. cinctus [Species] L. miles A. interpres [Species] Eudromias [Genus] Afribyx [Genus] A. melanocephala E. morinellus [Species] A. senegallus [Species] Limnodromus [Genus] Zonibyx [Genus] Stephanibyx [Genus] L. griseus [Species] Z. modestus [Species] S. lugubris [Species] L. semipalmatus Thinornis [Genus] S. melanopterus Coenocorypha [Genus] T. novaeseelandiae [Species] S. coronatus C. aucklandica [Species] Anarhynchus [Genus] Hoplopterus [Genus] Capella [Genus] A. frontalis [Species] H. spinosus [Species] C. solitaria [Species] Pluvianellus [Genus] H. armatus C. hardwickii P. socialis [Species] H. duvaucelii C. nemoricola Phegornis [Genus] Hoploxypterus [Genus] C. stenura P. mitchellii [Species] H. cayanus [Species] C. megala Ptilocelys [Genus] C. nigripennis Scopacidae [Family] P. resplendens [Species] Aechmorhynchus [Genus] C. macrodactyla Zonifer [Genus] A. cancellatus [Species] C. media Z. tricolor [Species] A. parvirostris C. gallinago Anomalophrys [Genus] Prosobonia [Genus] C. delicata A. superciliosus [Species] P. leucoptera [Species] C. paraguaiae Lobipluvia [Genus] Bartramia [Genus] C. nobilis

B. longicauda [Species]

L. malabarica [Species]

C. undulata

Steganopus [Genus] Chubbia [Genus] Stercorarius [Genus] C. imperialis [Species] S. tricolor [Species] S. pomarinus [Species] C. jamesoni Lobipes [Genus] S. parasiticus C. stricklandii L. lobatus [Species] S. longicaudus Scolopax [Genus] Dromadidae [Family] Laridae [Family] S. rusticola [Species] Dromas [Genus] Gabianus [Genus] S. saturata D. ardeola [Species] G. pacificus [Species] S. celebensis G. scoresbii S. rochussenii Burhinidae [Family] Pagophila [Genus] Philohela [Genus] Burhinus [Genus] P. eburnea [Species] P. minor [Species] B. oedicnemus [Species] Lymnocryptes [Genus] Larus [Genus] B. senegalensis L. minima [Species] L. fuliginosus [Species] B. vermiculatus Calidris [Genus] L. modestus B. capensis C. canutus [Species] L. heermanni B. bistriatus C. tenuirostris L. leucophthalmus B. superciliaris Crocethia [Genus] L. hemprichii B. magnirostris C. alba [Species] L. belcheri Esacus [Genus] Ereunetes [Genus] L. crassirostris E. recurvirostris [Species] E. pusillus [Species] L. audouinii Orthoramphus [Genus] E. mauri L. delawarensis O. magnirostris [Species] Eurynorhynchus [Genus] L. canus E. pygmeus [Species] Glareolidae [Family] L. argentatus Erolia [Genus] Pluvianus [Genus] L. fuscus E. ruficollis [Species] P. aegyptius [Species] L. californicus E. minuta Cursorius [Genus] L. occidentalis E. temminckii L. dominicanus C. cursor [Species] E. subminuta C. temminckii L. schistisagus E. minutilla C. coromandelicus L. marinus E. fuscicollis Rhinoptilus [Genus] L. glaucescens E. bairdii R. africanus [Species] L. hyperboreus E. melanotos R. cinctus L. leucopterus E. acuminata R. chalcopterus L. ichthyaetus E. maritima R. bitorquatus L. atricilla E. ptilocnemis Peltohyas [Genus] L. brunnicephalus E. alpina P. australis [Species] L. cirrocephalus E. testacea Stiltia [Genus] L. serranus Limicola [Genus] S. isabella [Species] L. pipixcan L. falcinellus [Species] Glareola [Genus] L. novaehollandiae Micropalama [Genus] G. pratincola [Species] L. melanocephalus M. himantopus [Species] G. maldivarum L. bulleri *Tryngites* [Genus] G. nordmanni L. maculipennis T. subruficollis [Species] G. ocularis L. ridibundus Philomachus [Genus] G. nuchalis L. genei P. pugnax [Species] G. cinerea L. philadelphia Recurvostridae [Family] G. lactea L. minutus Ibidorhyncha [Genus] Attagis [Genus] L. saundersi I. struthersii [Species] A. gayi [Species] Rhodostethia [Genus] Himantopus [Genus] A. malouinus R. rosea [Species] H. himantopus [Species] Thinocorus [Genus] Rissa [Genus] Cladorhynchus [Genus] T. orbignyianus [Species] R. tridactyla [Species] C. leucocephala [Species] T. rumicivorus R. brevirostris Recurvirostra [Genus] Creagrus [Genus] R. avosetta [Species] Chionididae [Family] C. furcatus [Species] R. americana Chionis [Genus] Xema [Genus] C. alba [Species] R. novaehollandiae X. sabini [Species] C. minor R. andina Chlidonias [Genus] Phalaropodidae [Family] Stercorariidae [Family] C. hybrida [Species] C. leucoptera Phalaropus [Genus] Catharacta [Genus] P. fulicarius [Species] C. skua [Species] C. nigra

Phaetusa [Genus]	Uria [Genus]	S. seimundi
P. simplex [Species]	U. lomvia [Species]	S. oxyura
Gelochelidon [Genus]	U. aalge	S. sphenurus
G. nilotica [Species]	Cepphus [Genus]	S. korthalsi
Hydroprogne [Genus]	C. grylle [Species]	S. sieboldii
H. tschegrava [Species]	C. columba	S. farmosae
Sterna [Genus]	C. carbo	Butreron [Genus]
S. aurantia [Species]	Brachyramphus [Genus]	
S. hirundinacea		B. capellei [Species]
S. hirundo	B. marmoratus [Species]	Treron [Genus]
	B. brevirostris	T. curvirostra [Species]
S. paradisaea	B. hypoleucus	T. pompadora
S. vittata	B. craveri	T. fulvicollis
S. virgata	Synthliboramphus [Genus]	T. olax
S. forsteri	S. antiquus [Species]	T. vernans
S. trudeaui	S. wumizusume	T. bicincta
S. dougallii	Ptychoramphus [Genus]	T. s. thomae
S. striata	P. aleuticus [Species]	T. australis
S. repressa	Cyclorrhynchus [Genus]	T. calva
S. sumatrana	C. psittacula [Species]	
S. melanogaster		T. delalandii
S. aleutica	Aethia [Genus]	T. waalia
S. lunata	A. cristatella [Species]	T. phoenicoptera
	A. pusilla	Phapitreron [Genus]
S. anaethetus	A. pygmaea	P. leucotis [Species]
S. fuscata	Cercorhinca [Genus]	P. amethystina
S. nereis	C. monocerata [Species]	Leucotreron [Genus]
S. albistriata	Fratercula [Genus]	L. occipitalis [Species]
S. superciliaris	F. arctica [Species]	L. fischeri
S. balaenarum	F. corniculata	L. jistheri L. merrilli
S. iorata	Lunda [Genus]	
		L. marchei
S. albifrons	I circhata [Species]	T 1 1 .
	L. cirrhata [Species]	L. subgularis
Thalasseus [Genus]	*	L. subgularis L. leclancheri
Thalasseus [Genus] T. hergii [Species]	Columbiformes [Order]	
Thalasseus [Genus] T. bergii [Species] T. maximus	Columbiformes [Order] Pteroclididae [Family]	L. leclancheri
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus]	L. leclancheri L. cincta L. dohertyi
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species]	L. leclancheri L. cincta L. dohertyi L. porphyrea
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus]
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species]
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] Procelsterna [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] Procelsterna [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. huttoni P. porphyraceus P. greyii P. richardsii
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. huttoni P. porphyraceus P. greyii P. richardsii P. ponapensis
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Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. huttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. pelewensis P. roseicapilla
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. pelewensis P. roseicapilla P. perousii
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. pelewensis P. roseicapilla P. perousii P. superbus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. polewensis P. roseicapilla P. perousii P. superbus P. pulchellus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. noseicapilla P. perousii P. superbus P. superbus P. pulchellus P. coronulatus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. polewensis P. roseicapilla P. perousii P. superbus P. pulchellus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. noseicapilla P. perousii P. superbus P. superbus P. pulchellus P. coronulatus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family] Plautus [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius Pezophaps [Genus]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. huttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. roseicapilla P. perousii P. superbus P. gulchellus P. coronulatus P. monacha
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family] Plautus [Genus] P. alle [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. huttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. neewensis P. pelewensis P. roseicapilla P. perousii P. superbus P. pulchellus P. coronulatus P. monacha P. iozonus
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family] Plautus [Genus] P. alle [Species] Pinguinis [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius Pezophaps [Genus] P. solitaria [Species]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. roseicapilla P. perousii P. superbus P. greybus P. nuchellus P. coronulatus P. monacha P. iozonus P. insolitus P. rivoli
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family] Plautus [Genus] P. alle [Species] Pinguinis [Genus] P. impennis [Species]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius Pezophaps [Genus] P. solitaria [Species] Columbidae [Family]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. pelewensis P. pelewensis P. roseicapilla P. perousii P. superbus P. pulchellus P. coronulatus P. iozonus P. insolitus P. rivoli P. miquelli
Thalasseus [Genus] T. bergii [Species] T. maximus T. bengalensis T. zimmermanni T. eurygnatha T. elegans T. sandvicensis Larosterna [Genus] L. inca [Species] Procelsterna [Genus] P. cerulea [Species] Anous [Genus] A. stolidus [Species] A. tenuirostris A. minutus Gygis [Genus] G. alba [Species] Rynchopidae [Family] Rynchops [Genus] R. nigra [Species] R. flavirostris R. albicollis Alcidae [Family] Plautus [Genus] P. alle [Species] Pinguinis [Genus]	Columbiformes [Order] Pteroclididae [Family] Syrrhaptes [Genus] S. tibetanus [Species] S. paradoxus Pterocles [Genus] P. alchata [Species] P. namaqua P. exustus P. senegallus P. orientalis P. coronatus P. gutturalis P. burchelli P. personatus P. decoratus P. lichtensteinii P. bicinctus P. indicus P. quadricinctus Raphidae [Family] Raphus [Genus] R. cucullatus [Species] R. solitarius Pezophaps [Genus] P. solitaria [Species]	L. leclancheri L. cincta L. dohertyi L. porphyrea Ptilinopus [Genus] P. dupetithouarsii [Species] P. regina P. mercierii P. purpuratus P. coralensis P. insularis P. rarotongensis P. buttoni P. porphyraceus P. greyii P. richardsii P. ponapensis P. roseicapilla P. perousii P. superbus P. gulchellus P. coronulatus P. monacha P. iozonus P. insolitus P. rivoli

Aves species list

P. viridis C. nigriristris D. radiata P. eugeniae D. rufigaster C. goodsoni D. finschii P. geelvinkiana C. subvinacea D. chalconota P. pectoralis C. plumbea P. naina D. zoeae C. chiriquensis P. hyogastra D. carola C. purpureotincta P. granulifrons Cryptophaps [Genus] C. delegorguei P. melanospila C. poecilorrhoa [Species] C. iriditorques P. jambu Hemiphaga [Genus] C. malherbii P. wallacii H. novaeseelandiae [Species] Nesoenas [Genus] P. aurantiifrons Lopholaimus [Genus] . mayeri [Species] P. ornatus L. antarcticus [Species] Turacoena [Genus] T. manadensis [Species] P. perlatus Gymnophaps [Genus] P. tannensis G. albertisii [Species] T. modesta Chrysoena [Genus] G. solomonensis Macropygia [Genus] C. victor [Species] G. mada M. unchall [Species] C. viridis Columba [Genus] M. amboinensis C. luteovirens M. ruficeps C. leuconota [Species] Alectroenas [Genus] M. magna C. rupestris A. pulcherrima [Species] C. livia M. phasianella A. sganzini C. oenas M. rufipennis A. madagascariensis C. eversmanni M. nigrirostris M. mackinlayi A. nitidissima C. oliviae Drepanoptila [Genus] C. albitorques Reinwardtoena [Genus] D. holosericea [Species] C. palumbus R. reinwardtsi [Species] Megaloprepia [Genus] C. trocaz R. browni M. magnifica [Species] C. junoniae Coryphoenas [Genus] M. formosa C. leucocephala C. crassirostris [Species] Ducula [Genus] C. picazuro Ectopistes [Genus] E. migratoria [Species] D. galeata [Species] C. gymnophtalmos D. aurorae C. squamosa Zenaidura [Genus] D. oceanica C. maculosa Z. macroura [Species] D. pacifica C. unicincta Z. graysoni D. rubricera C. guinea Z. auriculata Zenaida [Genus] D. myristicivora C. hodgsonii D. concinna C. arquatrix Z. aurita [Species] C. thomensis D. aenea Z. asiatica D. oenothorax C. albinucha Nesopelia [Genus] D. pistrinaria C. flavirostris N. galapagoensis [Species] D. whartoni C. oenops Streptopelia [Genus] Ŝ. turtur [Species] D. rosacea C. inornata D. perspicillata C. caribaea S. orientalis D. pickeringii C. rufina S. lugens D. latrans C. fasciata S. picturata D. bakeri C. albilinea S. decaocto D. brenchleyi C. araucana S. roseogrisea D. goliath C. elphinstonii S. semitorquata D. bicolor C. torringtoni S. decipiens D. luctuosa C. pulchricollis S. capicola C. punicea D. melanura S. vinacea C. palumboides S. reichenowi D. spilorrhoa D. cineracea C. janthina S. fulvopectoralis D. lacernulata C. versicolor S. bitorquata D. badia C. jouyi S. tranquebarica D. mullerii C. vitiensis S. chinensis D. pinon C. pallidiceps S. senegalensis D. melanochroa C. norfolciensis Geopelia [Genus] D. poliocephala C. argentina G. humeralis [Species] C. pollenii D. forsteni G. striata D. mindorensis G. cuneata C. speciosa

Metriopelia [Genus]	L. megalura	G. scheepmakeri
M. ceciliae [Species]	L. jamaicensis	G. victoria
M. morenoi	L. plumbeiceps	Didunculus [Genus]
M. melanoptera	L. rufaxilla	D. strigirostris [Species]
M. aymara	L. wellsi	Psittaciformes [Order]
Scardafella [Genus]	L. cassini	Psittacidae [Family]
S. inca [Species]	L. ochraceiventris	Strigops [Genus]
S. squammata	Osculatia [Genus]	S. habroptilus [Species]
Uropelia [Genus]	O. saphirina [Species]	Nestor [Genus]
U. campestris [Species]	Oreopeleia [Genus]	N. meridionalis [Species]
Columbina [Genus]	O. veraguensis [Species]	N. notabilis
C. picui [Species]	O. lawrencii	N. productus
Columbigallina [Genus]	O. goldmani	Chalcopsitta [Genus]
C. passerina [Species]	O. costaricensis	C. atra [Species]
C. talpacoti	O. chrysia	C. insignis
C. minuta	O. mystacea	C. sintillata
C. buckleyi	O. martinica	C. duivenbodei
C. cruziana	O. violacea	C. cardinalis
Oxypelia [Genus]	O. montana	Eos [Genus]
O. cyanopis [Species]	O. caniceps	E. cyanogenia [Species]
Claravis [Genus]	O. albifacies	E. reticulata
C. pretiosa [Species]	O. chiriquensis	E. squamata
C. mondetoura	O. linearis	E. histrio
C. godefrida	O. bourcieri	E. bornea
Oena [Genus]	O. erythropareia	E. semilarvata
O. capensis [Species]	Geotrygon [Genus]	E. goodfellowi
Tympanistria [Genus]	G. versicolor [Species]	Trichoglossus [Genus]
T. tympanistria [Species]	Gallicolumba [Genus]	T. ornatus [Species]
Turtur [Genus]	G. luzonica [Species]	T. haematod
T. afer [Species]	G. platenae	T. rubiginosus
T. abyssinicus	G. keayi	T. chlorolepidotus
T. chalcospilos	G. criniger	T. euteles
T. brehmeri	G. menagei	Psitteuteles [Genus]
Chalcophaps [Genus]	G. rufigula	P. flavoviridis [Species]
C. indica [Species]	G. tristigmata	P. johnstoniae P. goldini
C. stephani	G. beccarii	P. goldiei P. versicolor
Henicophaps [Genus]	G. salamonis	P. iris
H. albifrons [Species]	G. sanctaecrucis	Pseudeos [Genus]
H. foersteri	G. stairi	P. fuscata [Species]
Petrophassa [Genus]	G. canifrons	Domicella [Genus]
P. albipennis [Species]	G. xanthonura	D. hypoinochroa [Species]
P. rufipennis	G. kubaryi	D. amabilis
Phaps [Genus]	G. jobiensis	D. lory
P. chalcoptera [Species]	G. erythroptera	D. domicella
P. elegans	G. rubescens	D. tibialis
Ocyphaps [Genus]	G. hoedtii	D. chlorocercus
O. lophotes [Species]	Leucosarcia [Genus]	D. albidinucha
Lophophaps [Genus]	L. melanoleuca [Species]	D. garrula
L. plumifera [Species]	Trugon [Genus]	Phigys [Genus]
L. ferruginea	T. terrestris [Species]	P. solitarius [Species]
Geophaps [Genus]	Microgoura [Genus]	Vini [Genus]
G. scripta [Species]	M. meeki [Species]	V. australis [Species]
G. smithii	Starnoenas [Genus]	V. kuhlii
Histriophaps [Genus]	S. cyanocephala [Species]	V. stepheni
H. histrionica [Species]	Otidiphaps [Genus]	V. peruviana
Aplopelia [Genus]	O. nobilis [Species]	V. ultramarina
A. larvata [Species]	Caloenas [Genus]	Glossopsitta [Genus]
A. simplex	C. nicobarica [Species]	G. concinna [Species]
Leptotila [Genus] L. verreauxi [Species]	Goura [Genus] G. cristata [Species]	G. porphyrocephala G. pusilla
L. verreumi [species]	G. Wishim [Species]	G. pusilla

P. leucotis Charmosyna [Genus] Ara [Genus] C. palmarum [Species] A. ararauna [Species] P. picta A. caninde P. viridicata C. meeki C. rubrigularis P. egregria A. militaris C. aureicincta P. melanura A. ambigua C. diadema P. berlepschi A. macao C. toxopei P. rupicola A. chloroptera P. albipectus C. placentis A. tricolor C. rubronotata P. calliptera A. rubrogenys C. multistriata P. rhodocephala A. auricollis C. wilhelminae P. hoffmanni A. severa Microsittace [Genus] C. pulchella A. spixii M. ferruginea [Species] C. margarethae A. manilata C. josefinae Enicognathus [Genus] A. maracana C. papou E. leptorhynchus [Species] A. couloni Oreopsittacus [Genus] Myiopsitta [Genus] A. nobilis O. arfaki [Species] M. monachus [Species] Aratinga [Genus] Neopsittacus [Genus] Amoropsittaca [Genus] A. acuticaudata [Species] N. musschenbroekii [Species] A. aymara [Species] A. guarouba N. pullicauda Psilopsaigon [Genus] A. holochlora Psittaculirostris [Genus] P. aurifrons [Species] A. strenua P. desmaresti [Species] Bolborhynchus [Genus] A. finschi P. salvadorii B. lineola [Species] A. wagleri B. ferrugineifrons Opopsitta [Genus] A. mitrata P. gulielmitertii [Species] B. andicolus A. erythrogenys P. diophthalma Forpus [Genus] A. leucophthalmus F. cyanopygius [Species] Lathamus [Genus] A. chloroptera L. discolor [Species] F. passerinus A. euops Micropsitta [Genus] F. conspicillatus A. auricapillus M. bruijnii [Species] F. sclateri A. jandaya M. keiensis F. coelestis A. solstitialis M. geelvinkiana Brotogeris [Genus] A. weddellii M. pusio B. tirica [Species] A. astec M. meeki B. versicolurus A. nana B. pyrrhopterus M. finschii A. canicularis Probosciger [Genus] B. jugularis A. pertinax P. aterrimus [Species] B. gustavi A. cactorum B. chrysopterus Calyptorhynchus [Genus] A. aurea C. baudinii [Species] B. sanctithomae Nandayus [Genus] C. funereus Nannopsittaca [Genus] N. nenday [Species] C. magnificus N. panychlora [Species] Leptosittaca [Genus] C. lathami Touit [Genus] L. branickii [Species] Callocephalon [Genus] T. batavica [Species] Conuropsis [Genus] C. fimbriatum [Species] T. purpurata C. carolinensis [Species] T. melanonotus Kakatoe [Genus] Rhynchopsitta [Genus] K. galerita [Species] T. huetii R. pachyrhyncha [Species] K. sulphurea T. dilectissima Cyanoliseus [Genus] K. alba T. surda C. patagonus [Species] K. moluccensis T. stictoptera C. whitleyi K. Haematuropygia T. emmae K. leadbeateri Ognorhynchus [Genus] Pionites [Genus] K. ducrops O. icterotis [Species] P. melanocephala [Species] K. sanguinea Pyrrhura [Genus] P. leucogaster P. cruentata [Species] K. tenuirostris Pionopsitta [Genus] P. devillei K. roseicapilla P. pileata [Species] Nymphicus [Genus] P. frontalis P. haematotis N. hollandicus [Species] P. perlata P. caica P. rhodogaster P. barrabandi Anodorhynchus [Genus] A. hyacinthinus [Species] P. molinae P. pyrilia P. hypoxantha A. glaucus Hapalopsittaca [Genus] A. leari P. hoematotis H. melanotis [Species]

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H. fuertesi	Psittrichas [Genus]	A. taranta
H. amazonina	P. fulgidus [Species]	A. swinderniana
H. pyrrhops	Lorius [Genus]	A. fischeri
Gypopsitta [Genus]	L. roratus [Species]	A. personata
G. vulturina [Species]	Geoffroyus [Genus]	A. lilianae
Graydidascalus [Genus]	G. geoffroyi [Species]	A. nigrigenis
G. brachyurus [Species]	G. simplex	Loriculus [Genus]
Pionus [Genus]	G. heteroclitus	L. vernalis [Species]
P. menstruus [Species]	Prioniturus [Genus]	L. beryllinus
P. sordidus	P. luconensis [Species]	L. pusillus
P. maximiliani	P. discurus	L. philippensis
P. tumultuosus	P. flavicans	L. amabilis
P. seniloides	P. platurus	L. stigmatus
P. senilis	P. mada	L. galgulus L. exilis
P. chalcopterus	Tanygnathus [Genus]	
P. fuscus	T. lucionensis [Species]	L. flosculus
Amazona [Genus]	T. mulleri	L. aurantiifrons
A. collaria [Species]	T. gramineus	Platycercus [Genus]
A. leucocephala	T. heterurus	P. elegans [Species] P. caledonicus
A. ventralis	T. megalorynchos	P. eximius
A. xantholora	Mascarinus [Genus]	P. icterotis
A. albifrons	M. mascarin [Species]	P. adscitus
A. agilis	Psittacula [Genus]	P. venustus
A. vittata	P. eupatria [Species]	P. zonarius
A. pretrei	P. krameri	
A. viridigenalis	P. alexandri	Purpureicephalus [Genus]
A. finschi	P. caniceps	P. spurius [Species]
A. autumnalis	P. exsul	Northiella [Genus]
A. dufresniana	P. derbyana	N. haematogaster [Species] Psephotus [Genus]
A. brasiliensis	P. longicauda	P. haematonotus [Species]
A. arausiaca	P. cyanocephala	P. varius
A. festiva	P. intermedia	
A. xanthops	P. himalayana	P. pulcherrimus P. chrysopterygius
A. barbadensis	P. calthorpae	Neophema [Genus]
A. aestiva	P. columboides	N. elegans [Species]
A. ochrocephala	Polytelis [Genus]	N. chrysostomus
A. amazonica	P. swainsonii [Species]	N. chrysogaster
A. mercenaria	P. anthopeplus	N. petrophila
A. farinosa	P. alexandrae	N. pulchella
A. vinacea	Aprosmictus [Genus]	N. splendida
A. guildingii	A. jonquillaceus [Species]	N. bourkii
A. versicolor	A. erythropterus	Eunymphicus [Genus]
A. imperialis	Alisterus [Genus]	E. cornutus [Species]
Deroptyus [Genus]	A. amboinensis [Species]	Cyanoramphus [Genus]
D. accipitrinus [Species]	A. chloropterus	C. unicolor [Species]
Triclaria [Genus]	A. scapularis	C. novaezelandiae
T. malachitacea [Species]	Prosopeia [Genus]	C. zealandicus
Poicephalus [Genus]	P. tabuensis [Species]	C. auriceps
P. robustus [Species]	P. personata	C. malherbi
P. gulielmi	Psittacella [Genus]	C. ulietanus
P. flavifrons	P. brehmii [Species]	Melopsittacus [Genus]
P. cryptoxanthus	P. picta	M. undulatus [Species]
P. senegalus	P. modesta	Pezoporus [Genus]
P. meyeri	Bolbopsittacus [Genus]	P. wallicus [Species]
P. rufiventris	B. lunulatus [Species]	Geopsittacus [Genus]
P. ruppellii	Psittinus [Genus]	G. occidentalis [Species]
Psittacus [Genus]	P. cyanurus [Species]	*
P. erithacus [Species]	Agapornis [Genus]	Cuculiformes [Order]
Coracopsis [Genus]	A. cana [Species]	Musophagidae [Family]
C. vasa [Species]	A. pullaria	Tauraco [Genus]
C. nigra	A. roseicollis	T. persa [Species]

