

Preface

MOVEMENT IS THE HALLMARK of avian life. The freedom with which most birds fly through their environment shapes every aspect of their lives—from the food items they consume and their response to predators, to the size of their territories, and their dependence upon long-distance vocal signals to communicate. But mobility of birds plays its most dramatic role in migration. Migration is the regular movement from a breeding site to a location (or locations) to survive the rest of the year. We may never know when birds first started migrating, but over the tens of millions of years of these annual pilgrimages, migration has proliferated and lengthened, to the point that thousands of species migrate some distance and hundreds of species move thousands of miles between temperate, arctic, and tropical environments.

The attention of ornithologists is riveted on the very long temperate-tropical migration systems partly because of the spectacular feat of moving vast distances, often at high altitude and over some of the most formidable barriers. Behaviorists fascinated with how information is stored and processed have long been challenged by how birds find and remember their route between very precisely defined locations in different continents. Physiologists and morphologists probe the adaptations that allow birds to complete these Olympian journeys. Still other researchers wrestle with how genes and the environment interact to shape the precise physiological and behavioral programs that migration demands.

As fascinating and important as these inquiries into the machinery of migration are, the ultimate challenge is understanding how and why these systems evolved and

how the act of migration affects a species overall life history. Answering these broader questions requires the more reductionistic study of how birds accomplish these feats, but these pursuits need to be folded into a more holistic approach to the geography, history, ecology, and demographic trade-offs of the migratory strategy.

This holistic view of temperate-tropical migration systems has been evolving much the way that biological evolution proceeds: changes in perspective give rise to periods of rapid change followed by years of steady empirical progress. The evolution of thought on these migration systems can be traced through a series of major symposia that have punctuated the last 25 or so years.

In 1977, a group of about 50 bird ecologists held a meeting at the Smithsonian's Conservation and Research Center (CRC) in Front Royal, Virginia, to discuss the important findings and the most important questions remaining in migration ecology. The excited chatter of the conference focused on newly obtained information on how birds spent their time in the Tropics. The meeting was a small effort to redress the years of imbalanced concentration on the ecology of migratory birds on the temperate breeding grounds and culminated in a symposium volume entitled *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (Keast and Morton, eds., 1980). That volume became one of the most heavily cited bird books ever produced from a scientific meeting and an excellent complement to Moreau's classic volumes on the Palearctic-African migration system. Twelve years later, another meeting was held at the Manomet Bird Observatory, Massachusetts, and also resulted in a landmark volume, *Ecology and Conservation of Neotropical Migrant Landbirds* (Hagan and Johnston, eds., 1992). The Manomet symposium rode on the crest of a wave of renewed interest in the challenges facing the conservation of migratory species dependent upon habitat along their long journeys through the (predominantly Western) Hemisphere. Both conferences were influential in driving research agendas on New World migratory birds (primarily songbirds) at the end of the twentieth century.

It was only fitting that the Smithsonian Institution hosted the next conference, 25 years after the first, to synthesize the cutting-edge findings about the basic ecology and evolution of migratory birds of all worlds. "Birds of Two Worlds: Advances in the Ecology and Evolution of Temperate-Tropical Migration Systems" took place in March 2002 at the National Conservation and Training Center in Shepherdstown, West Virginia, and lasted 3½ days. The conference included a series of invited talks organized into symposia, round table discussions, and a contributed poster session.

The present volume, resulting from that conference, emphasizes basic evolutionary and ecological questions that surround the phenomenon of long-distance migration in birds and includes both New and the Old World examples. Rather than focusing on the mechanisms and adaptations for migration itself, we concentrate on how migration systems evolve and how the challenges of moving between

vastly different environments can influence the life history, morphology, and behavior of the species involved. What properties distinguish long-distance migrants from resident birds and how migratory birds cope with the transitions during the annual cycle are major threads woven through all the chapters. Finally, we explore the factors that underlie the distribution of migratory species across ecosystems and continents. Many of the questions addressed in this volume have haunted ornithologists for decades, but the recent advent of conceptual models and the technological tools for probing these difficult questions have allowed ornithologists to stretch the boundaries of our understanding.