T. livingstonii Misocalius [Genus] R. calyorbynchus [Species] T. corythaix M. osculans [Species] R. curvirostris T. schuttii Phaenicophaeus [Genus] Chrysococcyx [Genus] T. fischeri C. cupreus [Species] P. pyrrhocephalus [Species] T. erythrolophus Dasylophus [Genus] C. flavigularis D. superciliosus [Species] T. bannermani C. klaas Lepidogrammus [Genus] T. ruspolii C. caprius L. cumingi [Species] T. leucotis Chalcites [Genus] T. macrorbynchus Crotophaga [Genus] C. maculatus [Species] C. major [Species] T. bartlaubi C. xanthorhynchus C. ani T. leucolophus C. basalis C. sulcirostris Gallirex [Genus] C. lucidus G. porphyreolophus [Species] Guira [Genus] C. malayanus G. guira [Species] Ruwenzorornis [Genus] C. crassirostris Tapera [Genus] R. johnstoni [Species] C. ruficollis T. naevia [Species] Musophaga [Genus] C. meyeri M. violacea [Species] Morococcyx [Genus] Caliechthrus [Genus] M. erythropygus [Species] Corythaeola [Genus] C. leucolophus [Species] Dromococcyx [Genus] C. cristata [Species] Surniculus [Genus] D. phasianellus [Species] Crinifer [Genus] S. lugubris [Species] D. pavoninus C. leucogaster [Species] Microdynamis [Genus] Geococcyx [Genus] C. africanus M. parva [Species] G. californiana [Species] C. concolor Eudynamys [Genus] G. velox C. personata E. scolopacea [Species] Neomorphus [Genus] Urodynamis [Genus] Cuculidae [Family] N. geoffroyi [Species] U. taitensis [Species] Clamator [Genus] N. squaminger Scythrops [Genus] C. glandarius [Species] N. radiolosus S. novaehollandiae [Species] C. coromandus N. rufipennis Coccyzus [Genus] C. serratus N. pucheranii C. pumilus [Species] C. jacobinus Carpococcyx [Genus] C. cinereus C. cafer C. radiceus [Species] C. erythropthalmus Pachycoccyx [Genus] C. renauldi C. americanus P. audeberti [Species] Coua [Genus] C. euleri Cuculus [Genus] C. delalandei [Species] C. minor C. crassirostris [Species] C. gigas C. melacoryphus C. sparverioides C. coquereli C. lansbergi C. varius C. serriana Piaya [Genus] C. vagans C. reynaudii P. rufigularis [Species] C. fugax C. cursor P. pluvialis C. solitarius C. ruficeps P. cayana C. clamosus C. cristata P. melanogaster C. micropterus C. verreauxi P. minuta C. canorus C. caerulea Saurothera [Genus] C. saturatus Centropus [Genus] S. merlini [Species] C. poliocephalus C. milo [Species] S. vetula C. pallidus C. goliath Ceuthmochares [Genus] Cercococcyx [Genus] C. violaceus C. mechowi [Species] C. aereus [Species] C. menbeki C. olivinus Rhopodytes [Genus] C. ateralbus C. montanus R. diardi [Species] C. chalybeus Penthoceryx [Genus] R. sumatranus C. phasianinus P. sonneratii [Species] R. tristis C. spilopterus R. viridirostris Cacomantis [Genus] C. bernsteini C. merulinus [Species] Taccocua [Genus] C. chlororbynchus T. leschenaulti [Species] C. variolosus C. rectunguis C. castaneiventris Rhinortha [Genus] C. steerii C. heinrichi R. chlorophaea [Species] C. sinensis C. pyrrophanus Zanclostomus [Genus] C. andamanensis Rhamphomantis [Genus] Z. javanicus [Species] C. nigrorufus R. megarhynchus [Species] Rhamphococcyx [Genus] C. viridis

C. toulou	O. clarkii	Uroglaux [Genus]
C. bengalensis	O. albogularis	<i>Ū. dimorpha</i> [Species]
C. grillii	O. minimus	Ninox [Genus]
C. epomidis	O. leucotis	N. rufa [Species]
C. leucogaster	O. hartlaubi	N. strenua
C. anselli	Pyrroglaux [Genus]	N. connivens
C. monachus	P. podargina [Species]	N. novaeseelandiae
C. senegalensis	Mimizuku [Genus]	N. scutulata
C. superciliosus		N. affinis
	M. gurneyi [Species]	N. superciliaris
C. melanops	Jubula [Genus]	N. philippensis
C. celebensis	J. lettii [Species]	
C. unirufus	Lophostrix [Genus]	N. spilosoph ala
Strigiformes [Order]	L. cristata [Species]	N. spilocephala
Tytonidae [Family]	Bubo [Genus]	N. perversa
Tyto [Genus]	B. virginianus [Species]	N. squamipila
T. soumagnei [Species]	B. bubo	N. theomacha
T. alba	B. capensis	N. punctulata
	B. africanus	N. meeki
T. rosenbergii	B. poensis	N. solomonis
T. inexpectata	B. nipalensis	N. odiosa
T. novaehollandiae	B. sumatrana	N. jacquinoti
T. aurantia	B. shelleyi	Gymnoglaux [Genus]
T. tenebricosa	B. lacteus	G. lawrencii [Species]
T. capensis	B. coromandus	Sceloglaux [Genus]
T. longimembris	B. leucostictus	S. albifacies [Species]
Phodilus [Genus]		Athene [Genus]
P. badius [Species]	Pseudoptynx [Genus]	A. noctua [Species]
•	P. philippensis [Species]	A. brama
Strigidae [Family]	Ketupa [Genus]	A. blewitti
Otus [Genus]	K. blakstoni [Species]	Speotyto [Genus]
O. sagittatus [Species]	K. zeylonensis	S. cunicularia [Species]
O. rufescens	K. flavipes	Ciccaba [Genus]
O. icterorhynchus	K. ketupu	C. virgata [Species]
O. spilocephalus	Scotopelia [Genus]	C. nigrolineata
O. vandewateri	S. peli [Species]	C. huhula
O. balli	S. ussheri	
O. alfredi	S. bouvieri	C. albitarsus
O. brucei	Pulsatrix [Genus]	C. woodfordii
O. scops	P. perspicillata [Species]	Strix [Genus]
O. umbra	P. koeniswaldiana	S. butleri [Species]
	P. melanota	S. seloputo
O. senegalensis	Nyctea [Genus]	S. ocellata
O. flammeolus		S. leptogrammica
O. brookii	N. scandiaca [Species]	S. aluco
O. rutilus	Surnia [Genus]	S. occidentalis
O. manadensis	S. ulula [Species]	S. varia
O. beccarii	Glaucidium [Genus]	S. hylophila
O. silvicola	G. passerinum [Species]	S. rufipes
O. whiteheadi	G. gnoma	S. uralensis
O. insularis	G. siju	S. davidi
O. bakkamoena	G. minutissimum	S. nebulosa
O. asio	G. jardinii	Rhinoptynx [Genus]
O. trichopsis	G. brasilianum	R. clamator [Species]
O. barbarus	G. perlatum	Asio [Genus]
O. guatemalae	G. tephronotum	A. otus [Species]
O. roboratus	G. capense	A. stygius
O. cooperi	G. brodiei	
O. choliba	G. radiatum	A. abyssinicus
	G. vuutuum G. cuculoides	A. madagascariensis
O. atricapillus		A. flammeus
O. ingens	G. sjostedti	A. capensis
O. watsonii	Micrathene [Genus]	Pseudoscops [Genus]
O. nudipes	M. whitneyi [Species]	P. grammicus [Species]

E. diabolicus Nesasio [Genus] Macrodipteryx [Genus] N. solomonensis [Species] E. papuensis M. longipennis [Species] E. archboldi Semeiophorus [Genus] Aegolius [Genus] E. temminckii S. vexillarius [Species] A. funereus [Species] E. macrotis Hydropsalis [Genus] A. acadicus A. ridgwayi Veles [Genus] H. climacocerca [Species] V. binotatus [Species] A. harrisii H. brasiliana *Nyctidromus* [Genus] Uropsalis [Genus] Caprimulgiformes [Order] N. albicollis [Species] U. segmentata [Species] Steatornithidae [Family] Phalaenoptilus [Genus] U. lyra Steatornis [Genus] P. nuttallii [Species] Macropsalis [Genus] S. caripensis [Species] Siphonorhis [Genus] M. creagra [Species] S. americanus [Species] Eleothreptus [Genus] Podargidae [Family] Otophanes [Genus] E. anomalus [Species] Podargus [Genus] O. mcleodii [Species] P. strigoides [Species] **Apodiformes** [Order] O. yucatanicus P. papuensis Nyctiphrynus [Genus] P. ocellatus Apodidae [Family] N. ocellatus [Species] Batrachostomus [Genus] Collocalia [Genus] Caprimulgus [Genus] C. gigas [Species] B. auritus [Species] C. carolinensis [Species] C. whiteheadi B. harteri C. rufus B. septimus C. lowi C. cubanensis B. stellatus C. fuciphaga C. sericocaudatus B. moniliger C. brevirostris C. ridgwayi B. hodgsoni C. francica C. vociferus B. poliolophus C. inexpectata C. saturatus B. javensis C. inquieta C. longirostris B. affinis C. vanikorensis C. cayennensis C. leucophaea C. maculicaudus Nyctibiidae [Family] C. vestita C. parvulus Nyctibius [Genus] C. spodiopygia C. maculosus N. grandis [Species] C. birundinacea C. nigrescens N. aethereus C. troglodytes C. birundinaceus N. griseus C. marginata C. ruficollis N. leucopterus C. esculenta C. indicus N. bracteatus Hirundapus [Genus] C. europaeus H. caudacutus [Species] C. aegyptius Aegothelidae [Family] H. giganteus C. mahrattensis Aegotheles [Genus] H. ernsti C. nubicus A. crinifrons [Species] Streptoprocne [Genus] C. eximius A. insignis S. zonaris [Species] C. madagascariensis A. cristatus S. biscutata C. macrurus A. savesi Aerornis [Genus] A. bennettii C. pectoralis A. senex [Species] C. rufigena A. wallacii A. semicollaris C. donaldsoni A. albertisi Chaetura [Genus] C. poliocephalus Caprimulgidae [Family] C. chapmani [Species] C. asiaticus Lurocalis [Genus] C. pelagica C. natalensis L. semitorquatus [Species] C. vauxi C. inornatus Chordeiles [Genus] C. richmondi C. stellatus C. pusillus [Species] C. ludovicianus C. gaumeri C. rupestris C. monticolus C. leucopygialis C. acutipennis C. affinis C. sabini C. minor C. tristigma C. thomensis Nyctiprogne [Genus] C. sylvatica C. concretus N. leucopyga [Species] C. pulchellus C. nubicola C. cinereiventris Podager [Genus] C. enarratus P. nacunda [Species] C. spinicauda C. batesi Eurostopodus [Genus] Scotornis [Genus] C. martinica E. guttatus [Species] C. rutila S. fossii [Species] E. albogularis S. climacurus C. ussheri

C. andrei	R. naevius [Species]	A. nigricollis
C. melanopygia	R. dohrnii	A. veraguensis
C. brachyura	Glaucis [Genus]	A. dominicus
Zoonavena [Genus]	G. hirsuta [Species]	A. viridis
Z. grandidieri [Species]	Threnetes [Genus]	A. mango
Mearnsia [Genus]	T. niger [Species]	Avocettula [Genus]
M. picina [Species]	T. leucurus	A. recurvirostris [Species]
M. novaeguineae	T. ruckeri	Eulampis [Genus]
M. cassini	Phaethornis [Genus]	E. jugularis [Species]
M. bohmi	P. yaruqui [Species]	Sericotes [Genus]
Cypseloides [Genus]	P. guy	S. holosericeus [Species]
C. cherriei [Species]	P. syrmatophorus	Chrysolampis [Genus]
C. fumigatus	P. superciliosus	C. mosquitus [Species]
C. major	P. malaris	Orthorhyncus [Genus]
Nephoecetes [Genus]	P. eurynome	O. cristatus [Species]
N. niger [Species]	P. hispidus	Klais [Genus]
Apus [Genus]	P. anthophilus	K. guimeti [Species]
A. melba [Species]	P. bourcieri	Abeillia [Genus]
A. aequatorialis	P. philippii	A. albeillei [Species]
A. reichenowi	_ 1 111	Stephanoxis [Genus]
	P. squalidus	S. lalandi [Species]
A. apus A. sladeniae	P. augusti	Lophornis [Genus]
A. toulsoni	P. pretrei	L. ornata [Species]
	P. subochraceus	L. gouldii
A. pallidus A. acuticaudus	P. nattereri	L. magnifica
	P. gounellei	L. delattrei
A. pacificus A. unicolor	P. rupurumii	L. stictolopha
	P. porcullae	L. melaniae
A. myoptilus	P. ruber	Polemistria [Genus]
A. batesi	P. griseogularis	P. chalybea [Species]
A. caffer	P. longuemareus	P. pavonina
A. horus	P. zonura	Lithiophanes [Genus]
A. affinis	Eutoxeres [Genus]	L. insignibarbis [Species]
A. andecolus	E. aquila [Species]	Paphosia [Genus]
Aeronautes [Genus]	E. condamini	P. helenae [Species]
A. saxatalis [Species]	Phaeochroa [Genus]	P. adorabilis
A. montivagus	P. cuvierii [Species]	Popelairia [Genus]
Panyptila [Genus]	Campylopterus [Genus]	P. popelairii [Species]
P. sanctihieronymi [Species]	C. curvipennis [Species]	P. langsdorffi
P. cayennensis	C. largipennis	P. letitiae
Tachornis [Genus]	C. rufus	P. conversii
T. phoenicobia [Species]	C. hyperythrus	Discosura [Genus]
Micropanyptila [Genus]	C. hemileucurus	D. longicauda [Species]
M. furcata [Species]	C. ensipennis	Chlorestes [Genus]
Reinarda [Genus]	C. falcatus	C. notatus [Species]
R. squamata [Species]	C. phainopeplus	Chlorostilbon [Genus]
Cypsiurus [Genus]	C. villaviscensio	C. prasinus [Species]
C. parvus [Species]	Eupetomana [Genus]	C. vitticeps
Hemiprocnidae [Family]	E. macroura [Species]	C. aureoventris
Hemiprocne [Genus]	Florisuga [Genus]	C. canivetti
H. longipennis [Species]	F. mellivora [Species]	C. ricordii
H. mystacea	Melanotrochilus [Genus]	C. swainsonii
H. comata	M. fuscus [Species]	C. maugaeus
11. commu	Colibri [Genus]	C. russatus
Trochilidae [Family]	C. delphinae [Species]	C. gibsoni
Doryfera [Genus]	C. thalassinus	C. inexpectatus
D. johannae [Species]	C. coruscans	C. stenura
D. ludovicae	C. serrirostris	C. alice
Androdon [Genus]	Anthracothorax [Genus]	C. poortmani
A. aequatorialis [Species]	A. viridigula [Species]	C. euchloris
Ramphodon [Genus]	A. prevostii	C. auratus

A. luciae Cynanthus [Genus] Heliodoxa [Genus] C. sordidus [Species] A. fimbriata H. rubinoides [Species] A. lactea C. latirostris H. leadbeateri Ptochoptera [Genus] A. amabilis H. jacula A. cyaneotincta P. iolaima [Species] H. xanthogonys A. rosenbergi Cyanophaia [Genus] Ionolaima [Genus] C. bicolor [Species] A. boucardi I. schreibersii [Species] A. franciae Thalurania [Genus] Agapeta [Genus] A. veneta T. furcata [Species] A. gularis [Species] A. leucogaster T. watertonii Lampraster [Genus] A. cyanocephala T. glaucopis L. branickii [Species] A. microrhyncha T. lerchi Eugenia [Genus] A. cyanifrons Neolesbia [Genus] E. imperatrix [Species] A. beryllina N. nehrkorni [Species] Eugenes [Genus] A. cyanura Panterpe [Genus] E. fulgens [Species] A. saucerrottei P. insignis [Species] *Hylonympha* [Genus] A. tobaci Damophila [Genus] H. macrocerca [Species] A. viridigaster D. julie [Species] Sternoclyta [Genus] A. edward Lepidopyga [Genus] S. cyanopectus [Species] A. rutila L. coeruleogularis [Species] Topaza [Genus] A. yucatanensis L. goudoti T. pella [Species] A. tzacatl L. luminosa T. pyra A. castaneiventris Hylocharis [Genus] Oreotrochilus [Genus] A. amazilia H. xantusii [Species] O. chimborazo [Species] A. violiceps H. leucotis O. stolzmanni Eupherusa [Genus] H. eliciae O. melanogaster E. eximia [Species] O. estella H. sapphirina E. nigriventris O. bolivianus H. cyanus Elvira [Genus] H. chrysura O. leucopleurus E. chionura [Species] O. adela H. grayi E. cupreiceps Chrysuronia [Genus] Urochroa [Genus] Microchera [Genus] C. oenone [Species] U. bougueri [Species] M. albocoronata [Species] Patagona [Genus] Goldmania [Genus] Chalybura [Genus] G. violiceps [Species] P. gigas [Species] C. buffonii [Species] Goethalsia [Genus] Aglaeactis [Genus] C. urochrysia G. bella [Species] A. cupripennis [Species] Aphantochroa [Genus] Trochilus [Genus] A. aliciae A. cirrochloris [Species] A. castelnaudii T. polytmus [Species] Lampornis [Genus] Leucochloris [Genus] A. pamela L. clemenciae [Species] L. albicollis [Species] Lafresnaya [Genus] L. amethystinus Polytmus [Genus] L. lafresnayi [Species] L. viridipallens P. guainumbi [Species] Pterophanes [Genus] L. hemileucus Waldronia [Genus] P. cyanopterus [Species] L. castaneoventris W. milleri [Species] Coeligena [Genus] L. cinereicauda Smaragdites [Genus] C. coeligena [Species] Lamprolaima [Genus] S. theresiae [Species] C. wilsoni L. rhami [Species] Leucippus [Genus] C. prunellei Adelomyia [Genus] L. fallax [Species] C. torquata A. melanogenys [Species] C. phalerata L. baeri Anthocephala [Genus] C. eos L. chionogaster A. floriceps [Species] C. bonapartei L. viridicauda Urosticte [Genus] Talaphorus [Genus] U. ruficrissa [Species] C. helianthea T. hypostictus [Species] C. lutetiae U. benjamini T. taczanowskii C. violifer Phlogophilus [Genus] T. chlorocercus P. hemileucurus [Species] C. iris Amazilia [Genus] P. harterti Ensifera [Genus] A. candida [Species] E. ensifera [Species] Clytolaema [Genus] A. chionopectus C. rubricauda [Species] Sephanoides [Genus] A. versicolor Polyplancta [Genus] S. sephanoides [Species] A. hollandi P. aurescens [Species] S. fernandensis

Boissoneaua [Genus]	Oxypogon [Genus]	Atthis [Genus]
B. flavescens [Species]	O. guerinii [Species]	A. heloisa [Species]
B. matthewsii	Opisthoprora [Genus]	Myrtis [Genus]
B. jardini	O. euryptera [Species]	M. fanny [Species]
Heliangelus [Genus]	Taphrolesbia [Genus]	Eulidia [Genus]
H. mavors [Species]	T. griseiventris [Species]	E. yarrellii [Species]
H. clarisse		Myrmia [Genus]
	Aglaiocercus [Genus]	
H. amethysticollis	A. kingi [Species]	M. micrura [Species]
H. strophianus	A. emmae	Acestrura [Genus]
H. exortis	A. coelestis	A. mulsanti [Species]
H. viola	Oreonympha [Genus]	A. decorata
H. micraster	O. nobilis [Species]	A. bombus
H. squamigularis	Augastes [Genus]	A. heliodor
H. speciosa	A. scutatus [Species]	A. berlepschi
H. rothschildi	A. lumachellus	A. harteri
H. luminosus	Schistes [Genus]	Chaetocercus [Genus]
Eriocnemis [Genus]	S. geoffroyi [Species]	C. jourdanii [Species]
E. nigrivestis [Species]	Heliothryx [Genus]	Selasphorus [Genus]
E. soderstromi	H. barroti [Species]	S. platycercus [Species]
E. vestitus	H. aurita	S. rufus
E. godini	Heliactin [Genus]	S. sasin
E. cupreoventris	H. cornuta [Species]	S. flammula
E. luciani	Loddigesia [Genus]	S. torridus
E. isaacsonii	L. mirabilis [Species]	S. simoni
E. mosquera	Heliomaster [Genus]	S. ardens
E. glaucopoides	H. constantii [Species]	S. scintilla
E. alinae	H. longirostris	6 106 10 10
E. derbyi	H. squamosus	Coliiformes [Order]
Haplophaedia [Genus]	H. furcifer	Coliidae [Family]
H. aureliae [Species]	Rhodopis [Genus]	Colius [Genus]
H. lugens	R. vesper [Species]	C. striatus [Species]
Ocreatus [Genus]	Thaumastura [Genus]	C. castanotus
O. underwoodii [Species]	T. cora [Species]	C. colius
Lesbia [Genus]	Philodice [Genus]	C. leucocephalus
L. victoriae [Species]	P. evelynae [Species]	C. indicus
L. nuna	P. bryantae	C. macrourus
Sappho [Genus]	P. mitchellii	Trogoniformes [Order]
S. sparganura [Species]	Doricha [Genus]	Trogonidae [Family]
Polyonymus [Genus]	D. enicura [Species]	Pharomachrus [Genus]
	D. eliza	
P. caroli [Species] Zodalia [Genus]	Tilmatura [Genus]	P. mocinno [Species]
	T. dupontii [Species]	P. fulgidus
Z. glyceria [Species]	4	P. pavoninus
Ramphomicron [Genus]	Microstilbon [Genus]	Euptilotis [Genus]
R. microrhynchum [Species]	M. burmeisteri [Species]	E. neoxenus [Species]
R. dorsale	Calothorax [Genus]	Priotelus [Genus]
Metallura [Genus]	C. lucifer [Species]	P. temnurus [Species]
M. phoebe [Species]	C. pulcher	Temnotrogon [Genus]
M. theresiae	Archilochus [Genus]	T. roseigaster [Species]
M. purpureicauda	A. colubris [Species]	Trogon [Genus]
M. aeneocauda	A. alexandri	T. massena [Species]
M. melagae	Calliphlox [Genus]	T. clathratus
M. eupogon	C. amethystina [Species]	T. melanurus
M. williami	Mellisuga [Genus]	T. strigilatus
M. tyrianthina	M. minima [Species]	T. citreolus
M. ruficeps	Calypte [Genus]	T. mexicanus
Chalcostigma [Genus]	C. anna [Species]	T. elegans
C. olivaceum [Species]	C. costae	T. collaris
C. stanleyi	C. helenae	T. aurantiiventris
C. heteropogon	Stellula [Genus]	T. personatus
C. herrani	S. calliope [Species]	T. rufus

T. surrucura	Pelargopsis [Genus]	T. riedelii
T. curucui	P. amauroptera [Species]	T. carolinae
T. violaceus	P. capensis	T. ellioti
Apaloderma [Genus]	P. melanorhyncha	T. nympha
A. narina [Species]	Lacedo [Genus]	T. ďanae
A. aequatoriale	L. pulchella [Species]	T. sylvia
Heterotrogon [Genus]	Dacelo [Genus]	· ·
H. vittatus [Species]	D. novaeguineae [Species]	Todidae [Family]
Harpactes [Genus]	D. leachii	Todus [Genus]
H. reinwardtii [Species]	D. tyro	T. multicolor [Species]
H. fasciatus	D. gaudichaud	T. angustirostris
H. kasumba	Clytoceyx [Genus]	T. todus
H. diardii	C. rex [Species]	T. mexicanus
H. ardens	Melidora [Genus]	T. subulatus
H. whiteheadi	M. macrorrhina [Species]	M 11 FD 111
H. orrhophaeus	Cittura [Genus]	Momotidae [Family]
H. duvaucelii		Hylomanes [Genus]
H. oreskios	C. cyanotis [Species]	H. momotula [Species]
H. erythrocephalus	Halcyon [Genus]	Aspatha [Genus]
H. wardi	H. coromanda [Species]	A. gularis [Species]
11. www	H. badia	Electron [Genus]
Coraciiformes [Order]	H. smyrnensis	E. platyrhynchum [Species]
Alcedinidae [Family]	H. pileata	E. carinatum
Ceryle [Genus]	H. cyanoventris	Eumomota [Genus]
C. lugubris [Species]	H. leucocephala	E. superciliosa [Species]
C. maxima	H. senegalensis	Baryphthengus [Genus]
C. torquata	H. senegaloides	B. ruficapillus [Species]
C. alcyon	H. malimbica	Momotus [Genus]
C. rudis	H. albiventris	M. mexicanus [Species]
Chloroceryle [Genus]	H. chelicuti	M. momota
C. amazona [Species]	H. nigrocyanea	
C. americana	H. winchelli	Meropidae [Family]
C. inda	H. diops	Dicrocercus [Genus]
C. aenea	H. macleayii	D. hirundineus [Species]
Alcedo [Genus]	H. albonotata	Melittophagus [Genus]
A. hercules [Species]	H. leucopygia	M. revoilii [Species]
A. atthis	H. farquhari	M. pusillus
A. semitorquata	H. pyrrhopygia	M. variegatus
A. meninting	H. torotoro	M. lafresnayii
A. quadribrachys	H. megarhyncha	M. bullockoides
A. euryzona	H. australasia	M. bulocki
A. coerulescens	H. sancta	M. gularis
A. cristata	H. cinnamomina	M. mulleri
A. leucogaster	H. funebris	Aerops [Genus]
Myioceyx [Genus]	H. chloris	A. albicollis [Species]
M. lecontei [Species]	H. saurophaga	A. boehmi
Ispidina [Genus]	H. recurvirostris	Merops [Genus]
	H. venerata	M. leschenaulti [Species]
I. picta [Species]	H. tuta	M. apiaster
I. madagascariensis Ceyx [Genus]	H. gambieri	M. superciliosus
	H. godeffroyi	M. ornatus
C. cyanopectus [Species]	H. miyakoensis	M. orientalis
C. argentatus	H. bougainvillei	M. viridis
C. goodfellowi	H. concreta	M. malimbicus
C. lepidus		M. nubicus
C. azureus	H. lindsayi H. fulcida	M. nubicoides
C. websteri	H. fulgida	
C. pusillus	H. monacha	Bombylonax [Genus]
C. erithacus	H. princeps	B. breweri [Species]
C. rufidorsum	Tanysiptera [Genus]	Nyctyornis [Genus]
C. melanurus	T. hydrocharis [Species]	N. amicta [Species]
C. fallax	T. galatea	N. athertoni

Meropogon [Genus] Ptiloaemus [Genus] Facamerops [Genus] M. forsteni [Species] P. tickelli [Species] 7. aurea [Species] Anorrhinus [Genus] Leptosomatidae [Family] Bucconidae [Family] A. galeritus [Species] Leptosomus [Genus] Notharchus [Genus] Penelopides [Genus] L. discolor [Species] N. macrorhynchos [Species] P. panini [Species] N. pectoralis P. exarhatus Coraciidae [Family] N. ordii Aceros [Genus] Brachypteracias [Genus] N. tectus A. nipalensis [Species] B. leptosomus [Species] Bucco [Genus] A. corrugatus B. squamigera B. macrodactylus [Species] A. leucocephalus Atelornis [Genus] B. tamatia A. cassidix A. pittoides [Species] B. noanamae A. crossleyi A. undulatus B. capensis A. plicatus Uratelornis [Genus] Nystalus [Genus] A. everetti U. chimaera [Species] N. radiatus [Species] A. narcondami Coracias [Genus] N. chacuru Anthracoceros [Genus] C. garrulus [Species] N. striolatus A. malayanus [Species] C. abyssinica N. maculatus C. caudata A. malabaricus Hypnelus [Genus] C. spatulata A. coronatus H. ruficollis [Species] C. noevia A. montani H. bicinctus C. benghalensis A. marchei Malacoptila [Genus] C. temminckii Bycanistes [Genus] M. striata [Species] C. cyanogaster B. bucinator [Species] M. fusca Eurystomus [Genus] B. cylindricus M. fulvogularis E. glaucurus [Species] B. subcylindricus M. rufa E. gularis B. brevis E. orientalis M. panamensis Ceratogymna [Genus] M. mystacalis C. atrata [Species] Upupidae [Family] Micromonacha [Genus] C. elata *Upupa* [Genus] M. lanceolata [Species] Buceros [Genus] *U. epops* [Species] Nonnula [Genus] B. rhinoceros [Species] N. rubecula [Species] B. bicornis Phoeniculidae [Family] N. sclateri B. hydrocorax Phoeniculus [Genus] N. brunnea Rhinoplax [Genus] P. purpureus [Species] N. frontalis R. vigil [Species] P. bollei N. ruficapilla P. castaneiceps Bucorvus [Genus] N. amaurocephala P. aterrimus B. abyssinicus [Species] Hapaloptila [Genus] Rhinopomastus [Genus] B. leadheateri H. castanea [Species] R. minor [Species] Piciformes [Order] Monasa [Genus] R. cyanomelas Galbulidae [Family] M. atra [Species] Bucerotidae [Family] Galbalcyrhynchus [Genus] M. nigrifrons Tockus [Genus] G. leucotis [Species] T. birostris [Species] M. morphoeus Brachygalba [Genus] T. fasciatus M. flavirostris B. lugubris [Species] T. alboterminatus Chelidoptera [Genus] B. phaeonota T. bradfieldi C. tenebrosa [Species] B. goeringi T. pallidirostris B. salmoni Capitonidae [Family] T. nasutus B. albogularis Capito [Genus] T. hemprichii Facamaralcyon [Genus] C. aurovirens [Species] T. monteiri 7. tridactyla [Species] C. maculicoronatus T. griseus T. hartlaubi Galbula [Genus] C. squamatus C. hypoleucus T. camurus G. albirostris [Species] G. galbula C. dayi T. erythrorhynchus C. quinticolor T. flavirostris G. tombacea C. niger T. deckeni G. cyanescens G. pastazae Eubucco [Genus] T. jacksoni Berenicornis [Genus] G. ruficauda E. richardsoni [Species] E. bourcierii B. comatus [Species] G. leucogastra G. dea E. versicolor B. albocristatus

Semnornis [Genus] Lybius [Genus] Selenidera [Genus] S. frantzii [Species] L. undatus [Species] S. spectabilis [Species] S. ramphastinus L. vieilloti S. culik Psilopogon [Genus] L. torquatus S. reinwardtii L. guifsobalito S. langsdorffi P. pyrolophus [Species] L. rubrifacies S. nattereri Megalaima [Genus] M. virens [Species] L. chaplini S. maculirostris L. leucocephalus M. lagrandieri Andigena [Genus] A. bailloni [Species] M. zeylanica L. minor A. laminirostris M. viridis L. melanopterus A. hypoglauca M. faiostricta L. bidentatus A. cucullata M. corvina L. dubius L. rolleti A. nigrirostris M. chrysopogon Ramphastos [Genus] Trachyphonus [Genus] M. rafflesii R. vitellinus [Species] M. mystacophanos T. purpuratus [Species] R. dicolorus T. vaillantii M. javensis R. citreolaemus M. flavifrons T. erythrocephalus R. sulfuratus T. darnaudii M. franklinii R. swainsonii T. margaritatus M. oorti R. ambiguus M. asiatica Indicatoridae [Family] R. aurantiirostris M. incognita Prodotiscus [Genus] R. tucanus M. henricii P. insignis [Species] R. cuvieri M. armillaris P. regulus R. inca M. pulcherrima Melignomon [Genus] R. toco M. robustirostris M. zenkeri [Species] M. australis Picidae [Family] indicator [Genus] M. eximia *7ynx* [Genus] I. exilis [Species] M. rubricapilla 7. torquilla [Species] I. propinguus M. haemacephala 7. ruficollis I. minor Calorhamphus [Genus] Picumnus [Genus] I. conirostris C. fuliginosus [Species] P. cinnamomeus [Species] I. variegatus Gymnobucco [Genus] P. rufiventris I. maculatus G. calvus [Species] P. fuscus I. archipelagicus G. peli P. castelnau I. indicator G. sladeni P. leucogaster I. xanthonotus G. bonapartei P. limae Melichneutes [Genus] Smilorhis [Genus] P. olivaceus M. robustus [Species] S. leucotis [Species] P. granadensis Stactolaema [Genus] Ramphastidae [Family] P. nebulosus S. olivacea [Species] Aulacorhynchus [Genus] P. exilis S. anchietae A. sulcatus [Species] P. borbae S. whytii A. calorhynchus P. aurifrons Pogoniulus [Genus] A. derbianus P. temminckii P. duchaillui [Species] A. prasinus P. cirratus P. scolopaceus A. haematopygus P. sclateri P. leucomystax A. coeruleicinctis P. steindachneri P. simplex A. huallagae P. squamulatus P. coryphaeus Pteroglossus [Genus] P. minutissimus P. pusillus P. torquatus [Species] P. pallidus P. chrysoconus P. sanguineus P. albosquamatus P. bilineatus P. erythropygius P. guttifer P. subsulphureus P. castanotis P. varzeae P. atroflavus P. aracari P. pygmaeus Tricholaema [Genus] P. pluricinctus P. asterias T. lacrymosum [Species] P. viridis P. pumilus T. leucomelan P. bitorquatus P. innominatus T. diadematum P. olallae Nesoctites [Genus] T. melanocephalum P. flavirostris N. micromegas [Species] T. flavibuccale P. mariae Verreauxia [Genus] P. beauharnaesii T. hirsutum V. africana [Species]

Sasia [Genus]	P. viridanus	S. varius [Species]
S. ochracea [Species]	P. vittatus	S. thyroideus
S. abnormis	P. xanthopygaeus	Trichopicus [Genus]
Geocolaptes [Genus]	P. canus	T. cactorum [Species]
G. olivaceus [Species]	P. rabieri	Veniliornis [Genus]
Colaptes [Genus]	P. erythropygius	V. fumigatus [Species]
C. cafer [Species]	P. flavinucha	V. spilogaster
C. auratus	P. puniceus	V. passerinus
C. chrysoides	P. chlorolophus	V. frontalis
C. rupicola	P. mentalis P. mineaceus	V. maculifrons V. cassini
C. pitius C. campestris	Dinopium [Genus]	v . cassını V. affinis
Nesoceleus [Genus]	D. benghalense [Species]	V. kirkii
N. fernandinae [Species]	D. shorii	V. callonotus
Chrysoptilus [Genus]	D. javanense	V. sanguineus
C. melanochloros [Species]	D. rafflesii	V. dignus
C. punctigula	Gecinulus [Genus]	V. nigriceps
C. atricollis	G. grantia [Species]	Dendropicos [Genus]
Piculus [Genus]	G. viridis	D. fuscescens [Species]
P. rivolii [Species]	Meiglyptes [Genus]	D. stierlingi
P. auricularis	M. tristis [Species]	D. elachus
P. aeruginosus	M. jugularis	D. abyssinicus
P. rubiginosus	M. tukki	D. poecilolaemus
P. simplex	Mulleripicus [Genus]	D. gabonensis
P. flavigula	M. pulverulentus [Species]	D. lugubris
P. leucolaemus	M. funebris	Dendrocopos [Genus]
P. aurulentus	M. fuliginosus	D. major [Species]
P. chrysochloros	M. fulvus	D. leucopterus
Campethera [Genus]	Dryocopus [Genus]	D. syriacus
C. punctuligera [Species]	D. martius [Species]	D. assimilis
C. nubica C. bennettii	D. javensis	D. himalayensis
C. cailliautii	D. pileatus D. lineatus	D. darjellensis D. medius
C. notata	D. erythrops	D. leucotos
C. abingoni	D. schulzi	D. cathpharius
C. taeniolaema	D. galeatus	D. hyperythrus
C. tullbergi	Asyndesmus [Genus]	D. auriceps
C. maculosa	A. lewis [Species]	D. atratus
C. permista	Melanerpes [Genus]	D. macei
C. caroli	M. erythrocephalus [Species]	D. mahrattensis
C. nivosa	M. portoricensis	D. minor
Celeus [Genus]	M. herminieri	D. canicapillus
C. flavescens [Species]	M. formicivorus	D. wattersi
C. spectabilis	M. hypopolius	D. kizuki
C. castaneus	M. carolinus	D. moluccensis
C. immaculatus	M. aurifrons	D. maculatus
C. elegans	M. chrysogenys	D. temminckii
C. jumana	M. superciliaris	D. obsoletus
C. grammicus	M. caymanensis	D. dorae
C. loricatus C. undatus	M. radiolatus M. striatus	D. albolarvatus D. villosus
C. flavus C. torquatus	M. rubricapillus M. pucherani	D. pubescens D. borealis
Micropternus [Genus]	M. chrysauchen	D. nuttallii
M. brachyurus [Species]	M. flavifrons	D. scalaris
Picus [Genus]	M. cruentatus	D. arizonae
P. viridis [Species]	M. rubrifrons	D. stricklandi
P. vaillantii	Leuconerpes [Genus]	D. mixtus
P. awokera	L. candidus [Species]	D. lignarius
P. squamatus	Sphyrapicus [Genus]	Picoides [Genus]
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P. tridactylus [Species] C. viridis [Species] Campylorhamphus [Genus] C. hosii C. pucherani [Species] P. arcticus C. whiteheadi C. trochilirostris Sapheopipo [Genus] C. pusillus S. noguchii [Species] Dendrocolaptidae [Family] C. procurvoides *Xiphidiopicus* [Genus] Dendrocincla [Genus] X. percussus [Species] D. tyrannina [Species] Furnariidae [Family] Polipicus [Genus] D. macrorhyncha Geobates [Genus] P. johnstoni [Species] D. fuliginosa G. poecilopterus [Species] P. elliotii D. anabatina Geositta [Genus] Mesopicos [Genus] D. merula G. maritima [Species] M. goertae [Species] D. homochroa G. peruviana M. griseocephalus Deconychura [Genus] G. saxicolina Thripias [Genus] D. longicauda [Species] G. isabellina T. namaguus [Species] D. stictolaema G. rufipennis T. xantholophus Sittasomus [Genus] G. punensis T. pyrrhogaster S. griseicapillus [Species] G. cunicularia Hemicircus [Genus] Glyphorynchus [Genus] G. antarctica H. concretus [Species] G. spirurus [Species] G. tenuirostris H. canente Drymornis [Genus] G. crassirostris Blythipicus [Genus] D. bridgesii [Species] Upucerthia [Genus] Nasica [Genus] B. pyrrhotis [Species] U. dumetaria [Species] N. longirostris [Species] B. rubiginosus U. albigula Dendrexetastes [Genus] Chrysocolaptes [Genus] U. validirostris D. rufigula [Species] C. validus [Species] U. serrana Hylexetastes [Genus] C. festivus U. andaecola H. perrotii [Species] C. lucidus Ochetorhynchus [Genus] H. stresemanni Phloeoceastes [Genus] O. ruficaudus [Species] Xiphocolaptes [Genus] P. guatemalensis [Species] O. certhioides X. promeropirhynchus [Species] P. melanoleucos O. harteri X. albicollis P. leucopogon Eremobius [Genus] X. falcirostris P. rubricollis E. phoenicurus [Species] X. franciscanus P. robustus Chilia [Genus] X. major P. pollens C. melanura [Species] Dendrocolaptes [Genus] P. haematogaster Cinclodes [Genus] D. certhia [Species] Campephilus [Genus] C. antarcticus [Species] D. concolor C. principalis [Species] C. patagonicus D. hoffmannsi C. imperialis C. oustaleti D. picumnus C. magellanicus C. fuscus D. platyrostris C. comechingonus Xiphorhynchus [Genus] Passeriformes [Order] C. atacamensis X. picus [Species] Eurylaimidae [Family] C. palliatus X. necopinus Smithornis [Genus] C. taczanowskii X. obsoletus S. capensis [Species] C. nigrofumosus X. ocellatus S. rufolateralis C. excelsior X. spixii S. sharpei Clibanornis [Genus] X. elegans Pseudocalyptomena [Genus] C. dendrocolaptoides [Species] X. pardalotus P. graueri [Species] Furnarius [Genus] X. guttatus Corydon [Genus] F. rufus [Species] X. flavigaster C. sumatranus [Species] F. leucopus X. striatigularis Cymbirhynchus [Genus] F. torridus X. lachrymosus C. macrorhynchos [Species] X. erythropygius F. minor Eurylaimus [Genus] X. triangularis F. figulus E. javanicus [Species] Lepidocolaptes [Genus] F. cristatus E. ochromalus Limnornis [Genus] L. leucogaster [Species] E. steerii L. curvirostris [Species] L. souleyetii Serilophus [Genus] L. angustirostris Sylviorthorhynchus [Genus] S. lunatus [Species] L. affinis S. desmursii [Species] Psarisomus [Genus] L. squamatus Aphrastura [Genus] P. dalhousiae [Species] L. fuscus A. spinicauda [Species]

L. albolineatus

Calyptomena [Genus]

A. masafuerae

Phleocryptes [Genus]	Poecilurus [Genus]	Coryphistera [Genus]
P. melanops [Species]	P. candei [Species]	C. alaudina [Species]
Leptasthenura [Genus]	P. kollari	Anumbius [Genus]
L. andicola [Species]	P. scutatus	A. annumbi [Species]
L. striata	Cranioleuca [Genus]	Siptornis [Genus]
L. pileata	C. sulphurifera [Species]	S. striaticollis [Species]
L. xenothorax	C. semicinerea	Xenerpestes [Genus]
L. striolata	C. obsoleta	X. minlosi [Species]
L. aegithaloides	C. pyrrhophia	X. singularis
L. platensis	C. subcristata	Metopothrix [Genus]
L. fuliginiceps	C. hellmayri	M. aurantiacus [Species]
L. yanacensis	C. curtata	Roraimia [Genus]
L. setaria	C. furcata	R. adusta [Species]
Spartonoica [Genus]	C. demissa	Margarornis [Genus]
S. maluroides [Species]	C. erythrops	M. squamiger [Species]
Schizoeaca [Genus]	C. vulpina	M. bellulus
S. coryi [Species]	C. pallida	M. rubiginosus
S. fuliginosa	C. antisiensis	M. stellatus
S. griseomurina	C. marcapatae	Premnornis [Genus]
S. palpebralis	C. albiceps	P. guttuligera [Species]
S. ĥelleri	C. baroni	Premnoplex [Genus]
S. harterti	C. albicapilla	P. brunnescens [Species]
Schoeniophylax [Genus]	C. mulleri	Pseudocolaptes [Genus]
S. phryganophila [Species]	C. gutturata	P. lawrencii [Species]
Oreophylax [Genus]	Siptornopsis [Genus]	P. boissonneautii
O. moreirae [Species]	S. hypochondriacus [Species]	Berlepschia [Genus]
Synallaxis [Genus]	Asthenes [Genus]	B. rikeri [Species]
S. ruficapilla [Species]	A. pyrrholeuca [Species]	Pseudoseisura [Genus]
S. superciliosa	A. dorbignyi	P. cristata [Species]
S. poliophrys	A. berlepschi	P. lophotes
S. azarae	A. baeri	P. gutturalis
S. frontalis	A. patagonica	Hyloctistes [Genus]
S. moesta	A. steinbachi	H. subulatus [Species]
S. cabanisi	A. humicola	Ancistrops [Genus]
S. spixi	A. modesta	A. strigilatus [Species]
S. hypospodia	A. pudibunda	Anabazenops [Genus]
S. subpudica	A. ottonis	A. fuscus [Species]
S. albescens	A. heterura	Syndactyla [Genus]
S. brachyura	A. wyatti	S. rufosuperciliata [Species]
S. albigularis	A. humilis	S. subalaris
S. gujanensis	A. anthoides	S. guttulata
S. propinqua	A. sclateri	S. mirandae
S. cinerascens	A. hudsoni	Simoxenops [Genus]
S. tithys	A. virgata	S. ucayalae [Species]
S. cinnamomea	A. maculicauda	S. striatus
S. fuscorufa	A. flammulata A. urubambensis	Anabacerthia [Genus]
S. unirufa		A. striaticollis [Species]
S. rutilans	Thripophaga [Genus]	A. temporalis
S. erythrothorax	T. macroura [Species] T. cherriei	A. amaurotis
S. cherriei S. stictothorax	T. fusciceps	Philydor [Genus] P. atricapillus [Species]
Hellmayrea [Genus]	T. herlepschi	P. erythrocercus
H. gularis [Species]	Phacellodomus [Genus]	P. pyrrhodes
Gyalophylax [Genus]	P. sibilatrix [Species]	P. dimidiatus
G. hellmayri [Species]	P. rufifrons	P. baeri
Certhiaxis [Genus]	P. striaticeps	P. lichtensteini
C. cinnamomea [Species]	P. erythrophthalmus	P. rufus
C. mustelina	P. ruber	P. erythropterus
Limnoctites [Genus]	P. striaticollis	P. ruficaudatus
L. rectirostris [Species]	P. dorsalis	Automolus [Genus]
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S. bernardi A. leucophthalmus [Species] M. gularis A. infuscatus S. melanonotus M. gutturalis S. melanothorax M. fulviventris A. dorsalis A. rubiginosus S. luctuosus M. leucophthalma A. albigularis Biatas [Genus] M. haematonota A. ochrolaemus B. nigropectus [Species] M. ornata A. rufipileatus Thamnophilus [Genus] M. ervthrura A. ruficollis T. doliatus [Species] M. erythronotos A. melanopezus T. multistriatus M. axillaris Hylocryptus [Genus] T. palliatus M. schisticolor H. erythrocephalus [Species] T. bridgesi M. sunensis H. rectirostris T. nigriceps M. longipennis Cichlocolaptes [Genus] T. praecox M. minor C. leucophrus [Species] T. nigrocinereus M. iheringi Heliobletus [Genus] T. aethiops M. grisea H. contaminatus [Species] T. unicolor M. unicolor Thripadectes [Genus] T. schistaceus M. behni T. flammulatus [Species] T. murinus M. urosticta T. holostictus T. aroyae M. menetriesii T. melanorhynchus T. punctatus M. assimilis T. rufobrunneus T. amazonicus Dichrozona [Genus] T. virgaticeps T. insignis D. cincta [Species] T. scrutator Myrmorchilus [Genus] T. caerulescens T. ignobilis T. torquatus M. strigilatus [Species] Xenops [Genus] T. ruficapillus Herpsilochmus [Genus] X. milleri [Species] H. pileatus [Species] Pygiptila [Genus] X. tenuirostris P. stellaris [Species] H. sticturus X. rutilans H. stictocephalus Megastictus [Genus] X. minutus M. margaritatus [Species] H. dorsimaculatus Megaxenops [Genus] Neoctantes [Genus] H. roraimae M. parnaguae [Species] N. niger [Species] H. pectoralis Pygarrhichas [Genus] Clytoctantes [Genus] H. longirostris P. albogularis [Species] C. alixii [Species] H. axillaris Sclerurus [Genus] Xenornis [Genus] H. rufimarginatus S. scansor [Species] *X. setifrons* [Species] Microrhopias [Genus] S. albigularis Thamnistes [Genus] M. quixensis [Species] S. mexicanus T. anabatinus [Species] Formicivora [Genus] S. rufigularis F. iheringi [Species] Dysithamnus [Genus] S. caudacutus D. stictothorax [Species] F. grisea S. guatemalensis D. mentalis F. serrana Lochmias [Genus] D. striaticeps F. melanogaster L. nematura [Species] F. rufa D. puncticeps D. xanthopterus Drymophila [Genus] Formicariidae [Family] D. ardesiacus D. ferruginea [Species] Cymbilaimus [Genus] D. saturninus D. genei C. lineatus [Species] D. ochropyga D. occidentalis Hypoedaleus [Genus] D. plumbeus D. devillei H. guttatus [Species] Batara [Genus] Thamnomanes [Genus] D. caudata B. cinerea [Species] T. caesius [Species] D. malura Mackenziaena [Genus] Myrmotherula [Genus] D. squamata Terenura [Genus] M. leachii [Species] M. brachyura [Species] M. severa M. obscura T. maculata [Species] M. sclateri T. callinota Frederickena [Genus] F. viridis [Species] M. klagesi T. humeralis M. surinamensis T. sharpei U. unduligera Taraba [Genus] M. ambigua T. spodioptila T. major [Species] M. cherriei Cercomacra [Genus] Sakesphorus [Genus] M. guttata C. cinerascens [Species] S. canadensis [Species] M. longicauda C. brasiliana M. hauxwelli S. cristatus C. tyrannina