The volume is organized into seven thematic sections that establish a narrative trail. When this path is traversed the reader will see the breadth of biology required to understand the evolution and ecology of these migratory systems. Each section begins with a brief introduction by a leading ornithologist that is designed to provide a broad but cogent synthesis of the chapters that follow. To provide an overall roadmap, below we describe the parts of the volume and the big questions and research themes that illuminate the research described in the individual contributions.

Evolution of Migration Systems

Temperate-tropical migration systems represent the end point of evolutionary processes that select for shorter seasonal movements. For decades, ornithologists have grappled with the theoretical questions of what factors drive the evolution of seasonal movements. What are the demographic trade-offs for different migration strategies? Ornithologists have also speculated upon the historical aspects of the development of migration systems: How rapidly do they evolve? Did tropical resident populations give rise to temperate-tropical migrants? How often does long-distance migration evolve within particular taxa? Chapters in this section address these shared questions from distinctly different perspectives and methodologies.

Adaptations for Two Worlds

Migratory birds must often function efficiently and competitively in two highly divergent habitats. Nowhere is this more apparent than in the temperate-tropical migration systems. The contributors approach the problem of adaptive compromise facing migratory birds at the level of adaptations that characterize species and populations and the challenges that face individuals. Do these adaptive compromises have a tangible effect on highly migratory species when compared with birds that remain resident in a region throughout the year? How do birds obtain and use information about the environment at the ends and pathways of migration? And how do individual migrants balance the obvious need to display a high degree of ecological flexibility with the contravening demands for specialization, and what behavioral mechanisms maintain this balance?

Biogeography

Biogeographers search for patterns in the distribution of organisms across large spatial scales and develop hypotheses about what factors account for the patterns. Most biogeographers deal with a single geographic range for the species they study. What makes the study of the geography of migratory birds so interesting is that at least two ranges are involved, as well as the path between them. As migratory birds crisscross the globe, they often share their ranges and routes to varying degrees with many species (such as those that migrate from the Western Palearctic to sub-Saharan Africa), thus forming discernible migration systems. Authors in this section explore factors that account for the large-scale patterns of distribution of migratory birds and incorporate ecological, historical, and biophysical processes into their hypotheses.

Connectivity

Up until about 10 years ago, we knew almost nothing about dispersal into breeding populations or the geographic relationship between specific breeding and nonbreeding grounds of birds. A recent explosion of technological advances, from the application of molecular techniques to the use of stable isotopes, now allows scientists to address these issues and others. The chapters in this section describe the technology and, more importantly, explore the ecological and evolutionary implications of understanding population connectivity.

Migration Itself

Long-distance migration is one of the most physically demanding events in the animal kingdom. The adaptations and preparations for the journey have ramifications for their entire life history and give rise to many big questions: What factors influence departure and stopover schedules? How are migratory routes shaped by natural selection and how rapidly can they be modified? In keeping with the

theme of the volume, the chapters here explore and emphasize how these adaptations to the extreme sport of migration influence the performance of birds at other times of year.

Behavioral Ecology

The chapters in this section explore the mating systems, use of space, and flocking behavior of migratory birds during the breeding and, particularly, the nonbreeding season. The ultimate aim of this section is to improve our understanding of how cross-seasonal interactions influence the behavior and ecology of birds at both ends of their migratory trips.

Population Ecology

The dynamics of breeding populations of migratory birds vary considerably; many populations show long periods of stability, others display long-term cycles, and still others show less predictable annual fluctuations. Understanding why some population numbers change and others do not is a central issue in ecology and crucial to understanding the anthropogenic causes of population change. Are migrants most limited during the breeding season, the nonbreeding season, or migration? When are density-dependent factors, such as food supply, depredation, and habitat availability, important, and when do major climatic occurrences, such as an ill-timed hurricane or El Niño event, determine population size? What is the role of social factors, such as dominance and territoriality? And finally, can we improve our ability to predict population changes over time?

This is an exciting time in migratory bird research and we believe that this volume captures that enthusiasm and goes one step further to explicitly point aspiring students toward the research gaps still in need of attention. Our hope is that this volume will inspire students and researchers alike and continue to push the envelope of our understanding of migratory bird biology.