C. nigriscens	F. colma [Species]	G. milleri
C. serva	F. analis	G. bangsi
C. nigricans	F. nigricapillus	G. quitensis
C. carbonaria	F. rufipectus	G. erythrotis
C. melanaria	Chamaeza [Genus]	G. hypoleuca
C. ferdinandi	C. campanisona [Species]	G. przewalskii
Sipia [Genus]	C. nobilis	G. capitalis
S. berlepschi [Species]	C. ruficauda	G. nuchalis
S. rosenbergi	C. mollissima	G. albigula
Pyriglena [Genus]	Pithys [Genus]	G. ruficapilla
P. leuconota [Species]	P. albifrons [Species]	G. erythroleuca
P. atra	P. castanea	G. rufocinerea
P. leucoptera	Gymnopithys [Genus]	G. griseonucha
Rhopornis [Genus]	G. rufigula [Species]	G. rufula
R. ardesiaca [Species]	G. salvini	G. andicola
Myrmoborus [Genus]	G. lunulata	G. macularia
M. leucophrys [Species]	G. leucaspis	G. fulviventris
M. lugubris	Rhegmatorhina [Genus]	G. berlepschi
M. myotherinus	R. gymnops [Species]	G. perspicillata
M. melanurus	R. berlepschi	G. ochroleuca
Hypocnemis [Genus]	R. cristata	Conopophagidae [Family]
H. cantator [Species]	R. hoffmannsi	Conopophaga [Genus]
H. hypoxantha	R. melanosticta	C. lineata [Species]
Hypocnemoides [Genus]	Hylophylax [Genus]	C. cearae
H. melanopogon [Species]	H. naevioides [Species]	C. aurita
H. maculicauda	H. naevia	C. roberti
Myrmochanes [Genus]	H. punctulata	C. peruviana
M. hemileucus [Species]	H. poecilonota	C. ardesiaca
Gymnocichla [Genus]	Phlegopsis [Genus]	C. castaneiceps
G. nudiceps [Species] Sclateria [Genus]	P. nigromaculata [Species] P. erythroptera	C. melanops
S. naevia [Species]	P. borbae	C. melanogaster
Percnostola [Genus]	Phaenostictus [Genus]	Corythopis [Genus]
P. rufifrons [Species]	P. mcleannani [Species]	C. delalandi [Species]
P. schistacea	Myrmornis [Genus]	C. torquata
P. leucostigma	M. torquata [Species]	Rhinocryptidae [Family]
P. caurensis	Pittasoma [Genus]	Pteroptochos [Genus]
P. lophotes	P. michleri [Species]	P. castaneus [Species]
Myrmeciza [Genus]	P. rufopileatum	P. tarnii
M. longipes [Species]	Grallaricula [Genus]	P. megapodius
M. exsul	G. flavirostris [Species]	Scelorchilus [Genus]
M. ferruginea	G. ferrugineipectus	S. albicollis [Species]
M. ruficauda	G. nana	S. rubecula
M. laemosticta	G. loricata	Rhinocrypta [Genus]
M. disjuncta	G. peruviana	R. lanceolata [Species]
M. pelzelni	G. lineifrons	Teledromas [Genus]
M. hemimelaena	G. cucullata	T. fuscus [Species]
M. hyperythra	Myrmothera [Genus]	Liosceles [Genus]
M. goeldii	M. campanisona [Species]	L. thoracicus [Species]
M. melanoceps	M. simplex	Merulaxis [Genus]
M. fortis	Thamnocharis [Genus]	M. ater [Species]
M. immaculata	T. dignissima [Species]	Melanopareia [Genus]
M. griseiceps	Grallaria [Genus]	M. torquata [Species]
Myrmoderus [Genus]	G. squamigera [Species]	M. maximiliani
M. loricatus [Species]	G. excelsa	M. maranonicus
M. squamosus Movementholae [Copus]	G. gigantea	M. elegans
Myrmophylax [Genus] M. atrothorax [Species]	G. guatimalensis G. varia	Scytalopus [Genus]
M. atrothorax [Species] M. stictothorax	G. varia G. alleni	S. unicolor [Species] S. speluncae
Formicarius [Genus]	G. haplonota	S. speiuncue S. macropus
1 0 [Goildo]	a. wpronow	S. There opers

S. femoralis	E. spectabilis	M. oliveceus
S. argentifrons	E. albiceps	M. oleagineus
S. chiriquensis	E. parvirostris	M. macconnelli
S. panamensis	E. mesoleuca	M. rufiventris
S. latebricola	E. strepera	Leptopogon [Genus]
S. indigoticus	E. gigas	L. rufipectus [Species]
S. magellanicus	E. pelzelni	L. taczanowskii
Psilorhamphus [Genus]	E. cristata	L. amaurocephalus
P. guttatus [Species]	E. ruficeps	L. superciliaris
Myornis [Genus]	E. chiriquensis	Phylloscartes [Genus]
M. senilis [Species]	E. frantzii	P. nigrifrons [Species]
Eugralla [Genus]	E. obscura	P. poecilotis
E. paradoxa [Species]	E. dayi	P. chapmani
Acropternis [Genus]	E. pallatangae	P. ophthalmicus
A. orthonyx [Species]	E. fallax	P. eximius
2	Mecocerculus [Genus]	P. gualaquizae
Tyrannidae [Family]	M. leucophrys [Species]	P. flaviventris
Phyllomyias [Genus]	M. poecilocercus	P. venezuelanus
P. fasciatus [Species]	M. hellmayri	P. orbitalis
P. burmeisteri	ž .	
P. virescens	M. calopterus M. minor	P. flaveolus
P. sclateri		P. roquettei
P. griseocapilla	M. stictopterus	P. ventralis
P. griseiceps	Serpophaga [Genus]	P. paulistus
P. plumbeiceps	S. cinerea [Species]	P. oustaleti
P. nigrocapillus	S. hypoleuca	P. difficilis
P. cinereiceps	S. nigricans	P. flavovirens
P. uropygialis	S. araguayae	P. virescens
Zimmerius [Genus]	S. subcristata	P. superciliaris
Z. vilissimus [Species]	Inezia [Genus]	P. sylviolus
Z. bolivianus	I. inornata [Species]	Pseudotriccus [Genus]
Z. cinereicapillus	I. tenuirostris	P. pelzelni [Species]
Z. gracilipes	I. subflava	P. simplex
Z. viridiflavus	Stigmatura [Genus]	P. ruficeps
Ornithion [Genus]	S. napensis [Species]	Myiornis [Genus]
O. inerme [Species]	S. budytoides	M. auricularis [Species]
O. semiflavum	Anairetes [Genus]	M. albiventris
O. brunneicapillum	A. alpinus [Species]	M. ecaudatus
Camptostoma [Genus]	A. agraphia	Lophotriccus [Genus]
C. imberbe [Species]	A. agilis	L. pileatus [Species]
C. obsoletum	A. reguloides	L. eulophotes
Phaeomyias [Genus]	A. flavirostris	L. vitiosus
P. murina [Species]	A. fernandezianus	L. galeatus
Sublegatus [Genus]	A. parulus	Atalotriccus [Genus]
S. modestus [Species]	Tachuris [Genus]	A. pilaris [Species]
S. obscurior	T. rubrigastra [Species]	Poecilotriccus [Genus]
Suiriri [Genus]	Culicivora [Genus]	P. ruficeps [Species]
S. suiriri [Species]	C. caudacuta [Species]	P. capitale
Tyrannulus [Genus]	Polystictus [Genus]	P. tricolor
T. elatus [Species]	P. pectoralis [Species]	P. andrei
Myiopagis [Genus]	P. superciliaris	Oncostoma [Genus]
M. gaimardii [Species]	Pseudocolopteryx [Genus]	O. cinereigulare [Species]
M. caniceps	P. sclateri [Species]	O. olivaceum
M. subplacens	P. dinellianus	Hemitriccus [Genus]
M. flavivertex	P. acutipennis	H. minor [Species]
M. cotta	P. flaviventris	H. josephinae
M. viridicata	Euscarthmus [Genus]	H. diops
M. leucospodia	E. meloryphus [Species]	H. obsoletus
Elaenia [Genus]	E. rufomarginatus	H. flammulatus
E. martinica [Species]	Mionectes [Genus]	H. zosterops
E. flavogaster	M. striaticollis [Species]	H. aenigma
i. juvogustoi	111. Sit withouts [Species]	11. winigmu

H. orbitatus	M. flavicans [Species]	O. frontalis
H. iohannis	M. phoenicomitra	O. pulchella
H. striaticollis	M. inornatus	O. rufipectoralis
H. nidipendulus	M. roraimae M. lintoni	O. fumicolor
H. spodiops	M. lintoni	O. oenanthoides
H. margaritaceiventer	M. pulcher	O. parvirostris
H. inoratus	M. ochraceiventris	O. leucophrys
H. granadensis	M. cryptoxanthus	O. piurae
H. mirandae	M. fasciatus	O. littoralis
H. kaempferi	Aphanotriccus [Genus]	Myiotheretes [Genus]
H. rufigularis	A. capitalis [Species]	M. striaticollis [Species]
H. furcatus	A. audax	M. erythropygius
Todirostrum [Genus]	Xenotriccus [Genus]	M. rufipennis
T. senex [Species]	X. callizonus [Species] X. mexicanus	M. pernix
T. russatum		M. fumigatus
T. plumbeiceps	Pyrrhomyias [Genus]	M. fuscorufus
T. fumifrons	P. cinnamomea [Species]	Xolmis [Genus]
T. latirostre	Mitrephanes [Genus]	X. pyrope [Species] X. cinerea
T. sylvia	M. phaeocercus [Species] M. olivaceus	X. cinevea X. coronata
T. maculatum		X. velata
T. poliocephalum	Contopus [Genus]	X. dominicana
T. cinereum	C. borealis [Species]	
T. pictum	C. fumigatus C. ochraceus	X. irupero
T. chrysocrotaphum	C. sordidulus	Neoxolmis [Genus]
T. nigriceps	C. virens	N. rubetra [Species]
T. calopterum	C. cinereus	N. ruficentris
Cnipodectes [Genus]	C. nigrescens	Agriornis [Genus] A. montana [Species]
C. subbrunneus [Species]	C. albogularis	A. andicola
Ramphotrigon [Genus]	C. caribaeus	A. livida
R. megacephala [Species]	C. latirostris	
R. fuscicauda	Empidonax [Genus]	A. microptera A. murina
R. ruficauda	E. flaviventris [Species]	Muscisaxicola [Genus]
Rhynchocyclus [Genus]	E. virescens	M. maculirostris [Species]
R. brevirostris [Species]	E. alnorum	M. fluviatilis
R. olivaceus	E. traillii	M. macloviana
R. fulvipectus	E. albigularis	M. capistrata
Tolmomyias [Genus]	E. euleri	M. rufivertex
T. sulphurescens [Species]	E. griseipectus	M. juninensis
T. assimilis	E. minimus	M. albilora
T. poliocephalus	E. hammondii	M. alpina
T. flaviventris	E. wrightii	M. cinerea
Platyrinchus [Genus]	E. oberholseri	M. albifrons
P. saturatus [Species]	E. affinis	M. flavinucha
P. cancrominus	E. difficilis	M. frontalis
P. mystaceus	E. flavescens	Lessonia [Genus]
P. coronatus	E. fulvifrons	L. oreas [Species]
P. flavigularis	E. atriceps	L. rufa
P. platyrhynchos	Nesotriccus [Genus]	Knipolegus [Genus]
P. leucoryphus	N. ridgwayi [Species]	K. striaticeps [Species]
Onychorhynchus [Genus]	Cnemotriccus [Genus]	K. hudsoni
O. coronatus [Species]	C. fuscatus [Species]	K. poecilocercus
Myiotriccus [Genus]	Sayornis [Genus]	K. signatus
M. ornatus [Species]	S. phoebe [Species]	K. cyanirostris
Terenotriccus [Genus]	S. saya	K. poecilurus
T. erythrurus [Species]	S. nigricans	K. orenocensis
Myiobius [Genus]	Pyrocephalus [Genus]	K. aterrimus
M. villosus [Species]	P. rubinus [Species]	K. nigerrimus
M. barbatus	Ochthoeca [Genus]	K. lophotes
M. atricaudus	O. cinnamomeiventris [Species]	Hymenops [Genus]
Myiophobus [Genus]	O. diadema	H. perspicillata [Species]
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M. nugator Fluvicola [Genus] P. marginatus F. pica [Species] M. validus P. albogriseus F. nengeta M. sagrae P. major M. stolidus P. surinamus F. leucocephala P. aglaiae Colonia [Genus] M. antillarum P. homochrous C. colonus [Species] M. oberi Alectrurus [Genus] Deltarhynchus [Genus] P. minor A. tricolor [Species] D. flammulatus [Species] P. validus A. risora Pitangus [Genus] P. niger Tityra [Genus] P. lictor [Species] Gubernetes [Genus] T. cayana [Species] G. yetapa [Species] P. sulphuratus T. semifasciata Satrapa [Genus] Megarhynchus [Genus] T. inquisitor S. icterophrys [Species] M. pitangua [Species] T. leucura Tumbezia [Genus] Myiozetetes [Genus] T. salvini [Species] M. cayanensis [Species] Pipridae [Family] Muscigralla [Genus] M. similis Schiffornis [Genus] M. brevicauda [Species] M. granadensis S. major [Species] Hirundinea [Genus] M. luteiventris S. turdinus H. ferruginea [Species] Conopias [Genus] S. virescens Machetornis [Genus] C. inornatus [Species] Sapayoa [Genus] C. parva M. rixosus [Species] S. aenigma [Species] Muscipipra [Genus] C. trivirgata Piprites [Genus] C. cinchoneti M. vetula [Species] P. griseiceps [Species] Attila [Genus] Myiodynastes [Genus] P. chloris A. phoenicurus [Species] M. hemichrysus [Species] P. pileatus A. cinnamomeus M. chrysocephalus Neopipo [Genus] M. bairdii A. torridus N. cinnamomea [Species] M. maculatus A. citriniventris Chloropipo [Genus] A. bolivianus M. luteiventris C. flavicapilla [Species] A. rufus Legatus [Genus] C. holochlora L. leucophaius [Species] A. spadiceus C. uniformis Casiornis [Genus] Empidonomus [Genus] C. unicolor E. varius [Species] C. rufa [Species] Xenopipo [Genus] C. fusca E. aurantioatrocristatus X. atronitens [Species] Tyrannopsis [Genus] Rhytipterna [Genus] Antilophia [Genus] R. simplex [Species] T. sulphurea [Species] A. galeata [Species] R. holerythra Tyrannus [Genus] Tyranneutes [Genus] T. niveigularis [Species] R. immunda T. stolzmanni [Species] Laniocera [Genus] T. albogularis T. virescens L. hypopyrrha [Species] T. melancholicus Neopelma [Genus] L. rufescens T. couchii N. chrysocephalum [Species] Sirystes [Genus] T. vociferans N. pallescens S. sibilator [Species] T. crassirostris N. aurifrons Myiarchus [Genus] T. verticalis N. sulphureiventer M. semirufus [Species] T. forficata Heterocercus [Genus] M. yucatanensis T. savana H. flavivertex [Species] T. tyrannus M. barbirostris H. aurantiivertex M. tuberculifer T. dominicensis H. lineatus M. swainsoni T. caudifasciatus Machaeropterus [Genus] M. venezuelensis T. cubensis M. regulus [Species] M. panamensis Xenopsaris [Genus] M. pyrocephalus M. ferox X. albinucha [Species] M. deliciosus Pachyramphus [Genus] M. cephalotes Manacus [Genus] P. viridis [Species] M. phaeocephalus M. manacus [Species] M. apicalis P. versicolor Corapipo [Genus] M. cinerascens P. spodiurus C. leucorrhoa [Species] M. nuttingi P. rufus C. gutturalis M. crinitus P. castaneus Ilicura [Genus] M. tyrannulus P. cinnamomeus I. militaris [Species] M. magnirostris P. polychopterus Masius [Genus]

M. chrysopterus [Species]	L. cryptolophus	Pittidae [Family]
Chiroxiphia [Genus]	L. fuscocinereus	Pitta [Genus]
C. linearis [Species]	L. vociferans	P. phayrei [Species]
C. lanceolata	L. unirufus	P. nipalensis
C. pareola	L. lanioides	P. soror
C. caudata	L. streptophorus	P. oatesi
Pipra [Genus]	Chirocylla [Genus]	P. schneideri
P. pipra [Species]	C. uropygialis [Species]	P. caerulea
P. coronata	Porphyrolaema [Genus]	P. cyanea
P. isidorei	P. porphyrolaema [Species]	P. elliotii
P. coeruleocapilla	Cotinga [Genus]	P. guajana
P. nattereri	C. amabilis [Species]	P. gurneyi
P. vilasboasi	C. ridgwayi	P. kochi
P. iris	C. nattererii	P. erythrogaster
P. serena	C. maynana	P. arcuata
P. aureola	C. cotinga	P. granatina
P. fasciicauda	C. maculata	P. venusta
P. filicauda	C. cayana	P. baudii
P. mentalis	Xipholena [Genus]	P. sordida
P. erythrocephala	X. punicea [Species]	P. brachyura
P. rubrocapilla	X. lamellipennis	P. nympha
P. chloromeros P. cornuta	X. atropurpurea	P. angolensis
1. cornutu	Carpodectes [Genus]	P. superba
Cotingidae [Family]	C. nitidus [Species]	P. maxima
Phoenicircus [Genus]	C. antoniae	P. steerii
P. carnifex [Species]	C. hopkei	P. moluccensis
P. nigricollis	Conioptilon [Genus]	P. versicolor
Laniisoma [Genus]	C. mcilhennyi [Species]	P. anerythra
L. elegans [Species]	Gymnoderus [Genus]	Philepittidae [Family]
Phibalura [Genus]	G. foetidus [Species]	Philepitta [Genus]
P. flavirostris [Species]	Haematoderus [Genus]	P. castanea [Species]
Tijuca [Genus]	H. militaris [Species]	P. schlegeli
T. atra [Species]	Querula [Genus]	Neodrepanis [Genus]
Carpornis [Genus]	Q. purpurata [Species]	N. coruscans [Species]
C. cucullatus [Species]	Pyroderus [Genus]	N. hypoxantha
C. melanocephalus	P. scutatus [Species]	A
Ampelion [Genus]	Cephalopterus [Genus]	Acanthisittidae [Family]
A. rubrocristatus [Species]	C. glabricollis [Species]	Acanthisitta [Genus]
A. rufaxilla	C. penduliger	A. chloris [Species]
A. sclateri	C. ornatus	Xenicus [Genus]
A. stresemanni Pipreola [Genus]	Perissocephalus [Genus]	X. longipes [Species] X. gilviventris
P. riefferii [Species]	P. tricolor [Species]	X. lyalli
P. intermedia	Procnias [Genus]	21. tyuu
P. arcuata	P. tricarunculata [Species]	Menuridae [Family]
P. auroeopectus	P. alba	Menura [Genus]
P. frontalis	P. averano	M. novaehollandiae [Species]
P. chlorolepidota	P. nudicollis	M. alberti
P. formosa	Rupicola [Genus]	Atrichornithidae [Family]
P. whitelyi	R. rupicola [Species]	Attrichornis [Genus]
Ampelioides [Genus]	R. peruviana	A. clamosus [Species]
A. tschudii [Species]	Oxyruncidae [Family]	A. rufescens
Iodopleura [Genus]	Oxyruncus [Genus]	11. rujescens
<i>Î. pipra</i> [Species]	O. cristatus [Species]	Alaudidae [Family]
I. fusca	•	Mirafra [Genus]
I. isabellae	Phytotomidae [Family]	M. javanica [Species]
Calyptura [Genus]	Phytotoma [Genus]	M. hova
C. cristata [Species]	P. raimondii [Species]	M. cordofanica
Lipaugus [Genus]	P. rara	M. williamsi
L. subalaris [Species]	P. rutila	M. cheniana

M. albicauda C. conirostris C. leucosternum [Species] M. passerina C. starki Pseudhirundo [Genus] M. candida C. sclateri P. griseopyga [Species] M. pulpa C. fringillaris Riparia [Genus] M. hypermetra C. obbiensis R. paludicola [Species] C. personata M. somalica R. congica M. africana Chersophilus [Genus] R. riparia M. chuana C. duponti [Species] R. cincta Pseudalaemon [Genus] M. angolensis Phedina [Genus] P. fremantlii [Species] M. rufocinnamomea P. borbonica [Species] Galerida [Genus] M. apiata P. brazzae G. cristata [Species] M. africanoides Ptyonoprogne [Genus] G. theklae M. collaris P. rupestris [Species] G. malabarica M. assamica P. obsoleta G. deva M. rufa P. fuligula G. modesta M. gilleti P. concolor G. magnirostris M. poecilosterna Hirundo [Genus] Lullula [Genus] M. sabota H. rustica [Species] L. arborea [Species] M. erythroptera H. lucida Alauda [Genus] M. nigricans H. angolensis A. arvensis [Species] Heteromirafra [Genus] H. tahitica A. gulgula H. ruddi [Species] H. albigularis Eremophila [Genus] Certhilauda [Genus] H. aethiopica E. alpestris [Species] H. smithii C. curvirostris [Species] E. bilopha C. albescens H. atrocaerulea C. albofasciata H. nigrita Hirundinidae [Family] H. leucosoma Eremopterix [Genus] Pseudochelidon [Genus] E. australis [Species] H. megaensis P. eurystomina [Species] H. nigrorufa E. leucotis Tachycineta [Genus] E. signata H. dimidiata T. bicolor [Species] E. verticalis Cecropis [Genus] T. albilinea E. nigriceps C. cucullata [Species] T. albiventer C. abyssinica E. grisea T. leucorrhoa E. leucopareia C. semirufa T. leucopyga C. senegalensis Ammomanes [Genus] T. thalassina A. cincturus [Species] C. daurica Callichelidon [Genus] C. striolata A. phoenicurus C. cyaneoviridis [Species] A. deserti Petrochelidon [Genus] Kalochelidon [Genus] A. dunni P. rufigula [Species] K. euchrysea [Species] A. grayi P. preussi Progne [Genus] A. burrus P. andecola P. tapera [Species] Alaemon [Genus] P. nigricans P. subis A. alaudipes [Species] P. spilodera P. dominicensis A. hamertoni P. pyrrhonota P. chalybea Ramphocoris [Genus] P. fulva P. modesta *R. clotbey* [Species] P. fluvicola Notiochelidon [Genus] P. ariel Melanocorypha [Genus] N. murina [Species] M. calandra [Species] N. cyanoleuca P. fuliginosa Delichon [Genus] M. bimaculata N. flavipes M. maxima N. pileata D. urbica [Species] M. mongolica Atticora [Genus] D. dasypus M. leucoptera A. fasciata [Species] D. nipalensis Psalidoprocne [Genus] M. yeltoniensis A. melanoleuca Calandrella [Genus] Neochelidon [Genus] P. nitens [Species] C. cinerea [Species] N. tibialis [Species] P. fuliginosa C. blanfordi Alopochelidon [Genus] P. albiceps C. acutirostris A. fucata [Species] P. pristoptera C. raytal Stelgidopteryx [Genus] P. oleaginea P. antinorii C. rufescens S. ruficollis [Species] C. razae Cheramoeca [Genus] P. petiti

P. holomelaena	A. gutturalis	L. leucomela
P. orientalis	A. sokokensis	L. maculosa
P. mangebettorum	A. crenatus	L. sharpei
P. chalybea	A. lineiventris	L. leucopygia
P. obscura	A. chloris	Campephaga [Genus]
Matacilidas (Famila)	Commonly mides [Femily]	C. phoenicea [Species]
Motacillidae [Family]	Campephagidae [Family]	C. quiscalina
Dendronanthus [Genus]	Pteropodocys [Genus]	C. lobata
D. indicus [Species]	P. maxima [Species]	Pericrocotus [Genus]
Motacilla [Genus]	Coracina [Genus]	P. roseus [Species]
M. flava [Species]	C. novaehollandiae [Species]	P. divaricus
M. citreola	C. fortis	P. cinnamomeus
M. cinerea M. alba	C. atriceps	P. lansbergei
	C. pollens C. schistacea	P. erythropygius
M. grandis	C. saledonica	P. solaris
M. madaraspatensis		P. ethologus
M. aguimp M. clara	C. caeruleogrisea C. temminckii	P. brevirostris
	C. larvata	P. miniatus
M. capensis		P. flammeus
M. flaviventris	C. striata C. bicolor	Hemipus [Genus]
Tmetothylacus [Genus]	C. lineata	H. picatus [Species]
T. tenellus [Species]	21.21.11111	H. hirundinaceus
Macronyx [Genus]	C. boyeri	Tephrodornis [Genus]
M. capensis [Species]	C. leucopygia	T. gularis [Species]
M. croceus M. full-homeii	C. papuensis C. robusta	T. pondicerianus
M. fullebornii M. alagutai		Decomposidos [Family]
M. sharpei	C. longicauda	Pycnonotidae [Family]
M. flavicollis M. gargantiigada	C. parvula C. abbotti	Spizixos [Genus]
M. aurantiigula M. ameliae	C. analis	S. canifrons [Species]
	C. caesia	S. semitorques
M. grimwoodi		Pycnonotus [Genus]
Anthus [Genus]	C. pectoralis	P. zeylanicus [Species] P. striatus
A. novaeseelandiae [Species]	C. graueri C. cinerea	
A. leucophrys A. vaalensis	C. azurea	P. leucogrammicus P. tympanistrigus
A. vaaiensis A. pallidiventris		P. melanoleucos
A. melindae	C. typica C. newtoni	P. priocephalus
A. campestris	C. coerulescens	P. atriceps
A. godlewskii	C. dohertyi	P. melanicterus
A. berthelotii	C. tenuirostris	_
A. similis	C. morio	P. squamatus P. cyaniventris
A. brachyurus	C. schisticeps	P. jocosus
A. caffer	C. melaena	P. xanthorrhous
A. trivialis	C. montana	P. sinensis
A. nilghiriensis	C. holopolia	P. taivanus
A. hodgsoni	C. mcgregori	P. leucogenys
A. gustavi	C. panayensis	P. cafer
A. pratensis	C. polioptera	P. aurigaster
A. cervinus	C. melaschistos	P. xanthopygos
A. roseatus	C. fimbriata	P. nigricans
A. spinoletta	C. melanoptera	P. capensis
A. sylvanus	Campochaera [Genus]	P. barbatus
A. spragueii	C. sloetii [Species]	P. eutilotus
A. furcatus	Chlamydochaera [Genus]	P. nieuwenhuisii
A. hellmayri	C. jefferyi [Species]	P. urostictus
A. chacoensis	Lalage [Genus]	P. bimaculatus
A. lutescens	L. melanoleuca [Species]	P. finlaysoni
A. correndera	L. nigra	P. xantholaemus
A. nattereri	L. sueurii	P. penicillatus
A. bogotensis	L. aurea	P. flavescens
A. antarcticus	L. atrovirens	P. goiavier
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N. chloris [Species] P. luteolus E. ruppelli [Species] P. plumosus N. gularis E. anguitimens P. blanfordi N. vireo Laniidae [Family] P. simplex Criniger [Genus] Prionops [Genus] C. barbatus [Species] P. brunneus P. plumata [Species] P. erythropthalmos C. calurus P. poliolopha P. masukuensis C. ndussumensis P. caniceps P. montanus C. olivaceus P. alberti P. virens C. finschii P. retzii C. flaveolus P. gracilis P. gabela C. pallidus P. ansorgei P. scopifrons C. ochraceus P. curvirostris Lanioturdus [Genus] C. bres P. importunus L. torquatus [Species] C. phaeocephalus P. latirostris Nilaus [Genus] Setornis [Genus] P. gracilirostris N. afer [Species] S. criniger [Species] P. tephrolaemus Dryoscopus [Genus] Hypsipetes [Genus] P. milanjensis D. pringlii [Species] H. viridescens [Species] Calyptocichla [Genus] D. gambensis H. propinguus C. serina [Species] D. cubla H. charlottae Baeopogon [Genus] D. senegalensis H. palawanensis B. indicator [Species] D. angolensis H. criniger B. clamans D. sabini H. philippinus Ixonotus [Genus] Tchagra [Genus] H. siquijorensis I. guttatus [Species] T. minuta [Species] H. everetti Chlorocichla [Genus] T. senegala H. affinis C. falkensteini [Species] T. tchagra H. indicus C. simplex T. australis H. mcclellandii C. flavicollis T. jamesi H. malaccensis C. flaviventris T. cruenta H. virescens C. laetissima Laniarius [Genus] H. flavala Thescelocichla [Genus] L. ruficeps [Species] H. amaurotis T. leucopleura [Species] L. luhderi H. crassirostris Phyllastrephus [Genus] L. ferrugineus H. borbonicus P. scandens [Species] L. barbarus H. madagascariensis P. terrestris L. mufumbiri H. nicobariensis P. strepitans L. atrococcineus H. thompsoni P. cerviniventris L. atroflavus Neolestes [Genus] P. fulviventris L. fulleborni N. torquatus [Species] P. poensis L. funebris Tylas [Genus] P. hypochloris L. leucorhynchus T. eduardi [Species] P. baumanni Telophorus [Genus] P. poliocephalus Irenidae [Family] T. bocagei [Species] P. flavostriatus Aegithina [Genus] T. sulfureopectus P. debilis A. tiphia [Species] T. olivaceus P. lorenzi A. nigrolutea T. nigrifrons P. albigularis A. viridissima T. multicolor P. fischeri A. lafresnayei T. kupeensis P. orostruthus Chloropsis [Genus] T. zeylonus P. icterinus C. flavipennis [Species] T. viridis P. xavieri C. palawanensis T. quadricolor P. madagascariensis C. sonnerati T. dohertyi P. zosterops C. cyanopogon Malaconotus [Genus] C. cochinchinensis P. tenebrosus M. cruentus [Species] P. xanthophrys C. aurifrons M. lagdeni P. cinereiceps C. hardwickei M. gladiator Bleda [Genus] C. venusta M. blanchoti B. syndactyla [Species] Irena [Genus] M. alius B. eximia I. puella [Species] Corvinella [Genus] B. canicapilla I. cyanogaster C. corvina [Species] Nicator [Genus] Eurocephalus [Genus] C. melanoleuca

Lanius [Genus]	Hypocolius [Genus]	T. rufalbus
L. tigrinus [Species]	H. ampelinus [Species]	T. nicefori
L. souzae		T. sinaloa
L. bucephalus	Dulidae [Family]	T. modestus
L. cristatus	Dulus [Genus]	T. leucotis
L. collurio	D. dominicus [Species]	T. superciliaris
L. collueioides	Cinalidas [Esmilal	T. guarayanus
L. gubernator	Cinclidae [Family]	T. longirostris
L. vittatus	Cinclus [Genus]	T. griseus
L. schach	C. cinclus [Species]	Troglodytes [Genus]
L. validirostris	C. pallasii	T. troglodytes [Species]
L. mackinnoni	C. mexicanus	T. aedon
L. minor	C. leucocephalus	T. solstitialis
L. ludovicianus	Tracladutidas [Family]	T. rufulus
L. excubitor	Troglodytidae [Family] <i>Campylorhynchus</i> [Genus]	T. browni
	20 0	Uropsila [Genus]
L. excubitoroides	C. jocosus [Species]	-
L. sphenocercus	C. gularis	U. leucogastra [Species] Henicorhina [Genus]
L. cabanisi	C. yucatanicus	
L. dorsalis	C. brunneicapillus	H. leucosticta [Species]
L. somalicus	C. griseus	H. leucophrys
L. collaris	C. rufinucha	Microcerculus [Genus]
L. newtoni	C. turdinus	M. marginatus [Species]
L. senator	C. nuchalis	M. ustulatus
L. nubicus	C. fasciatus	M. bambla
Pityriasis [Genus]	C. zonatus	Cyphorhinus [Genus]
P. gymnocephala [Species]	C. megalopterus	C. thoracicus [Species]
Vancidae [Family]	Odontorchilus [Genus]	C. aradus
Vangidae [Family]	O. cinereus [Species]	Mimidae [Family]
Calicalicus [Genus]	O. branickii	Dumetalla [Genus]
C. madagascariensis [Species]	Salpinctes [Genus]	D. carolinensis [Species]
Schetba [Genus]	S. obsoletus [Species]	Melanoptila [Genus]
S. rufa [Species]	S. mexicanus	M. glabrirostris [Species]
Vanga [Genus]	Hylorchilus [Genus]	Melanotis [Genus]
V. curvirostris [Species]	H. sumichrasti [Species]	
Xenopirostris [Genus]	Cinnycerthia [Genus]	M. caerulescens [Species]
X. xenopirostris [Species]	C. unirufa [Species]	M. hypoleucus
X. damii	C. peruana	Mimus [Genus]
X. polleni	Cistothorus [Genus]	M. polyglottos [Species]
Falculea [Genus]	C. platensis [Species]	M. gilvus
F. palliata [Species]	C. meridae	M. gundlachii
Leptopterus [Genus]	C. apolinari	M. thenca
L. viridis [Species]	C. palustris	M. longicaudatus
L. chabert	Thryomanes [Genus]	M. saturninus
L. madagascarinus		M. patagonicus
Oriolia [Genus]	T. bewickii [Species] T. sissonii	M. triurus
O. bernieri [Species]		M. dorsalis
Euryceros [Genus]	Ferminia [Genus]	Nesomimus [Genus]
E. prevostrii [Species]	F. cerverai [Species]	N. trifasciatus [Species]
P 1 1111 1 1 1 1 1 1 1	Thryothorus [Genus]	Mimodes [Genus]
Bombycillidae [Family]	T. atrogularis [Species]	M. graysoni [Species]
Bombycilla [Genus]	T. fasciatoventris	Oreoscoptes [Genus]
B. garrulus [Species]	T. euophrys	O. montanus [Species]
B. japonica	T. genibarbis	Toxostoma [Genus]
B. cedrorum	T. coraya	T. rufum [Species]
Ptilogonys [Genus]	T. felix	T. longirostre
P. cinereus [Species]	T. maculipectus	T. guttatum
P. caudatus	T. rutilus	T. cinereum
Phainopepla [Genus]	T. nigricapillus	T. bendirei
P. nitens [Species]	T. thoracicus	T. ocellatum
Phainoptila [Genus]	T. pleurostictus	T. curvirostre
P. melanoxantha [Species]	T. ludovicianus	T. lecontei

T. redivivum P. swynnertoni C. saularis [Species] T. dorsale Erithacus [Genus] C. sechellarum Cinclocerthia [Genus] C. albospecularis E. gabela [Species] C. ruficauda [Species] C. malabaricus E. cyornithopsis Ramphocinclus [Genus] E. aequatorialis C. stricklandii R. brachyurus [Species] E. erythrothorax C. luzoniensis Donacobius [Genus] E. sharpei C. niger D. atricapillus [Species] E. gunningi C. pyrropygus Allenia [Genus] E. rubecula Irania [Genus] A. fusca [Species] E. akahige I. gutturalis [Species] Margarops [Genus] E. komadori Phoenicurus [Genus] M. fuscatus [Species] E. sibilans P. alaschanicus [Species] E. luscinia P. erythronotus Prunellidae [Family] E. megarhynchos P. caeruleocephalus Prunella [Genus] E. calliope P. ochruros P. collaris [Species] E. svecicus P. phoenicurus P. himalayana E. pectoralis P. hodgsoni P. rubeculoides E. ruficeps P. frontalis P. strophiata E. obscurus P. schisticeps P. montanella E. pectardens P. auroreus P. fulvescens E. brunneus P. moussieri P. ocularis E. cyane P. erythrogaster P. atrogularis E. cyanurus Rhyacornis [Genus] P. koslowi E. chrysaeus R. bicolor [Species] P. modularis E. indicus R. fuliginosus P. rubida E. hyperythrus Hodgsonius [Genus] P. immaculata E. johnstoniae H. phaenicuroides [Species] Cossypha [Genus] Cinclidium [Genus] Turdidae [Family] C. roberti [Species] C. leucurum [Species] Brachypteryx [Genus] C. bocagei C. diana B. stellata [Species] C. polioptera C. frontale B. hyperythra C. archeri Grandala [Genus] B. major C. isabellae B. calligyna G. coelicolor [Species] C. natalensis Sialia [Genus] B. leucophrys C. dichroa S. sialis [Species] B. montana C. semirufa S. mexicana Zeledonia [Genus] C. heuglini S. currucoides Z. coronata [Species] C. cyanocampter Enicurus [Genus] Erythropygia [Genus] C. caffra E. scouleri [Species] E. coryphaeus [Species] C. anomala E. velatus E. leucophrys C. humeralis E. ruficapillus E. hartlaubi C. ansorgei E. immaculatus E. galactotes C. niveicapilla E. schistaceus E. paena E. leucosticta C. heinrichi E. leschenaulti C. albicapilla E. maculatus E. quadrivirgata E. barbata Modulatrix [Genus] Cochoa [Genus] E. signata M. stictigula [Species] C. purpurea [Species] Namibornis [Genus] Cichladusa [Genus] C. viridis N. herero [Species] C. guttata [Species] C. azurea Cercotrichas [Genus] C. arquata Myadestes [Genus] C. ruficauda *C. podobe* [Species] M. townsendi [Species] Pinarornis [Genus] Alethe [Genus] M. obscurus P. plumosus [Species] A. diademata [Species] M. elisabeth Chaetops [Genus] A. poliophrys M. genibarbis A. fuelleborni M. ralloides C. frenatus [Species] Drymodes [Genus] A. montana M. unicolor D. brunneopygia [Species] A. lowei M. leucogenys Entomodestes [Genus] D. superciliaris A. poliocephala Pogonocichla [Genus] A. choloensis E. leucotis [Species] P. stellata [Species] Copsychus [Genus] E. coracinus

Stizorhina [Genus]	Saxicoloides [Genus]	N. eremita [Species]
S. fraseri [Species]	S. fulicata [Species]	Cichlherminia [Genus]
S. finschii	Pseudocossyphus [Genus]	C. lherminieri [Species]
Neocossyphus [Genus]	P. imerinus [Species]	Phaeornis [Genus]
N. rufus [Species]	Monticola [Genus]	P. obscurus [Species]
N. poensis	M. rupestris [Species]	P. palmeri
Cercomela [Genus]	M. explorator	Catharus [Genus]
C. sinuata [Species]	M. brevipes	C. gracilirostris [Species]
C. familiaris	M. rufocinereus	C. aurantiirostris
C. tractrac	M. angolensis	C. fuscater
C. schlegelii	M. saxatilis	C. occidentalis
C. fusca	M. cinclorhynchus	C. mexicanus
C. dubia	M. rufiventris	C. dryas
C. melanura	M. solitarius	C. fuscescens
C. scotocerca	Myophonus [Genus]	C. minimus
C. sordida	M. blighi [Species]	C. ustulatus
Saxicola [Genus]	M. melanurus	C. guttatus
S. rubetra [Species]	M. glaucinus	Hylocichla [Genus]
S. macrorhyncha	M. robinsoni	H. mustelina [Species]
S. insignis	M. horsfieldii	Platycichla [Genus]
S. dacotiae	M. insularis	P. flavipes [Species]
S. torquata	M. caeruleus	P. leucops
S. leucura	Geomalia [Genus]	Turdus [Genus]
S. caprata	G. heinrichi [Species]	T. bewsheri [Species]
S. jerdoni	Zoothera [Genus]	T. olivaceofuscus
S. ferrea	Z. schistacea [Species]	T. olivaceus
S. gutturalis	Z. dumasi	T. abyssinicus
Myrmecocichla [Genus]	Z. interpres	T. helleri
M. tholloni [Species]	Z. erythronota	T. libonyanus
M. aethiops	Z. wardii	T. tephronotus
M. formicivora	Z. cinerea	T. menachensis
M. nigra	Z. peronii	T. ludoviciae
M. arnotti	Z. citrina	T. litsipsirupa
M. albifrons	Z. everetti	T. dissimilis
M. melaena	Z. sibirica	T. unicolor
Thamnolaea [Genus]	Z. naevia	T. cardis
T. cinnamomeiventris [Species]	Z. pinicola	T. albocinctus
T. coronata	Z. piaggiae	T. torquatus
T. semirufa	Z. oberlaenderi	T. boulboul
Oenanthe [Genus]	Z. gurneyi	T. merula
O. bifasciata [Species]	Z. cameronensis	T. poliocephalus
O. isabellina	Z. princei	T. chrysolaus
O. bottae	Z. crossleyi	T. celaenops
O. xanthoprymna	Z. guttata	T. rubrocanus
O. oenanthe	Z. spiloptera	T. kessleri
O. deserti	Z. andromedae	T. feae
O. hispanica	Z. mollissima	T. pallidus
O. finschii	Z. dixoni	T. obscurus
O. picata	Z. dauma	T. ruficollis
O. lugens	Z. talaseae	T. naumanni
O. monacha	Z. margaretae	T. pilaris
O. alboniger	Z. monticola	T. iliacus
O. pleschanka	Z. marginata	T. philomelos
O. leucopyga	Z. terrestris	T. mupinensis
O. leucura	Amalocichla [Genus]	T. viscivorus
O. monticola	A. sclateriana [Species]	T. aurantius
O. moesta	A. incerta	T. ravidus
O. pileata	Cataponera [Genus]	T. plumbeus
Chaimarrornis [Genus]	C. turdoides [Species]	T. chiguanco
C. leucocephalus [Species]	Nesocichla [Genus]	T. nigriscens
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T. fuscater	Trichastoma [Genus]	N. atrigularis
T. serranus	T. tickelli [Species]	N. macrodactyla
T. nigriceps	T. pyrrogenys	N. marmorata
T. reevei	T. malaccense	N. crispifrons
T. olivater	T. cinereiceps	N. brevicaudata
T. maranonicus	T. rostratum	N. crassa
T. fulviventris	T. bicolor	N. rabori
T. rufiventris	T. separium	N. epilepidota
T. falcklandii	T. celebense	Pnoepyga [Genus]
T. leucomelas	T. abbotti	P. albiventer [Species]
T. amaurochalinus	T. perspicillatum	P. pusilla
T. plebejus	T. vanderbilti	Spelaeornis [Genus]
T. ignobilis	T. pyrrhopterum	S. caudatus [Species]
T. lawrencii	T. cleaveri	S. troglodytoides
T. fumigatus	T. albipectus	S. formosus
T. hauxwelli		S. chocolatinus
T. haplochrous	T. rufescens	
T. grayi	T. rufipenne	S. longicaudatus
	T. fulvescens	Sphenocichla [Genus]
T. nudigenis	T. puveli	S. humei [Species]
T. jamaicensis	T. poliothorax	Neomixis [Genus]
T. albicollis	Leonardina [Genus]	N. tenella [Species]
T. rufopalliatus	L. woodi [Species]	N. viridis
T. swalesi	Ptyrticus [Genus]	N. striatigula
T. rufitorques	P. turdinus [Species]	N. flavoviridis
T. migratorius	Malacopteron [Genus]	Stachyris [Genus]
Orthonychidae [Family]	M. magnirostre [Species]	S. rodolphei [Species]
Orthonyx [Genus]	M. affine	S. rufifrons
O. temminckii [Species]	M. cinereum	S. ambigua
O. spaldingii	M. magnum	S. ruficeps
1 0	M. palawanense	S. pyrrhops
Androphobus [Genus]	M. albogulare	S. chrysaea
A. viridis [Species]	Pomatorhinus [Genus]	S. plateni
Psophodes [Genus]	P. hypoleucos [Species]	S. capitalis
P. olivaceus [Species]	P. erythrogenys	S. speciosa
P. nigrogularis	P. horsfieldii	S. whiteheadi
Sphenostoma [Genus]	P. schisticeps	S. striata
S. cristatum [Species]	P. montanus	S. nigrorum
Cinclostoma [Genus]	P. ruficollis	S. hypogrammica
C. punctatum [Species]	P. ochraceiceps	S. grammiceps
C. castanotum	P. ferruginosus	S. herberti
C. cinnamomeum	Garritornis [Genus]	S. nigriceps
C. ajax	G. isidorei [Species]	S. poliocephala
Ptilorrhoa [Genus]	Pomatostomus [Genus]	S. striolata
P. leucosticta [Species]	P. temporalis [Species]	S. oglei
P. caerulescens	P. superciliosus	S. maculata
P. castanonota	P. ruficeps	S. leucotis
Eupetes [Genus]	Xiphirhynchus [Genus]	S. nigricollis
E. macrocercus [Species]	X. superciliaris [Species]	S. thoracica
Melampitta [Genus]	Jabouilleia [Genus]	S. erythroptera
M. lugubris [Species]		
M. gigantea	J. danjoui [Species]	S. melanothorax
<i>Ifrita</i> [Genus]	Rimator [Genus]	Dumetia [Genus]
I. kowaldi [Species]	R. malacoptilus [Species]	D. hyperythra [Species]
•	Ptilocichla [Genus]	Rhopocichla [Genus]
Timaliidae [Family]	P. leucogrammica [Species]	R. atriceps [Species]
Pellorneum [Genus]	P. mindanensis	Macronous [Genus]
P. ruficeps [Species]	P. falcata	M. flavicollis [Species]
P. palustre	Kenopia [Genus]	M. gularis
P. fuscocapillum	K. striata [Species]	M. kelleyi
P. capistratum	Napothera [Genus]	M. striaticeps
P. albiventre	N. rufipectus [Species]	M. ptilosus

Micromacronus [Genus]	G. davidi	A. ruficapilla
M. leytensis [Species]	G. sukatschewi	A. cinereiceps
Timalia [Genus]	G. cineraceus	A. rufogularis
T. pileata [Species]	G. rufogularis	A. brunnea
Chrysomma [Genus]	G. lunulatus	A. brunneicauda
C. sinense [Species]	G. maximus	A. poioicephala
Moupinia [Genus]	G. ocellatus	A. pyrrhoptera
M. altirostris [Species]	G. caerulatus	A. peracensis
M. poecilotis	G. mitratus	A. morrisonia
Chamaea [Genus]	G. ruficollis	A. nipalensis
C. fasciata [Species]	G. merulinus	A. abyssinica
Turdoides [Genus]	G. canorus	A. atriceps
T. nipalensis [Species]	G. sannio	Lioptilus [Genus]
T. altirostris	G. cachinnans	L. nigricapillus [Species]
T. caudatus	G. lineatus	L. gilberti
T. earlei		L. rufocinctus
	G. virgatus	L. chapini
T. gularis	G. austeni	Parophasma [Genus]
T. longirostris	G. squamatus	P. galinieri [Species]
T. malcolmi	G. subunicolor	
T. squamiceps	G. elliotii	Phyllanthus [Genus]
T. fulvus	G. henrici	P. atripennis [Species]
T. aylmeri	G. affinis	Crocias [Genus]
T. rubiginosus	G. erythrocephalus	C. langbianis [Species]
T. subrufus	G. yersini	C. albonotatus
T. striatus	G. formosus	Heterophasia [Genus]
T. affinis	G. milnei	H. annectens [Species]
T. melanops	Liocichla [Genus]	H. capistrata
T. tenebrosus	L. phoenicea [Species]	H. gracilis
T. reinwardtii	L. steerii	H. melanoleuca
T. plebejus	Leiothrix [Genus]	H. auricularis
T. jardineii	L. argentauris [Species]	H. pulchella
T. squamulatus	L. lutea	H. picaoides
T. leucopygius	Cutia [Genus]	Yuhina [Genus]
T. hindei	C. nipalensis [Species]	Y. castaniceps [Species]
T. hypoleucus	Pteruthius [Genus]	Y. bakeri
T. bicolor	P. rufiventer [Species]	Y. flavicollis
T. gymnogenys	P. flaviscapis	Y. gularis
Babax [Genus]	P. xanthochlorus	Y. diademata
B. lanceolatus [Species]	P. melanotis	Y. occipitalis
B. waddelli	P. aenobarbus	Y. brunneiceps
B. koslowi	Gampsorhynchus [Genus]	Y. nigrimenta
Garrulax [Genus]	1 5 -	Y. zantholeuca
	G. rufulus [Species]	Malia [Genus]
G. cinereifrons [Species]	Actinodura [Genus]	M. grata [Species]
G. palliatus	A. egertoni [Species]	Myzornis [Genus]
G. rufifrons	A. ramsayi	M. pyrrhoura [Species]
G. perspicillatus	A. nipalensis	Horizorhinus [Genus]
G. albogularis	A. waldeni	H. dohrni [Species]
G. leucolophus	A. souliei	Oxylabes [Genus]
G. monileger	A. morrisoniana	O. madagascariensis [Species]
G. pectoralis	Minla [Genus]	Mystacornis [Genus]
G. lugubris	M. cyanouroptera [Species]	M. crossleyi [Species]
G. striatus	M. strigula	w. trosseyt [Species]
G. strepitans	M. ignotincta	Panuridae [Family]
G. milleti	Alcippe [Genus]	Panurus [Genus]
G. maesi	A. chrysotis [Species]	P. biarmicus [Species]
G. chinensis	A. variegaticeps	Conostoma [Genus]
G. vassali	A. cinerea	C. oemodium [Species]
G. galbanus	A. castaneceps	Paradoxornis [Genus]
G. delesserti	A. vinipectus	P. paradoxus [Species]
G. variegatus	A. striaticollis	P. unicolor

P. flavirostris Bradypterus [Genus] Chaetornis [Genus] P. guttaticollis B. baboecala [Species] C. striatus [Species] P. conspicillatus Graminicola [Genus] B. graueri P. ricketti B. grandis G. bengalensis [Species] P. webbianus Schoenicola [Genus] B. carpalis P. alphonsianus B. alfredi S. platyura [Species] P. zappeyi B. sylvaticus Locustella [Genus] P. przewalskii B. barratti L. lanceolata [Species] P. fulvifrons L. naevia B. victorini P. nipalensis L. certhiola B. cinnamomeus P. davidianus L. ochotensis B. thoracicus P. atrosuperciliaris L. pleskei B. major P. ruficeps L. fluvialtilis B. tacsanowskius P. gularis L. luscinioides B. luteoventris L. fasciolata P. heudei B. palliseri L. amnicola B. seebohmi Picathartidae [Family] Acrocephalus [Genus] B. caudatus Picathartes [Genus] A. melanopogon [Species] B. accentor P. gymnocephalus [Species] A. paludicola B. castaneus P. oreas A. schoenobaenus Bathmocercus [Genus] A. sorghophilus Polioptilidae [Family] B. cerviniventris [Species] A. bistrigiceps Microbates [Genus] B. rufus A. agricola M. collaris [Species] B. winifredae A. concinens M. cinereiventris Dromaeocercus [Genus] A. scirpaceus Ramphocaenus [Genus] D. brunneus [Species] A. cinnamomeus R. melanurus [Species] D. seeboehmi A. baeticatus Polioptila [Genus] Nesillas [Genus] A. palustris P. caerulea [Species] N. typica [Species] A. dumetorum P. melanura N. aldabranus A. arundinaceus P. lembeyei N. mariae A. stentoreus P. albiloris Thamnornis [Genus] A. orinus P. plumbea T. chloropetoides [Species] A. orientalis P. lactea Melocichla [Genus] A. luscinia P. guianensis M. mentalis [Species] A. familiaris P. schistaceigula Achaetops [Genus] A. aequinoctialis P. dumicola A. pycnopygius [Species] A. caffer Sphenoeacus [Genus] Sylviidae [Family] A. atyphus S. afer [Species] Oligura [Genus] A. vaughani Megalurus [Genus] O. castaneocoronata [Species] A. rufescens M. pryeri [Species] Tesia [Genus] A. brevipennis M. timoriensis T. superciliaris [Species] A. gracilirostris M. palustris T. olivea A. newtoni M. albolimbatus T. cyaniventer A. aedon M. gramineus Urosphena [Genus] Bebrornis [Genus] M. punctatus U. subulata [Species] B. rodericanus [Species] Cincloramphus [Genus] U. whiteheadi B. sechellensis C. cruralis [Species] U. squameiceps Hippolais [Genus] U. pallidipes C. mathewsi H. caligata [Species] Eremiornis [Genus] Cettia [Genus] H. pallida E. carteri [Species] C. diphone [Species] H. languida Megalurulus [Genus] C. annae H. olivetorum C. parens M. bivittata [Species] H. polyglotta M. mariei C. ruficapilla H. icterina C. fortipes Cichlornis [Genus] Chloropeta [Genus] C. vulcania C. whitneyi [Species] C. natalensis [Species] C. major C. llaneae C. similis C. flavolivacea C. grosvenori C. gracilirostris C. robustipes Ortygocichla [Genus] Cisticola [Genus] C. brunnifrons O. rubiginosa [Species] C. erythrops [Species] C. cetti O. rufa C. lepe

C. cantans	P. socialis	C. brevicauda
C. lateralis	P. subflava	C. harterti
C. woosnami	P. somalica	C. superciliaris
C. anonyma	P. fluviatilis	C. chloronota
C. bulliens	P. maculosa	Calamonastes [Genus]
C. chubbi	P. flavicans	C. simplex [Species]
C. hunteri	P. substriata	C. stierlingi
C. nigriloris	P. molleri	C. fasciolatus
C. aberrans	P. robertsi	Euryptila [Genus]
C. bodessa	P. leucopogon	E. subcinnamomea [Species]
C. chiniana	P. leontica	Poliolais [Genus]
C. cinereola	P. bairdii	P. lopesi [Species]
C. ruficeps	P. erythroptera	Graueria [Genus]
C. rufilata	P. pectoralis	G. vittata [Species]
C. subruficapilla	Drymocichla [Genus]	Eremomela [Genus]
C. lais	D. incana [Species]	E. icteropygialis [Species]
C. restricta	Urolais [Genus]	E. flavocrissalis
C. njombe	U. epichlora [Species]	E. scotops
C. galactotes	Spiloptila [Genus]	E. pusilla
C. pipiens	S. clamans [Species]	E. canescens
C. carruthersi	Apalis [Genus]	E. gregalis
C. tinniens	A. thoracica [Species]	E. badiceps
C. robusta	A. pulchra	E. turneri
C. aberdare	A. ruwenzori	E. atricollis
C. natalensis	A. nigriceps	E. usticollis
C. fulvicapilla	A. jacksoni	Randia [Genus]
C. angusticauda	A. chariessa	R. pseudozosterops [Species]
C. melanura	A. binotata	Newtonia [Genus]
C. brachyptera	A. flavida	N. brunneicauda [Species]
C. rufa	A. ruddi	N. amphichroa
C. troglodytes	A. rufogularis	N. archboldi
C. nana	A. sharpii	N. fanovanae
C. incana	A. goslingi	Sylvietta [Genus]
C. juncidis	A. bamendae	S. virens [Species]
C. cherina	A. porphyrolaema	S. denti
C. haesitata	A. melanocephala	S. leucophrys
C. aridula	A. chirindensis	S. brachyura
C. textrix	A. cinerea	S. philippae
C. eximia	A. alticola	S. whytii
C. dambo	A. karamojae	S. ruficapilla
C. brunnescens	A. rufifrons	S. rufescens
C. ayresii	Stenostira [Genus]	S. isabellina
C. exilis	S. scita [Species]	Hemitesia [Genus]
Scotocerca [Genus]	Phyllolais [Genus]	H. neumanni [Species]
S. inquieta [Species]	P. pulchella [Species]	Macrosphenus [Genus]
Rhopophilus [Genus]	Orthotomus [Genus]	M. kempi [Species]
R. pekinensis [Species]	O. metopias [Species]	M. flavicans
Prinia [Genus]	O. moreaui	M. concolor
P. burnesi [Species]	O. cucullatus	M. pulitzeri
P. criniger	O. sutorius	M. kretschmeri
P. polychroa	O. atrogularis	Amaurocichla [Genus]
P. atrogularis	O. derbianus	A. bocagei [Species]
P. cinereocapilla	O. sericeus	Hypergerus [Genus]
P. buchanani	O. ruficeps	H. atriceps [Species]
P. rufescens	O. sepium	H. lepidus
P. hodgsoni	O. cinereiceps	Hyliota [Genus]
P. gracilis	O. nigriceps	H. flavigaster [Species]
P. sylvatica	O. samaransis	H. australis
P. familiaris	Camaroptera [Genus]	H. violacea
P. flaviventris	C. brachyura [Species]	Hylia [Genus]

H. prasina [Species] Parisoma [Genus] Muscicapa [Genus] Phylloscopus [Genus] P. buryi [Species] M. striata [Species] P. ruficapilla [Species] P. lugens M. gambagae P. laurae P. boehmi M. griseisticta P. layardi P. laetus M. sibirica P. subcaeruleum P. herberti M. dauurica P. budongoensis Sylvia [Genus] M. ruficauda S. atricapilla [Species] P. umbrovirens M. muttui S. borin P. trochilus M. ferruginea S. communis P. collybita M. sordida S. curruca P. sindianus M. thalassina S. nana P. neglectus M. panayensis P. bonelli S. nisoria M. albicaudata S. hortensis P. sibilatrix M. indigo S. leucomelaena P. fuscatus M. infuscata S. rueppelli P. fuligiventer M. ussheri S. melanocephala P. affinis M. boehmi S. melanothorax P. griseolus M. aquatica S. mystacea P. armandii M. olivascens S. cantillans P. schwarzi M. lendu S. conspicillata P. pulcher M. adusta S. deserticola P. maculipennis M. epulata S. undata P. proregulus M. sethsmithii S. sarda P. subviridis M. comitata Regulus [Genus] P. inornatus M. tessmanni R. ignicapillus [Species] P. borealis M. cassini R. regulus P. trochiloides M. caerulescens R. goodfellowi P. nitidus M. griseigularis R. satrapa P. plumbeitarsus Myioparus [Genus] R. calendula P. tenellipes M. plumbeus [Species] *Leptopoecile* [Genus] P. magnirostris Humblotia [Genus] L. sophiae [Species] P. tytleri H. flavirostris [Species] L. elegans P. occipitalis Ficedula [Genus] P. coronatus Muscicapidae [Family] F. hypoleuca [Species] P. ijimae Melaenornis [Genus] F. albicollis P. reguloides M. semipartitus [Species] F. zanthopygia P. davisoni M. pallidus F. narcissina P. cantator M. infuscatus F. mugimaki P. ricketti M. mariquensis F. hodgsonii P. olivaceus M. microrhynchus F. dumetoria P. cebuensis M. chocolatinus F. strophiata P. trivirgatus M. fischeri F. parva P. sarasinorum M. brunneus F. subruba P. presbytes M. edolioides F. monileger P. poliocephalus M. pammelaina F. solitaris P. makirensis M. ardesiacus F. hyperythra P. amoenus M. annamarulae F. basilanica Seicercus [Genus] M. ocreatus F. rufigula S. burkii [Species] M. cinerascens F. buruensis S. xanthoschistos M. silens F. henrici S. affinis Rhinomyias [Genus] F. harterti S. poliogenys R. addita [Species] S. castaniceps F. platenae R. oscillans F. bonthaina S. montis R. brunneata F. westermanni S. grammiceps R. olivacea Tickellia [Genus] F. superciliaris R. umbratilis F. tricolor T. hodgsoni [Species] R. ruficauda R. colonus F. sapphira Abroscopus [Genus] A. albogularis [Species] R. gularis F. nigrorufa A. schisticeps R. insignis F. timorensis A. superciliaris R. goodfellowi F. cyanomelana

Niltava [Genus]	P. chalybea	S. arfakianus
N. grandis [Species]	P. jamesoni	S. magnus
N. macgrigoriae	P. concreta	Pyrrholaemus [Genus]
N. davidi	Maluridae [Family]	P. brunneus [Species]
N. sundara	Clytomyias [Genus]	Chthonicola [Genus]
N. sumatrana	5 5	C. sagittatus [Species]
N. vivida	C. insignis [Species]	Calamanthus [Genus]
N. hyacinthina	malurus [Genus]	C. fuliginosus [Species]
N. hoevelli	M. wallacii [Species]	C. campestris
N. sanfordi	M. grayi	Hylacola [Genus]
N. concreta	M. alboscapulatus	H. pyrrhopygius [Species]
N. ruecki	M. melanocephalus	H. cautus
N. herioti	M. leucopterus	Acanthiza [Genus]
N. hainana	M. cyaneus	A. murina [Species]
N. pallipes	M. splendens	A. inornata
N. poliogenys	M. lamberti	A. reguloides
N. unicolor	M. amabilis	A. iredalei
N. rubeculoides	M. pulcherrimus	A. katherina
N. banyumas	M. elegans	A. pusilla
N. superba	M. coronatus	-
N. caerulata	M. cyanocephalus	A. apicalis
N. turcosa	Stipiturus [Genus]	A. ewingii
N. tickelliae	S. malachurus [Species]	A. chrysorrhoa
N. rufigastra	S. mallee	A. uropygialis
N. hodgsoni	M. ruficeps	A. robustirostris
Culicicapa [Genus]	Amytornis [Genus]	A. nana
C. ceylonensis [Species]	A. textilis [Species]	A. lineata
C. helianthea	A. purnelli	Smicrornis [Genus]
G. Bettuntbet	A. housei	S. brevirostris [Species]
Platysteiridae [Family]	A. woodwardi	Gerygone [Genus]
Bias [Genus]	A. dorotheae	G. cinerea [Species]
B. flammulatus [Species]	A. striatus	G. chloronota
B. musicus	A. barbatus	G. palpebrosa
Pseudobias [Genus]	A. goyderi	G. olivacea
P. wardi [Species]	11. goyuuri	G. dorsalis
Batis [Genus]	Acanthizidae [Family]	G. chrysogaster
B. diops [Species]	Dasyornis [Genus]	G. ruficauda
B. margaritae	D. brachypterus [Species]	G. magnirostris
B. mixta	D. broadbenti	G. sulphurea
B. dimorpha	Pycnoptilus [Genus]	G. inornata
B. capensis	P. floccosus [Species]	G. ruficollis
B. fratrum	Origma [Genus]	G. fusca
B. molitor	O. solitaria [Species]	G. tenebrosa
B. soror	Crateroscelis [Genus]	G. laevigaster
B. pririt	C. gutturalis [Species]	G. flavolateralis
B. senegalensis	C. murina	G. insularis
B. orientalis	C. nigrorufa	G. mouki
B. minor	C. robusta	G. modesta
B. perkeo	Sericornis [Genus]	G. igata
B. minulla	S. citreogularis [Species]	G. albofrontata
B. minima	S. maculatus	Aphelocephala [Genus]
B. ituriensis	S. humilis	A. leucopsis [Species]
B. poensis	S. frontalis	A. pectoralis
Platysteira [Genus]	S. beccarii	A. nigricincta
P. cyanea [Species]	S. nouhuysi	Mohoua [Genus]
		M. ochrocephala [Species]
P. albifrons P. peltata	S. magnirostris S. keri	Finschia [Genus]
P. laticincta		F. novaeseelandiae [Species]
_	S. spilodera S. perspicillatus	
P. castanea P. tonsa	S. perspicillatus	Epthianura [Genus] E. albifrons [Species]
P. blissetti	S. rufescens S. papuensis	E. tricolor
1. 00035000	S. papuensis	Li. II WOIOI

Aves species list

E. aurifrons	M. rugensis [Species]	R. phoenicura
E. crocea	Monarcha [Genus]	R. nigrocinnamomea
Ashbyia [Genus]	M. axillaris [Species]	R. albicollis
A. lovensis [Species]	M. rubiensis	R. euryura
	M. cinerascens	R. aureola
Monarchidae [Family]	M. melanopsis	R. javanica
Erythrocercus [Genus]	M. frater	R. perlata
E. mccallii [Species]	M. erythrostictus	R. leucophrys
E. holochlorus	M. castaneiventris	R. rufiventris
E. livingstonei	M. richardsii	R. cockerelli
Elminia [Genus]	M. leucotis	R. albolimbata
E. longicauda [Species]	M. guttulus	R. hyperythra
E. albicauda	M. mundus	R. threnothorax
Trochocercus [Genus]	M. sacerdotum	R. maculipectus
T. nigromitratus [Species]	M. trivirgatus	R. leucothorax
T. albiventris	M. leucurus	R. atra
T. albonotatus	M. julianae	R. fuliginosa
T. cyanomelas	M. manadensis	R. drownei
T. nitens	M. brehmii	R. tenebrosa
Philentoma [Genus]	M. infelix	R. rennelliana
P. pyrhopterum [Species]	M. menckei	R. spilodera
P. velatum	M. verticalis	R. nebulosa
Hypothymis [Genus]	M. barbatus	R. brachyrhyncha
H. azurea [Species]	M. browni	R. personata
H. helenae	M. viduus	R. dedemi
H. coelestris	M. godeffroyi	R. superflua
Eutrichomyias [Genus]	M. takatsukasae	R. teysmanni
E. rowleyi [Species]	M. chrysomela	R. lepida
Terpsiphone [Genus]	Arses [Genus]	R. opistherythra
T. rufiventer [Species]	A. insularis [Species]	R. rufidorsa
T. bedfordi		R. dahli
T. rufocinerea	A. telescophthalmus	R. matthiae
T. viridis	A. kaupi	R. malaitae
T. paradisi	Myiagra [Genus]	
T. atrocaudata	M. oceanica [Species]	R. rufifrons
T. cyanescens	M. galeata M. atra	Eopsaltriidae [Family]
T. cinnamomea	M. rubecula	Monachella [Genus]
T. atrochalybeia		M. muelleriana [Species]
T. mutata	M. ferrocyanea	Microeca [Genus]
T. corvina	M. cervinicauda	M. leucophaea [Species]
T. bourbonnensis	M. caledonica	M. flavigaster
Chasiempis [Genus]	M. vanikorensis	M. hemixantha
C. sandwichensis [Species]	M. albiventris	M. griseoceps
Pomarea [Genus]	M. azureocapilla	M. flavovirescens
P. dimidiata [Species]	M. ruficollis	M. papuana
P. nigra	M. cyanoleuca	Eugerygone [Genus]
P. mendozae	M. alecto	E. rubra [Species]
P. iphis	M. hebetior	Petroica [Genus]
P. whitneyi	M. inquieta	P. bivittata [Species]
Mayrornis [Genus]	Lamprolia [Genus]	P. archboldi
M. versicolor [Species]	L. victoriae [Species]	P. multicolor
M. lessoni	Machaerirhynchus [Genus]	P. goodenovii
M. schistaceus	M. flaviventer [Species]	P. phoenicea
Neolalage [Genus]	M. nigripectus	P. rosea
N. banksiana [Species]	Peltops [Genus]	P. rodinogaster
Clytorhynchus [Genus]	P. blainvillii [Species]	P. cucullata
C. pachycephaloides [Species]	P. montanus	P. vittata
C. vitiensis	Rhipidura [Genus]	P. macrocephala
C. nigrogularis	R. hypoxantha [Species]	P. australis
C. hamlini	R. superciliaris	P. traversi
Metabolus [Genus]	R. cyaniceps	Tregellasia [Genus]

T. capito [Species]	P. nudigula	P. superciliosus	
T. leucops	P. lorentzi	P. davidi	
Eopsaltria [Genus]	P. schlegelii	P. cinctus	
E. australis [Species]	P. aurea	P. hudsonicus	
E. flaviventris	P. rufiventris	P. rufescens	
E. georgiana	P. lanioides	P. wollweberi	
Peneoenanthe [Genus]	Colluricincla [Genus]	P. rubidiventris	
P. pulverulenta [Species]	C. megarhyncha [Species]	P. melanolophus	
Peocilodryas [Genus]	C. parvula	P. ater	
P. brachyura [Species]	C. boweri	P. venustulus	
P. hypoleuca	C. harmonica	P. elegans	
P. placens	C. woodwardi	P. amabilis	
P. albonotata	Pitohui [Genus]	P. cristatus	
P. superciliosa	P. kirhocephalus [Species]	P. dichrous	
Peneothello [Genus]	P. dichrous	P. afer	
P. sigillatus [Species]	P. incertus	P. griseiventris	
P. cryptoleucus	P. ferrugineus	P. niger	
P. cyanus	P. cristatus	P. leucomelas	
P. bimaculatus	P. nigrescens	P. albiventris	
Heteromyias [Genus]	P. tenebrosus	P. leuconotus	
H. cinereifrons [Species]	Turnagra [Genus]	P. funereus	
H. albispecularis	T. capensis [Species]	P. fasciiventer	
Pachycephalopsis [Genus]	Aggithalidaa [Family]	P. fringillinus	
P. hattamensis [Species]	Aegithalidae [Family]	P. rufiventris	
P. poliosoma	Aegithalos [Genus]	P. major	
Pachycephalidae [Family]	A. caudatus [Species]	P. bokharensis P. monticolus	
Eulacestoma [Genus]	A. leucogenys		
E. nigropectus [Species]	A. concinnus A. iouschistos	P. nuchalis	
Falcunculus [Genus]		P. xanthogenys	
F. frontatus [Species]	A. fuliginosus	P. spilonotus P. holsti	
Oreoica [Genus]	Psaltria [Genus]	P. hoisti P. caeruleus	
O. gutturalis [Species]	P. exilis [Species]		
Pachycare [Genus]	Psaltriparus [Genus]	P. cyanus	
P. flavogrisea [Species]	P. minimus [Species]	P. varius P. semilarvatus	
Rhagologus [Genus]	P. melanotis	P. inornatus	
R. leucostigma [Species]	Remizidae [Family]	P. bicolor	
Hylocitrea [Genus]	Remiz [Genus]	Melanochlora [Genus]	
H. bonensis [Species]	R. pendulinus [Species]		
Pachycephala [Genus]	Anthoscopus [Genus]	M. sultanea [Species]	
P. raveni [Species]	A. punctifrons [Species]	Sylviparus [Genus] S. modestus [Species]	
P. rufinucha	A. parvulus	Hypositta [Genus]	
P. tenebrosa	A. musculus	H. corallirostris [Species]	
P. olivacea	A. flavifrons	11. torum ostris [opecies]	
P. rufogularis	A. caroli	Sittidae [Family]	
P. inornata	A. sylviella	Sitta [Genus]	
P. hypoxantha	A. minutus	S. europaea [Species]	
P. cinerea	Auriparus [Genus]	S. nagaensis	
P. phaionota	A. flaviceps [Species]	S. castanea	
P. hyperythra	Cephalopyrus [Genus]	S. himalayensis	
P. modesta	C. flammiceps [Species]	S. victoriae	
P. philippensis		S. pygmaea	
P. sulfuriventer	Paridae [Family]	S. pusilla	
P. meyeri	Parus [Genus]	S. whiteheadi	
P. soror	P. palustris [Species]	S. yunnanensis	
P. simplex	P. lugubris	S. canadensis	
P. orpheus	P. montanus	S. villosa	
P. pectoralis	P. atricapillus	S. leucopsis	
P. flavifrons	P. carolinensis	S. carolinensis	
P. caledonica	P. sclateri	S. krueperi	
P. implicata	P. gambeli	S. neumayer	

Aves species list

S. tephronota D. vincens Hypogramma [Genus] S. frontalis D. aureolimbatum H. hypogrammicum [Species] D. nigrilore S. solangiae Nectarina [Genus] D. anthonyi S. azurea N. seimundi [Species] D. bicolor S. magna N. batesi D. quadricolor S. formosa N. olivacea D. australe Neositta [Genus] N. ursulae D. retrocinctum N. chrysoptera [Species] N. veroxii D. trigonostigma N. papuensis N. balfouri D. hypoleucum Daphoenositta [Genus] N. reichenbachii D. erythrorhynchos D. miranda [Species] N. hartlaubii D. concolor Tichodroma [Genus] N. newtonii D. pygmaeum T. muraria [Species] N. thomensis D. nebrkorni N. oritis Certhiidae [Family] D. vulneratum N. alinae Certhia [Genus] D. erythrothorax N. bannermani F. familiaris [Species] D. pectorale N. verticalis F. brachydactyla D. eximium N. cyanolaema F. himalayana D. aeneum N. fuliginosa F. nipalensis D. tristrami N. rubescens F. discolor D. igniferum N. amethystina Salpornis [Genus] D. maugei N. senegalensis S. spilonotus [Species] D. sanguinolentum N. adelberti D. birundinaceum Rhabdornithidae [Family] N. zeylonica D. celebicum N. minima Rhabdornis [Genus] D. monticolum N. sperata R. mysticalis [Species] D. ignipectus N. sericea R. inornatus D. cruentatum N. calcostetha D. trochileum Climacteridae [Family] N. dussumeiri Oreocharis [Genus] Climacteris [Genus] N. lotenia O. arfaki [Species] C. erythrops [Species] N. jugularis Paramythia [Genus] C. affinis N. buettikoferi P. montium [Species] C. picumnus N. solaris Pardalotus [Genus] C. rufa P. quadragintus [Species] N. asiatica C. melanura N. souimanga P. punctatus C. leucophaea P. xanthopygus N. humbloti P. rubricatus N. comorensis Dicaeidae [Family] P. striatus N. coquerellii Melanocharis [Genus] P. ornatus N. venusta M. arfakiana [Species] P. substriatus N. talatala M. nigra P. melanocephalus N. oustaleti M. longicauda N. fusca M. versteri Nectariniidae [Family] N. chalybea M. striativentris Anthreptes [Genus] N. afra Rhamphocharis [Genus] A. gabonicus [Species] N. mediocris R. crassirostris [Species] A. fraseri N. preussi Prionochilus [Genus] A. reichenowi N. neergaardi P. olivaceus [Species] A. anchietae N. chloropygia P. maculatus A. simplex P. percussus N. minulla A. malacensis N. regia P. plateni A. rhodolaema N. loveridgei P. xanthopygius A. singalensis P. thoracicus N. rockefelleri A. longuemarei N. violacea Dicaeum [Genus] A. orientalis N. habessinica D. annae [Species] A. neglectus N. bouvieri D. agile A. aurantium D. everetti A. pallidogaster N. osea D. aeruginosum N. cuprea A. pujoli D. proprium A. rectirostris N. tacazze D. chrysorrheum A. collaris N. bocagii D. melanoxanthum A. platurus N. purpureiventris

N. shelleyi	Z. uropygialis	L. squamiceps
N. mariquensis	Z. anomala	L. javanica
N. bifasciata	Z. atriceps	L. superciliaris
N. pembae	Z. atrifrons	L. dohertyi
N. chalcomelas	Z. mysorensis	Oculocincta [Genus]
N. coccinigastra	Z. mysorensis Z. fuscicapilla	O. squamifrons [Species]
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N. erythrocerca	Z. buruensis	Heleia [Genus]
N. congensis	Z. kuehni	H. muelleri [Species]
N. pulchella	Z. novaeguineae	H. crassirostris
N. nectarinioides	Z. metcalfi	Chlorocharis [Genus]
N. famosa	Z. natalis	C. emiliae [Species]
N. johnstoni	Z. lutea	Hypocryptadius [Genus]
N. notata	Z. griseotincta	H. cinnamomeus [Species]
N. johannae	Z. rennelliana	Speirops [Genus]
N. superba	Z. vellalavella	S. brunnea [Species]
N. kilimensis	Z. luteirostris	S. leucophoeca
N. reichenowi	Z. rendovae	S. lugubris
Aethopyga [Genus]		8
A. primigenius [Species]	Z. murphyi	Meliphagidae [Family]
A. boltoni	Z. ugiensis	Timeliopsis [Genus]
	Z. stresemanni	T. fulvigula [Species]
A. flagrans	Z. sanctaecrucis	T. griseigula
A. pulcherrima	Z. samoensis	Melilestes [Genus]
A. duyvenbodei	Z. explorator	M. megarhynchus [Species]
A. shelleyi	Z. flavifrons	
A. gouldiae	Z. minuta	M. bouganvillei Towark graphy (Convol
A. nipalensis	Z. xanthochroa	Toxorhamphus [Genus]
A. eximia	Z. lateralis	T. novaeguineae [Species]
A. christinae	Z. strenua	T. poliopterus
A. saturata	Z. tenuirostris	Oedistoma [Genus]
A. siparaja		O. iliolophum [Species]
A. mysticalis	Z. albogularis	О. рудтаеит
A. ignicauda	Z. inornata	Glycichaera [Genus]
	Z. cinerea	G. fallax [Species]
Arachnothera [Genus]	Z. abyssinica	Lichmera [Genus]
A. longirostra [Species]	Z. pallida	L. lombokia [Species]
A. crassirostris	Z. senegalensis	L. argentauris
A. robusta	Z. virens	L. indistincta
A. flavigaster	Z. borbonica	L. incana
A. chrysogenys	Z. ficedulina	
A. clarae	Z. griseovirescens	L. alboauricularis
A. affinis	Z. maderaspatana	L. squamata
A. magna		L. deningeri
A. everetti	Z. mayottensis	L. monticola
A. juliae	Z. modesta	L. flavicans
•	Z. mouroniensis	L. notabilis
Zosteropidae [Family]	Z. olivacea	L. cockerelli
Zosterops [Genus]	Z. vaughani	Myzomela [Genus]
Z. erythropleura [Species]	Woodfordia [Genus]	M. blasii [Species]
Z. japonica	W. superciliosa [Species]	M. albigula
Z. palpebrosa	W. lacertosa	M. cineracea
Z. ceylonensis	Rukia [Genus]	M. eques
Z. conspicillata	R. palauensis [Species]	M. obscura
Z. salvadorii	R. oleaginea	M. cruentata
Z. atricapilla	R. ruki	M. nigrita
	R. longirostra	e e e e e e e e e e e e e e e e e e e
Z. everetti		M. pulchella
Z. nigrorum	Tephrozosterops [Genus]	M. kuehni
Z. montana	T. stalkeri [Species]	M. erythrocephala
Z. wallacei	Madanga [Genus]	M. adolphinae
Z. flava	M. ruficollis [Species]	M. sanguinolenta
Z. chloris	Lophozosterops [Genus]	M. cardinalis
Z. consibrinorum	L. pinaiae [Species]	M. chermesina
Z. grayi	L. goodfellowi	M. sclateri
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M. lafargei M. lunatus Moho [Genus] M. braccatus [Species] M. melanocephala M. albogularis M. eichhorni M. bishopi M. affinis M. malaitae M. gularis M. apicalis M. laetior M. nobilis M. tristrami Chaetoptila [Genus] M. jugularis M. validirostris M. erythromelas Entomyzon [Genus] C. angustipluma [Species] M. vulnerata E. cyanotis [Species] Phylidonyris [Genus] P. pyrrhoptera [Species] M. rosenbergii Notiomystis [Genus] P. novaehollandiae Certhionyx [Genus] *N. cincta* [Species] P. nigra C. niger [Species] Pycnopygius [Genus] P. albifrons C. variegatus P. ixoides [Species] P. melanops Meliphaga [Genus] P. cinereus P. undulata M. mimikae [Species] P. stictocephalus P. notabilis Philemon [Genus] M. montana Ramsayornis [Genus] M. orientalis P. meyeri [Species] R. fasciatus [Species] M. albonotata P. brassi R. modestus M. aruensis P. citreogularis Plectorbyncha [Genus] M. analoga P. inornatus P. lanceolata [Species] M. vicina P. gilolensis Conopophila [Genus] P. fuscicapillus M. gracilis C. whitei [Species] M. notata P. subcorniculatus C. albogularis M. flavirictus P. moluccensis C. rufogularis M. lewinii P. buceroides C. picta M. flava P. novaeguineae Xanthomyza [Genus] P. cockerelli M. albilineata X. phrygia [Species] M. virescens P. eichhorni Cissomela [Genus] $M.\ versicolor$ P. albitorques C. pectoralis [Species] M. fasciogularis P. argenticeps Acanthorbynchus [Genus] M. inexpectata P. corniculatus A. tenuirostris [Species] M. fusca P. diemenensis A. superciliosus M. plumula Ptiloprora [Genus] Manorina [Genus] M. chrysops P. plumbea [Species] M. melanophrys [Species] M. cratitia P. meekiana M. melanocephala M. keartlandi P. erythropleura M. flavigula M. penicillata P. guisei M. melanotis M. ornata P. perstriata Anthornis [Genus] M. reticulata Melidectes [Genus] A. melanura [Species] M. leucotis M. fuscus [Species] Anthochaera [Genus] M. flavicollis M. princeps A. rufogularis [Species] M. melanops M. nouhuysi A. chrysoptera M. cassidix M. ochromelas A. carunculata M. unicolor M. leucostephes A. paradoxa M. flaviventer M. belfordi Prosthemadera [Genus] M. polygramma M. torquatus P. novaseelandiae [Species] M. macleayana Melipotes [Genus] Promerops [Genus] M. frenata M. gymnops [Species] P. cafer [Species] M. subfrenata M. fumigatus P. gurneyi M. obscura M. ater Oreornis [Genus] Vosea [Genus] Emberizidae [Family] O. chrysogenys [Species] V. whitemanensis [Species] Melophus [Genus] Foulehaio [Genus] *Myza* [Genus] M. lathami [Species] F. carunculata [Species] M. celebensis [Species] Latoucheornis [Genus] F. provocator M. sarasinorum L. siemsseni [Species] Cleptornis [Genus] Meliarchus [Genus] Emberiza [Genus] C. marchei [Species] M. sclateri [Species] E. calandra [Species] Apalopteron [Genus] Gymnomyza [Genus] E. citrinella A. familiare [Species] G. viridis [Species] E. leucocephala Melithreptus [Genus] G. samoensis E. cia M. brevirostris [Species] G. aubryana E. cioides

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E. jankowskii	A. leconteii	L. pusillus [Species]
E. buchanani	A. bairdii	L. griseocristatus
E. stewarti	A. baileyi	Donacospiza [Genus]
E. cineracea	A. henslowii	D. albifrons [Species]
E. hortulana	A. savannarum	Rowettia [Genus]
E. caesia	A. humeralis	R. goughensis [Species]
E. cirlus	A. aurifrons	Nesospiza [Genus]
E. striolata	Spizella [Genus]	N. acunhae [Species]
E. impetuani	S. arborea [Species]	N. wilkinsi
E. tahapisi	S. passerina	Diuca [Genus]
E. socotrana	S. pusilla	D. speculifera [Species]
E. capensis	S. atrogularis	D. diuca
E. yessoensis	S. pallida	Idiopsar [Genus]
E. tristami	S. breweri	<i>I. brachyrus</i> [Species]
E. fucata	Pooecetes [Genus]	Piezorbina [Genus]
E. pusilla	P. gramineus [Species]	P. cinerea [Species]
E. chrysophrys	Chondestes [Genus]	Xenospingus [Genus]
E. rustica	C. grammacus [Species]	X. concolor [Species]
E. elegans	Amphispiza [Genus]	Incaspiza [Genus]
E. aureola	A. bilineata [Species]	I. pulchra [Species]
E. poliopleura	A. belli	I. ortizi
E. flaviventris	Aimophila [Genus]	I. laeta
E. affinis	A. mystacalis [Species]	I. watkinsi
E. cabanisi	A. humeralis	Poospiza [Genus]
E. rutila	A. ruficauda	P. thoracica [Species]
E. koslowi	A. sumichrasti	P. boliviana
E. melanocephala	A. stolzmanni	P. alticola
E. bruniceps	A. strigiceps	P. hypochondria
E. sulphurata	A. aestivalis	P. erythrophrys
E. spodocephala	A. botterii	P. ornata
E. variabilis	A. cassinii	P. nigrorufa
E. pallasi	A. quinquestriata	P. lateralis
E. schoeniclus	A. carpalis	P. rubecula
Calcarius [Genus]	A. ruficeps	P. garleppi
C. mccownii [Species]	A. notosticta	P. baeri
C. lapponicus	A. rufescens	P. caesar
C. pictus	Torreornis [Genus]	P. hispaniolensis
C. ornatus	T. inexpectata [Species]	P. torquata
Plectrophenax [Genus]	Oriturus [Genus]	P. cinerea
P. nivalis [Species]	O. superciliosus [Species]	Sicalis [Genus]
Calamospiza [Genus]	Phrygilus [Genus]	S. citrina [Species]
C. melanocorys [Species]	P. atriceps [Species]	S. lutea
Zonotrichia [Genus]	P. gayi	S. uropygialis
Z. iliaca [Species]	P. patagonicus	S. luteocephala
Z. melodia	P. fruticeti	S. auriventris S. olivascens
Z. lincolnii	P. unicolor	S. columbiana
Z. georgiana	P. dorsalis	
Z. capensis	P. erythronotus	S. flaveola S. luteola
Z. querula	P. plebejus	S. raimondii
Z. leucophrys	P. carbonarius	S. taczanowskii
Z. albicollis	P. alaudinus	Emberizoides [Genus]
Z. atricapilla	Melanodera [Genus]	E. herbicola [Species]
Junco [Genus]	M. melanodera [Species]	E. nervicou [Species] Embernagra [Genus]
J. vulcani [Species]	M. xanthogramma	E. platensis [Species]
7. hyemalis	Haplospiza [Genus]	E. longicauda
J. phaeonotus	H. rustica [Species]	Volatinia [Genus]
Ammodramus [Genus]	H. unicolor	V. jacarina [Species]
A. sandwichensis [Species]	Acanthidops [Genus]	Sporophila [Genus]
A. maritimus	A. bairdii [Species]	S. frontalis [Species]
A. caudacutus	Lophospingus [Genus]	S. falcirostris
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S. schistacea	G. fuliginosa	Pezopetes [Genus]
S. intermedia	G. difficilis	P. capitalis [Species]
S. plumbea	G. scandens	
~ ·	G. conirostris	Oreothraupis [Genus]
S. americana		O. arremonops [Species]
S. torqueola	Camarhynchus [Genus]	Pselliophorus [Genus]
S. collaris	C. crassirostris [Species]	P. tibialis [Species]
S. lineola	C. psittacula	P. luteoviridis
S. luctuosa	C. pauper	Lysurus [Genus]
S. nigricollis	C. parvulus	L. castaneiceps [Species]
S. ardesiaca	C. pallidus	Urothraupis [Genus]
S. melanops	C. heliobates	U. stolzmanni [Species]
S. obscura	Certhidea [Genus]	Charitospiza [Genus]
S. caerulescens	C. olivacea [Species]	C. eucosma [Species]
S. albogularis	Pinaroloxias [Genus]	Coryphaspiza [Genus]
S. leucoptera	P. inornata [Species]	C. melanotis [Species]
S. peruviana	Pipilo [Genus]	Saltatricula [Genus]
S. simplex	P. chlorurus [Species]	S. multicolor [Species]
S. nigrorufa	P. ocai	Gubernatrix [Genus]
S. bouvreuil	P. erythrophthalmus	G. cristata [Species]
S. insulata	P. socorroensis	Coryphospingus [Genus]
S. minuta	P. fuscus	C. pileatus [Species]
S. hypoxantha	P. aberti	C. cucullatus
S. hypochroma	P. albicollis	Rhodospingus [Genus]
S. ruficollis	Melozone [Genus]	R. cruentus [Species]
S. palustris	M. kieneri [Species]	Paroaria [Genus]
S. castaneiventris	M. biarcuatum	P. coronata [Species]
S. cinnamomea	M. leucotis	P. dominicana
S. melanogaster	Arremon [Genus]	P. gularis
S. telasco	A. taciturnus [Species]	P. baeri
Oryzoborus [Genus]	A. flavirostris	P. capitata
O. crassirostris [Species]	A. aurantiirostris	Catamblyrhynchus [Genus]
	A. schlegeli	
O. angolensis	A. abeillei	C. diadema [Species]
Amaurospiza [Genus]	Arremonops [Genus]	Spiza [Genus]
A. concolor [Species]	A. rufivirgatus [Species]	S. americana [Species]
A. moesta	A. tocuyensis	Pheucticus [Genus]
Melopyrrha [Genus]	A. chlorinotus	P. chrysopeplus [Species]
M. nigra [Species]	A. conirostris	P. aureoventris
Dolospingus [Genus]	Atlapetes [Genus]	P. ludovicianus
D. fringilloides [Species]	\hat{A} . albinucha [Species]	P. melanocephalus
Catamenia [Genus]	A. pallidinucha	Cardinalis [Genus]
C. analis [Species]	A. rufinucha	C. cardinalis [Species]
C. inornata	A. leucopis	C. phoeniceus
C. homochroa	A. pileatus	C. sinuatus
C. oreophila	A. melanocephalus	Caryothraustes [Genus]
Tiaris [Genus]	A. flaviceps	C. canadensis [Species]
T. canora [Species]	A. fuscoolivaceus	C. humeralis
T. olivacea	A. tricolor	Rhodothraupis [Genus]
T. bicolor	A. albofrenatus	R. celaeno [Species]
T. fuliginosa	A. schistaceus	Periporphyrus [Genus]
Loxipasser [Genus]	A. nationi	P. erythromelas [Species]
L. anoxanthus [Species]	A. leucopterus	Pitylus [Genus]
Loxigilla [Genus]	A. albiceps	P. grossus [Species]
L. portorocensis [Species]	A. pallidiceps	Saltator [Genus]
L. violacea	A. rufigenis	S. atriceps [Species]
L. noctis	A. semirufus	S. maximus
Melanospiza [Genus]	A. personatus	S. atripennis
M. richardsoni [Species]	A. fulviceps	S. similis
Geospiza [Genus]	A. citrinellus	S. coerulescens
G. magnirostris [Species]	A. brunneinucha	S. orenocensis
G. fortis	A. torquatus	S. maxillosus
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S. aurantiirostris	H. frontalis	T. rufus
S. cinctus	H. melanotis	T. phoenicius
S. atricollis	H. goeringi	Trichothraupis [Genus]
S. rufiventris	H. verticalis	T. melanops [Species]
S. albicollis	H. xanthophthalmus	Habia [Genus]
Passerina [Genus]	H. trifasciatus	H. rubica [Species]
P. glaucocaerulea [Species]	Pyrrhocoma [Genus]	H. fuscicauda
P. cyanoides	P. ruficeps [Species]	H. atrimaxillaris
P. brissonii	Thlypopsis [Genus]	H. gutturalis
P. parellina	T. fulviceps [Species]	H. cristata
P. caerulea	T. ornata	Piranga [Genus]
P. cyanea	T. pectoralis	P. bidentata [Species]
P. amoena	T. sordida	P. flava
P. versicolor	T. inornata	P. rubra
P. ciris	T. ruficeps	P. roseogularis
P. rositae	Hemithraupis [Genus]	P. olivacea
P. leclancherii	H. guira [Species]	P. ludoviciana
P. caerulescens	H. ruficapilla	P. leucoptera
Orchesticus [Genus]	H. flavicollis	P. erythrocephala
O. albeillei [Species]	Chrysothlypis [Genus]	P. rubriceps
Schistochlamys [Genus]	C. chrysomelas [Species]	Calochaetes [Genus]
S. ruficapillus [Species]	C. salmoni	C. coccineus [Species]
	Nemosia [Genus]	
S. melanopis		Ramphocelus [Genus]
Neothraupis [Genus]	N. pileata [Species] N. rourei	R. sanguinolentus [Species]
N. fasciata [Species]		R. nigrogularis R. dimidiatus
Cypsnagra [Genus]	Phaenicophilus [Genus]	
C. hirundinacea [Species]	P. palmarum [Species]	R. melanogaster
Conothraupis [Genus]	P. poliocephalus	R. carbo
C. speculigera [Species]	Calyptophilus [Genus]	R. bresilius
C. mesoleuca	C. frugivorus [Species]	R. passerinii
Lamprospiza [Genus]	Rhodinocichla [Genus]	R. flammigerus
L. melanoleuca [Species]	R. rosea [Species]	Spindalis [Genus]
Cissopis [Genus]	Mitrospingus [Genus]	S. zena [Species]
C. leveriana [Species]	M. cassinii [Species]	Thraupis [Genus]
Chlorornis [Genus]	M. oleagineus	T. episcopus [Species]
C. reifferii [Species]	Chlorothraupis [Genus]	T. sayaca
Compsothraupis [Genus]	C. carmioli [Species]	T. cyanoptera
C. loricata [Species]	C. olivacea	T. ornata
Sericossypha [Genus]	C. stolzmanni	T. abbas
S. albocristata [Species]	Orthogonys [Genus]	T. palmarum
Nesospingus [Genus]	O. chloricterus [Species]	T. cyanocephala
N. speculiferus [Species]	Eucometis [Genus]	T. bonariensis
Chlorospingus [Genus]	E. penicillata [Species]	Cyanicterus [Genus]
C. ophthalmicus [Species]	Lanio [Genus]	C. cyanicterus [Species]
C. tacarcunae	L. fulvus [Species]	Buthraupis [Genus]
C. inornatus	L. versicolor	B. arcaei [Species]
C. punctulatus	L. aurantius	B. melanochlamys
C. semifuscus	L. leucothorax	B. rothschildi
C. zeledoni	Creurgops [Genus]	B. edwardsi
C. pileatus	C. verticalis [Species]	B. aureocincta
C. parvirostris	C. dentata	B. montana
C. flavigularis	Heterospingus [Genus]	B. eximia
C. flavovirens	H. xanthopygius [Species]	B. wetmorei
C. canigularis	Tachyphonus [Genus]	Wetmorethraupis [Genus]
Cnemoscopus [Genus]	T. cristatus [Species]	W. sterrhopteron [Species]
C. rubrirostris [Species]	T. rufiventer	Anisognathus [Genus]
Hemispingus [Genus]	T. surinamus	A. lacrymosus [Species]
H. atropileus [Species]	T. luctuosus	A. igniventris
H. superciliaris	T. delatrii	A. flavinuchus
H. reyi	T. coronatus	A. notabilis
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Aves species list

T. schrankii D. carbonaria Stephanophorus [Genus] S. diadematus [Species] T. florida D. venezuelensis D. albilatera Iridosornis [Genus] T. arthus D. duidae I. porphyrocephala [Species] T. icterocephala D. major T. xanthocephala I. analis D. indigotica I. jelskii T. chrysotis I. rufivertex T. parzudakii D. glauca Dubusia [Genus] T. xanthogastra D. caerulescens D. taeniata [Species] T. punctata D. cyanea Euneornis [Genus] T. guttata Delothraupis [Genus] D. castaneoventris [Species] T. varia *E. campestris* [Species] Tersina [Genus] Pipraeidea [Genus] T. rufigula T. viridis [Species] P. melanonota [Species] T. gyrola Euphonia [Genus] T. lavinia Parulidae [Family] E. jamaica [Species] T. cayana Mniotilta [Genus] E. plumbea T. cucullata M. varia [Species] E. affinis T. peruviana Vermivora [Genus] E. luteicapilla T. preciosa V. bachmanii [Species] T. vitriolina E. chlorotica V. chrysoptera E. trinitatis T. rufigenis V. pinus T. ruficervix E. concinna V. peregrina E. saturata T. labradorides V. celata E. finschi T. cyanotis V. ruficapilla E. violacea T. cyanicollis V. virginiae E. laniirostris T. larvata V. crissalis E. birundinacea T. nigrocincta V. luciae E. chalybea T. dowii V. gutturalis E. musica T. nigroviridis V. superciliosa E. fulvicrissa T. vassorii Parula [Genus] E. imitans T. heinei P. americana [Species] E. gouldi T. viridicollis P. pitiayumi E. chrysopasta T. argyrofenges Dendroica [Genus] E. mesochrysa T. cyanoptera D. petechia [Species] E. minuta T. pulcherrima D. pensylvanica T. velia E. anneae D. cerulea E. xanthogaster T. callophrys D. caerulescens E. rufiventris Dacnis [Genus] D. plumbea D. albiventris [Species] E. pectoralis D. pharetra E. cayennensis D. lineata D. pinus Chlorophonia [Genus] D. flaviventer D. graciae C. flavirostris [Species] D. hartlaubi D. adelaidae D. nigripes C. cyanea D. pityophila C. pyrrhophrys D. venusta D. dominica C. occipitalis D. cayana D. nigrescens Chlorochrysa [Genus] D. viguieri D. townsendi C. phoenicotis [Species] D. berlepschi D. occidentalis C. calliparaea Chlorophanes [Genus] D. chrysoparia C. nitidissima C. spiza [Species] D. virens Tangara [Genus] Cyanerpes [Genus] D. discolor T. inornata [Species] C. nitidus [Species] D. vitellina T. cabanisi C. lucidus D. tigrina T. palmeri C. caeruleus D. fusca T. mexicana C. cyaneus D. magnolia T. chilensis Xenodacnis [Genus] D. coronata T. fastuosa X. parina [Species] D. palmarum T. seledon Oreomanes [Genus] D. kirtlandii T. cyanocephala O. fraseri [Species] D. striata T. desmaresti Diglossa [Genus] D. castanea T. cyanoventris D. baritula [Species] Catharopeza [Genus] T. johannae D. lafresnayii C. bishopi [Species]

Setophaga [Genus]	B. chrysogaster	Hemignathus [Genus]
S. ruticilla [Species]	B. flaveolus	H. obscurus [Species]
Seiurus [Genus]	B. luteoviridis	H. lucidus
S. aurocapillus [Species]	B. signatus	H. wilsoni
S. noveboracensis	B. nigrocristatus	Loxops [Genus]
S. motacilla	B. griseiceps	L. coccinea [Species]
	B. basilicus	Paroreomyza [Genus]
Limnothlypis [Genus]	B. cinereicollis	P. maculata [Species]
L. swainsonii [Species]	B. conspicillatus	Pseudonester [Genus]
Helmitheros [Genus]		
H. vermivorus [Species]	B. coronatus	P. xanthophrys [Species]
Protonotaria [Genus]	B. culicivorus	Psittirostra [Genus]
P. citrea [Species]	B. rufifrons	P. psittacea [Species]
Geothlypis [Genus]	B. belli	Loxioides [Genus]
G. trichas [Species]	B. melanogenys	L. cantans [Species]
G. beldingi	B. tristriatus	L. palmeri
G. flavovelata	B. trifasciatus	L. flaviceps
G. rostrata	B. hypoleucus	L. bailleui
G. semiflava	B. leucoblepharus	L. kona
G. speciosa	B. leucophrys	Vireonidae [Family]
G. nelsoni	Phaeothlypis [Genus]	Cyclarhis [Genus]
G. chiriquensis	P. fulvicauda [Species]	C. gujanensis [Species]
G. aequinoctialis	P. rivularis	C. nigrirostris
G. poliocephala	Peucedramus [Genus]	
G. formosa	P. taeniatus [Species]	Vireolanius [Genus]
G. agilis	Xenoligea [Genus]	V. melitophrys [Species]
G. philadelphia	X. montana [Species]	V. pulchellus
G. tolmiei	Granatellus [Genus]	V. leucotis
Microligea [Genus]	G. venustus [Species]	Vireo [Genus]
M. palustris [Species]	G. sallaei	V. brevipennis [Species]
Teretistris [Genus]	G. pelzelni	V. huttoni
T. fernandinae [Species]	Icteria [Genus]	V. atricapillus
T. fornsi	I. virens [Species]	V. griseus
Leucopeza [Genus]	Conirostrum [Genus]	V. pallens
L. semperi [Species]	C. speciosum [Species]	V. caribaeus
Wilsonia [Genus]	C. leucogenys	V. bairdi
W. citrinia [Species]	C. bicolor	V. gundlachii
W. pusilla	C. margaritae	V. crassirostris
W. canadensis	C. cinereum	V. bellii
Cardellina [Genus]	C. ferrugineiventre	V. vicinior
C. rubrifrons [Species]	C. rufum	V. nelsoni
	C. sitticolor	V. hypochryseus
Ergaticus [Genus]	C. albifrons	V. modestus
E. ruber [Species]	Coereba [Genus]	V. nanus
E. versicolor	C. flaveola [Species]	V. latimeri
Myioborus [Genus]	•	V. osburni
M. pictus [Species]	Drepanididae [Family]	V. carmioli
M. miniatus	Himatione [Genus]	V. solitarius
M. brunniceps	H. sanguinea [Species]	V. flavifrons
M. pariae	Palmeria [Genus]	V. philadelphicus
M. cardonai	P. dolei [Species]	V. olivaceus
M. torquatus	Vestiaria [Genus]	V. magister
M. ornatus	V. coccinea [Species]	V. altiloquus
M. melanocephalus	Drepanis [Genus]	V. gilvus
M. albifrons	D. funerea [Species]	Hylophilus [Genus]
M. flavivertex	D. pacifica	H. poicilotis [Species]
M. albifacies	Ciridops [Genus]	H. thoracicus
Euthlypis [Genus]	C. anna [Species]	H. semicinereus
E. lachrymosa [Species]	Viridonia [Genus]	H. pectoralis
Basileuterus [Genus]	V. virens [Species]	H. sclateri
B. fraseri [Species]	V. parva	H. muscicapinus
B. bivittatus	V. sagittirostris	H. brunneiceps

H. semibrunneus Gymnomystax [Genus] Fringillidae [Family] H. aurantifrons G. mexicanus [Species] Fringilla [Genus] F. coelebs [Species] H. hypoxanthus Xanthocephalus [Genus] H. flavipes X. xanthocephalus [Species] F. teydea H. ochraceiceps Agelaius [Genus] F. montifringilla H. decurtatus A. thilius [Species] Serinus [Genus] A. phoeniceus S. pusillus [Species] Icteridae [Family] A. tricolor S. serinus Psarocolius [Genus] A. icterocephalus S. syriacus P. oseryi [Species] A. humeralis S. canaria P. latirostris A. xanthomus S. citrinella P. decumanus A. cyanopus S. thibetanus P. viridis A. ruficapillus S. canicollis P. atrovirens Leistes [Genus] S. nigriceps P. angustifrons L. militaris [Species] S. citrinelloides P. wagleri Pezites [Genus] S. frontalis P. montezuma P. militaris [Species] S. capistratus P. cassini Sturnella [Genus] S. koliensis P. bifasciatus S. magna [Species] S. scotops P. guatimozinus S. neglecta S. leucopygius P. yuracares Pseudoleistes [Genus] S. atrogularis Cacicus [Genus] P. guiraburo [Species] S. citrinipectus C. cela [Species] S. mozambicus P. virescens C. uropygialis Amblyramphus [Genus] S. donaldsoni C. chrysopterus A. holosericeus [Species] S. flaviventris C. koepckeae Hypopyrrhus [Genus] S. sulphuratus C. leucoramphus H. pyrohypogaster [Species] S. albogularis C. chrysonotus Curaeus [Genus] S. gularis C. sclateri S. mennelli C. curaeus [Species] C. solitarius C. forbesi S. tristriatus C. melanicterus Gnorimopsar [Genus] S. menschensis C. holosericeus S. striolatus G. chopi [Species] Icterus [Genus] Oreopsar [Genus] S. burtoni I. cayanensis [Species] O. bolivianus [Species] S. rufobrunneus I. chrysater Lampropsar [Genus] S. leucopterus I. nigrogularis L. tanagrinus [Species] S. totta I. leucopteryx Macroagelaius [Genus] S. alario I. auratus M. subalaris [Species] S. estherae I. mesomelas Dives [Genus] Neospiza [Genus] I. auricapillus D. atroviolacea [Species] N. concolor [Species] I. graceannae D. dives Linurgus [Genus] I. xantholemus Quiscalus [Genus] L. olivaceus [Species] I. pectoralis Q. mexicanus [Species] Rhynchostruthus [Genus] I. gularis Q. major *R. socotranus* [Species] I. pustulatus Q. palustris Carduelis [Genus] I. cucullatus Q. nicaraguensis C. chloris [Species] I. icterus Q. quiscula C. sinica I. galbula I. spurius Q. niger C. spinoides Q. lugubris I. dominicensis C. ambigua Euphagus [Genus] I. wagleri C. spinus E. carolinus [Species] I. laudabilis C. pinus I. bonana E. cyanocephalus C. atriceps Molothrus [Genus] C. spinescens I. oberi I. graduacauda M. badius [Species] C. yarrellii C. cucullata I. maculialatus M. rufoaxillaris I. parisorum M. bonariensis C. crassirostris Nesopsar [Genus] M. aeneus C. magellanica N. nigerrimus [Species] M. ater C. dominicensis Xanthopsar [Genus] Scaphidura [Genus] C. siemiradzkii X. flavus [Species] C. olivacea S. oryzivorus [Species]

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C. notata	Loxia [Genus]	Euschistospiza [Genus]
C. xanthogastra	L. pytyopsittacus [Species]	E. dybowskii [Species]
C. atrata	L. curvirostra	E. cinereovinacea
C. uropygialis	L. leucoptera Lagonosticta [Genus]	
C. barbata	Pyrrhula [Genus]	L. rara [Species]
C. tristis	P. nipalensis [Species]	L. rufopicta
C. psaltria	P. leucogenys	L. nitidula
C. lawrencei	P. aurantiaca	L. senegala
C. carduelis	P. erythrocephala	L. rubricata
Acanthis [Genus]	P. erythaca	L. landanae
A. flammea [Species]	P. pyrrhula	L. rhodopareia
A. hornemanni	Coccothraustes [Genus]	L. larvata
A. flavirostris	C. coccothraustes [Species]	Uraeginthus [Genus]
A. cannabina	C. migratorius	U. angolensis [Species]
A. yemenensis	C. personatus	U. bengalus
A. johannis	C. icterioides	U. cyanocephala
Leucosticte [Genus]	C. affinis	U. granatina
L. nemoricola [Species]	C. melanozanthos	U. ianthinogaster
L. brandti	C. carnipes	Estrilda [Genus]
L. arctoa	C. vespertinus	E. caerulescens [Species]
Callacanthis [Genus]	C. abeillei	E. perreini
C. burtoni [Species]	Pyrrhoplectes [Genus]	E. thomensis
Rhodopechys [Genus]	P. epauletta [Species]	E. melanotis
R. sanguinea [Species]	E	E. paludicola
R. githaginea	Estrildidae [Family]	E. melpoda
R. mongolica	Parmoptila [Genus]	E. rhodopyga
R. obsoleta	P. woodhousei [Species]	E. rufibarba
Uragus [Genus]	Nigrita [Genus]	E. troglodytes
U. sibiricus [Species]	N. fusconota [Species]	E. astrild
Urocynchramus [Genus]	N. bicolor	E. nigriloris
U. pylzowi [Species]	N. luteifrons	E. nonnula
Carpodacus [Genus]	N. canicapilla	E. atricapilla
	Nesocharis [Genus]	-
C. rubescens [Species]	N. shelleyi [Species]	E. erythronotos
C. nipalensis	N. ansorgei	E. charmosyna
C. erythrinus	N. capistrata	Amandava [Genus]
C. purpureus	Pytilia [Genus]	A. amandava [Species]
C. cassinii	P. phoenicoptera [Species]	A. formosa
C. mexicanus	P. hypogrammica	A. subflava
C. pulcherrimus	P. afra	Ortygospiza [Genus]
C. eos	P. melba	O. atricollis [Species]
C. rhodochrous	Mandingoa [Genus]	O. gabonensis
C. vinaceus	M. nitidula [Species]	O. locustella
C. edwardsii	Cryptospiza [Genus]	Aegintha [Genus]
C. synoicus	C. reichenovii [Species]	A. temporalis [Species]
C. roseus	C. salvadorii	Emblema [Genus]
C. trifasciatus	C. jacksoni	E. picta [Species]
C. rhodopeplus	C. shelleyi	E. bella
C. thura	Pyrenestes [Genus]	E. oculata
C. rhodochlamys	P. sanguineus [Species]	E. guttata
C. rubicilloides	P. ostrinus	Oreostruthus [Genus]
C. rubicilla	P. minor	O. fuliginosus [Species]
C. puniceus	Spermophaga [Genus]	Neochmia [Genus]
C. roborowskii	P. poliogenys [Species]	N. phaeton [Species]
Chaunoproctus [Genus]	P. haematina	N. ruficauda
C. ferreorostris [Species]	P. ruficapilla	Poephila [Genus]
Pinicola [Genus]	Clytospiza [Genus]	P. guttata [Species]
P. enucleator [Species]	C. monteiri [Species]	P. bichenovii
P. subhimachalus	Hypargos [Genus]	P. personata
Haematospiza [Genus]	H. margaritatus [Species]	P. acuticauda
H. sipahi [Species]	H. niveoguttatus	P. cincta
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Erythrura [Genus] V. chalybeata [Species] Ploceus [Genus] E. hyperythra [Species] V. funerea P. baglafecht [Species] P. bannermani E. prasina V. wilsoni E. viridifacies P. batesi V. hypocherina E. tricolor P. nigrimentum V. fischeri E. coloria P. bertrandi V. regia E. trichroa P. pelzelni V. macroura P. subpersonatus E. papuana V. paradisaea P. luteolus E. psittacea V. orientalis E. cyaneovirens P. ocularis Bubalornis [Genus] P. nigricollis E. kleinschmidti B. albirostris [Species] P. alienus Chloebia [Genus] Dinemellia [Genus] P. melanogaster C. gouldiae [Species] D. dinemelli [Species] P. capensis Aidemosyne [Genus] Plocepasser [Genus] P. subaureus A. modesta [Species] P. mahali [Species] P. xanthops Lonchura [Genus] P. superciliosus P. aurantius L. malabarica [Species] P. donaldsoni P. heuglini L. griseicapilla P. rufoscapulatus P. bojeri L. nana Histurgops [Genus] P. castaneiceps L. cucullata H. ruficauda [Species] P. princeps L. bicolor Pseudonigrita [Genus] P. xanthopterus L. fringilloides P. arnaudi [Species] P. castanops L. striata P. cabanisi P. galbula L. leucogastroides Philetairus [Genus] P. taeniopterus L. fuscans P. socius [Species] P. intermedius L. molucca Passer [Genus] P. velatus L. punctulata P. ammodendri [Species] P. spekei L. kelaarti P. domesticus P. spekeoides L. leucogastra P. hispaniolensis P. cucullatus L. tristissima P. pyrrhonotus P. grandis L. leucosticta P. castanopterus P. nigerrimus L. quinticolor P. rutilans P. weynsi L. malacca P. flaveolus P. golandi L. maja P. moabiticus P. dicrocephalus L. pallida P. iagoensis P. melanocephalus L. grandis P. melanurus P. jacksoni L. vana P. griseus P. badius L. caniceps P. simplex P. rubiginosus L. nevermanni P. montanus P. aureonucha L. spectabilis P. luteus P. tricolor L. forbesi P. eminibey P. albinucha L. hunsteini Petronia [Genus] P. nelicourvi L. flaviprymna P. brachydactyla [Species] P. sakalava L. castaneothorax P. xanthocollis P. hypoxanthus L. stygia P. petronia P. superciliosus L. teerinki P. superciliaris P. benghalensis L. monticola P. dentata P. manyar L. montana Montifringilla [Genus] P. philippinus L. melaena M. nivalis [Species] P. megarhynchus L. pectoralis M. adamsi P. bicolor Padda [Genus] M. taczanowskii P. flavipes P. fuscata [Species] M. davidiana P. preussi P. oryzivora M. ruficollis P. dorsomaculatus Amadina [Genus] M. blanfordi P. olivaceiceps A. erythrocephala [Species] M. theresae P. insignis A. fasciata Sporopipes [Genus] P. angolensis Pholidornis [Genus] S. squamifrons [Species] P. sanctithomae P. rushiae [Species] S. frontalis Malimbus [Genus] Ploceidae [Family] Amblyospiza [Genus] M. coronatus [Species] Vidua [Genus] A. albifrons [Species] M. cassini

M. scutatus	A. metallica	Necropsar [Genus]
M. racheliae	A. mystacea	N. leguati [Species]
M. ibadanensis	A. brunneicapilla	Fregilupus [Genus]
M. nitens	Poeoptera [Genus]	F. varius [Species]
M. rubricollis	P. kenricki [Species] Sturnus [Genus]	
M. erythrogaster	P. stuhlmanni S. senex [Species]	
M. malimbicus	P. lugubris S. malabaricus	
M. rubriceps	Grafisia [Genus]	S. erythropygius
Quelea [Genus]	G. torquata [Species]	S. pagodarum
Q. cardinalis [Species]	Onychognathus [Genus]	S. sericeus
Q. erythrops	O. walleri [Species]	S. philippensis
Q. quelea	O. nabouroup	S. sturninus
Foudia [Genus]	O. morio	S. roseus
F. madagascariensis [Species]	O. blythii	S. vulgaris
F. eminentissima	O. frater	S. unicolor
F. rubra	O. tristramii	S. cinerascens
F. bruante	O. fulgidus	S. contra
F. sechellarum	O. tenuirostris	S. nigricollis
F. flavicans	O. albirostris	S. burmannicus
Euplectes [Genus]	O. salvadorii	S. melanopterus
E. anomalus [Species]	Lamprotornis [Genus]	S. sinensis
E. afer		Leucopsar [Genus]
E. diadematus	L. iris [Species]	L. rothschildi [Species]
E. gierowii	L. cupreocauda	Acridotheres [Genus]
E. nigroventris	L. purpureiceps	A. tristis [Species]
E. hordeaceus	L. curruscus	A. ginginianus
E. orix	L. purpureus	A. fuscus
E. aureus	L. nitens	A. grandis
E. capensis	L. chalcurus	A. albocinctus
E. axillaris	L. chalybaeus	A. cristatellus
E. macrourus	L. chloropterus	Ampeliceps [Genus]
E. hartlaubi	L. acuticaudus	A. coronatus [Species]
E. albonotatus	L. splendidus	Mino [Genus]
E. ardens	L. ornatus	M. anais [Species]
E. progne	L. australis	M. dumontii
E. jacksoni	L. mevesii	Basilornis [Genus]
Anomalospiza [Genus]	L. purpuropterus	B. celebensis [Species]
A. imberbis [Species]	L. caudatus	B. galeatus
*	Cinnyricinclus [Genus]	B. corythaix
Sturnidae [Family]	C. femoralis [Species]	B. miranda
Aplonis [Genus]	C. sharpii	Streptocitta [Genus]
A. zelandica [Species]	C. leucogaster	S. albicollis [Species]
A. santovestris	Speculipastor [Genus]	S. albertinae
A. pelzelni	S. bicolor [Species]	Sarcops [Genus]
A. atrifusca	Neocichla [Genus]	S. calvus [Species]
A. corvina	N. gutturalis [Species]	Gracula [Genus]
A. mavornata	Spreo [Genus]	G. ptilogenys [Species]
A. cinerascens	S. fischeri [Species]	G. religiosa
A. tabuensis	S. bicolor	Enodes [Genus]
A. striata	S. albicapillus	E. erythrophris [Species]
A. fusca	S. superbus	Scissirostrum [Genus]
A. opaca	S. pulcher	S. dubium [Species]
A. cantoroides	S. hildebrandti	Buphagus [Genus]
A. crassa	Cosmopsarus [Genus]	B. africanus [Species]
A. feadensis	C. regius [Species]	B. erythrorhynchus
A. insularis	C. unicolor	B. crytistoris yncisus
A. dichroa	Saroglossa [Genus]	Oriolidae [Family]
A. mysolensis	S. aurata [Species]	Oriolus [Genus]
A. magna	S. spiloptera	O. szalayi [Species]
A. minor	Creatophora [Genus]	O. phaeochromus
A. panayensis	C. cinerea [Species]	O. forsteni
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O. bouroensis G. cyanoleuca [Species] Paradisaeidae [Family] O. viridifuscus G. brujini Loria [Genus] Corcorax [Genus] L. loriae [Species] O. sagittatus O. flavocinctus C. melanorhamphos [Species] Loboparadisea [Genus] L. sericea [Species] O. xanthonotus Struthidea [Genus] Cnemophilus [Genus] O. albiloris S. cinerea [Species] O. isabellae C. macgregorii [Species] Artamidae [Family] Macgregoria [Genus] O. oriolus Artamus [Genus] M. pulchra [Species] O. auratus A. fuscus [Species] Lycocorax [Genus] O. chinensis A. leucorhynchus L. pyrrhopterus [Species] O. chlorocephalus A. monachus Manucodia [Genus] O. crassirostris A. maximus M. ater [Species] O. brachyrhynchus A. insignis M. jobiensis O. monacha A. personatus M. chalybatus O. larvatus A. superciliosus M. comrii O. nigripennis A. cinereus Phonygammus [Genus] O. xanthornus A. cyanopterus P. keraudrenii [Species] O. hosii A. minor Ptiloris [Genus] O. crentus P. paradiseus [Species] O. traillii Cracticidae [Family] P. victoriae O. mellianus Cracticus [Genus] P. magnificus Sphecotheres [Genus] C. mentalis [Species] Semioptera [Genus] S. vieilloti [Species] C. torquatus S. wallacei [Species] S. flaviventris C. cassicus Seleucidis [Genus] S. viridis C. louisiadensis S. melanuleuca [Species] S. hypoleucus C. nigrogularis Paradigalla [Genus] C. quoyi P. carunculata [Species] Dicruridae [Family] Gymnorhina [Genus] Drepanornis [Genus] Chaetorhynchus [Genus] G. tibicen [Species] D. albertisi [Species] C. papuensis [Species] Strepera [Genus] D. brujini Dicrurus [Genus] S. graculina [Species] Epimachus [Genus] D. ludwigii [Species] S. fuliginosa E. fastuosus [Species] D. atripennis S. versicolor E. meyeri D. adsimilis Astrapia [Genus] D. fuscipennis Ptilonorhynchidae [Family] A. nigra [Species] D. aldabranus Ailuroedus [Genus] A. splendidissima D. forficatus A. buccoides [Species] A. mayeri D. waldenii A. crassirostris A. stephaniae D. macrocercus Scenopoeetes [Genus] A. rothschildi D. leucophaeus S. dentirostris [Species] Lophorina [Genus] D. caerulescens Archboldia [Genus] L. superba [Species] D. annectans A. papuensis [Species] Parotia [Genus] D. aeneus Amblyornis [Genus] P. sefilata [Species] D. remifer A. inornatus [Species] P. carolae D. balicassius A. macgregoriae P. lawesii D. hottentottus A. subalaris P. wahnesi D. megarhynchus A. flavifrons Pteridophora [Genus] D. montanus Prionodura [Genus] P. alberti [Species] D. andamanensis P. newtoniana [Species] Cicinnurus [Genus] D. paradiseus Sericulus [Genus] C. regius [Species] S. aureus [Species] Diphyllodes [Genus] Callaeidae [Family] S. bakeri D. magnificus [Species] Callaeas [Genus] S. chrysocephalus D. respublica C. cinerea [Species] Ptilonorhynchus [Genus] Paradisaea [Genus] Creadion [Genus] P. violaceus [Species] P. apoda [Species] C. carunculatus [Species] Chlamydera [Genus] P. minor Heterolocha [Genus] C. maculata [Species] P. decora H. acutirostris [Species] C. nuchalis P. rubra P. guilielmi Grallinidae [Family] C. lauterbachi C. cerviniventris Grallina [Genus] P. rudolphi

Corvidae [Family] G. glandarius [Species] N. columbiana [Species] Platylophus [Genus] G. lanceolatus N. caryocatactes P. galericulatus [Species] G. lidthi Platysmurus [Genus] Perisoreus [Genus] P. leucopterus [Species] P. canadensis [Species] Gymnorhinus [Genus] P. infaustus G. cyanocephala [Species] P. internigrans Cyanocitta [Genus] Urocissa [Genus] C. cristata [Species] *U. ornata* [Species] C. stelleri U. caerulea U. flavirostris Aphelocoma [Genus] A. coerulescens [Species] U. erythrorhyncha U. whiteheadi A. ultramarina A. unicolor Cissa [Genus] Cyanolyca [Genus] C. chinensis [Species] C. viridicyana [Species] C. thalassina Cyanopica [Genus] C. pulchra C. cucullata C. cyana [Species] C. pumilo Dendrocitta [Genus] C. nana D. vagabunda [Species] C. mirabilis D. occipitalis C. argentigula D. formosae Cissilopha [Genus] D. leucogastra C. melanocyanea [Species] D. frontalis C. sanblasiana D. baileyi Crypsirina [Genus] C. beecheii Cyanocorax [Genus] C. temia [Species] C. caeruleus [Species] C. cucullata C. cyanomelas Temnurus [Genus] C. violaceus T. temnurus [Species] C. cristatellus Pica [Genus] C. heilprini P. pica [Species] C. cayanus P. nuttali C. affinis Zavattariornis [Genus] Z. stresemanni [Species] C. chrysops C. mysticalis Podoces [Genus] P. hendersoni [Species] C. dickeyi C. yncas P. biddulphi Psilorhinus [Genus] P. panderi

P. pleskei

Pseudopodoces [Genus]

Nucifraga [Genus]

P. humilis [Species]

Pyrrhocorax [Genus] P. pyrrhocorax [Species] P. graculus Ptilostomus [Genus] P. afer [Species] Corvus [Genus] C. monedula [Species] C. dauuricus C. splendens C. moneduloides C. enca C. typicus C. florensis C. kubaryi C. validus C. woodfordi C. fuscicapillus C. tristis C. capensis C. frugilegus C. brachyrhynchos C. caurinus C. imparatus C. ossifragus C. palmarum C. jamaicensis C. nasicus C. leucognaphalus C. corone C. macrorhynchos C. orru C. bennetti C. coronoides C. torquatus C. albus C. tropicus C. cryptoleucus C. ruficollis C. corax C. rhipidurus C. albicollis

C. crassirostris

P. morio [Species]

C. formosa [Species]

Calocitta [Genus]

Garrulus [Genus]

A brief geologic history of animal life

A note about geologic time scales: A cursory look will reveal that the timing of various geological periods differs among textbooks. Is one right and the others wrong? Not necessarily. Scientists use different methods to estimate geological time—methods with a precision sometimes measured in tens of millions of years. There is, however, a general agreement on the magnitude and relative timing associated with modern time scales. The closer in geological time one comes to the present, the more accurate science can be—and sometimes the more disagreement there seems to be. The following account was compiled using the more widely accepted boundaries from a diverse selection of reputable scientific resources.

Era	Period	Epoch	Dates	Life forms
Proterozoic			2,500-544 mya*	First single-celled organisms, simple plants, and invertebrates (such as algae, amoebas, and jellyfish)
Paleozoic	Cambrian		544-490 mya	First crustaceans, mollusks, sponges, nautiloids, and annelids (worms)
	Ordovician		490-438 mya	Trilobites dominant. Also first fungi, jawless vertebrates, starfish, sea scorpions, and urchins
	Silurian		438-408 mya	First terrestrial plants, sharks, and bony fish
	Devonian		408-360 mya	First insects, arachnids (scorpions), and tetrapods
	Carboniferous	Mississippian	360-325 mya	Amphibians abundant. Also first spiders, land snails
		Pennsylvanian	325-286 mya	First reptiles and synapsids
	Permian		286-248 mya	Reptiles abundant. Extinction of trilobytes
Mesozoic Triassic	Triassic		248-205 mya	Diversification of reptiles: turtles, crocodiles, therapsids (mammal-like reptiles), first dinosaurs
	Jurassic		205-145 mya	Insects abundant, dinosaurs dominant in later stage. First mammals, lizard frogs, and birds
Cret	Cretaceous		145-65 mya	First snakes and modern fish. Extinction of dinosaurs, rise and fall of toothed birds
Cenozoic Tertiar	Tertiary	Paleocene	65-55.5 mya	Diversification of mammals
		Eocene	55.5-33.7 mya	First horses, whales, and monkeys
		Oligocene	33.7-23.8 mya	Diversification of birds. First anthropoids (higher primates)
		Miocene	23.8-5.6 mya	First hominids
		Pliocene	5.6-1.8 mya	First australopithecines
	Quaternary	Pleistocene	1.8 mya-8,000 ya	Mammoths, mastodons, and Neanderthals
		Holocene	8,000 ya-present	First modern humans