PREFACE

But how to begin a beginning? A strange sound interrupted my tossing. I went to the window, the cold air against my eyes. At first I saw only starlight. Then they were there. Up in the March blackness, two entwined skeins of snow and blue geese honking north, an undulating W-shaped configuration across the deep sky, white bellies glowing eerily with the reflected light from town, necks stretched northward. Then another flock pulled by who knows what out of the south to breed and remake itself. A new season. Answer: begin by following spring as they did—darkly, with neck stuck out.

So begins William Least Heat Moon's *Blue Highways*, with the avian semi-annual journey through the blue standing in not only for the physical investigation of byways but also for metaphysical exploration. It seems to be an appropriate metaphorical beginning for this book as well because while several fine reviews of the voluminous literature on bird migration have already been published (e.g., Keast and Morton 1980; Gwinner 1990; Hagan and Johnston 1992; Alerstam and Hedenström 1998a; Berthold et al. 2003; Greenberg and Marra 2005; Newton 2008), none has taken the particular road I intend to travel. In this treatment, I will use the structure of the annual cycle as a means for examining how the avian migrant

differs from its resident counterparts. The basic thesis is that these differences represent milestones along the evolutionary pathway that shape a migrant lifestyle through the process of natural selection. I am hopeful that this slight shift in emphasis, from a cataloging and description of the various aspects of bird migration to a synthesis and consideration of the larger picture into which the migrant fits, will result in a deeper understanding. Perforce, my treatment is selective rather than exhaustive, and topics considered important by others may not be addressed.

Pronouns are always a concern in a book of this kind, especially when the author has spent much of his life investigating many aspects of the topic in the field. Starting every sentence with "I" is not only annoying for the reader but also misleading in my own case, as more than 90 percent of my work has been done with the help of colleagues whose contributions were very large indeed—not to mention the fact that all inquirers, regardless of subject matter, stand on the shoulders of giants. Therefore, throughout this work, when referring to my published research and perceptions on major issues, I use the royal "we." This practice, however, is not meant to incriminate my collaborators. I take full responsibility for the opinions expressed.

The approach taken in this treatment is to provide "reflective inquiry" (*sensu* Reese 2012) on what a migrant is and how it came to be. In pursuing this end, I will strive to summarize what is known, what we think we know, and what we still don't understand about topics I consider to be critical. The reader will be referred to other sources for greater detail and will be exposed to competing hypotheses.

Ideas, of course, are the currency of the research biologist's profession, and it has been a concern of mine throughout to honor that concept. Therefore, my policy for literature citation in general is as follows:

- Cite the first-published or most influential paper that presents an important idea.
- Cite the most recent reviews and research of which I am aware.
- Cite my own work where it applies.
- Cite alternative explanations as pertinent.

Continental and epochal biases in literature citation characterize nearly all published scientific work and are, perhaps, not surprising given that a person's thought is formed largely in a particular intellectual milieu in space and time. I originally approached Barbara Helm, formerly of Germany's Max Planck Institute for Ornithology and currently lecturer at the University of Glasgow, to serve as co-author for this work, not only because of her brilliant and original work in collaboration with Eberhard Gwinner but also as a result of a conscious effort to address this problem; that is, my own intellectual consciousness was formed in the 1970s in the New World, whereas Barbara's was formed in the European tradition in the early 2000s. Unfortunately, work-level and other concerns forced her withdrawal, but she reviewed large portions of the manuscript in an attempt to help me address these

issues. Nevertheless, biases of these kinds are, to some extent, unavoidable, and I apologize in advance where I have allowed them to creep in and persist.

One aspect of the continental divide is in the use of bird names: Old World biologists tend to follow different authorities from New World scientists. The procedure followed in this book represents an uneasy compromise. I use the taxonomic sequence and terminology of the American Ornithologists' Union (2012) *Check-list of North American Birds* wherever possible and Gill and Wright (2006) for everything else. This procedure results in some odd choices because the two references disagree substantially in some places, but it seemed best for my purposes.

The taxonomic focus for my research has been on passerines, and there is no doubt that a tendency to use examples from this group disproportionately exists in my treatment of the hypotheses and literature of migration. I mention this slant not only as an apology to colleagues who work with one of the many other orders in class Aves but also as a theoretical caveat. These other avian groups have ancient evolutionary histories and ecologies that are quite different from songbirds (e.g., several are pelagic). Certainly, there is room for future syntheses involving greater incorporation of what is known about migration among orders other than Passeriformes than I have attempted, and I look forward to reading the results of such efforts.

Much of what I will summarize and analyze concerning the adaptations of migrants in the following chapters is based on field observations. A generation ago, the great theoretical ecologist Robert MacArthur (1972) suggested that the era of descriptive biology was over: it was time for synthesis. In many ways, he was right. It was time for ecology to move beyond the descriptive work of field biologists with their dusty specimen collections and pedantic ways and begin to try and make some effort at understanding the larger picture using rigorous theoretical reasoning supported by modeling, mathematics, and statistics. An unintended consequence of this change in focus was the severe weakening of the authority of field biology as an important scientific endeavor relative to other branches of biological science. Yet this view ignores three contributions made by field biology studies to the understanding of the natural world that are of fundamental importance: (1) they provide the original data on which explanatory models, hypotheses, and theories are based; (2) they test the assumptions for these theoretical efforts; and (3) they track change. Of course, the latter two of these contributions are not always appreciated by the scientific establishment since they often involve presentation of negative data—that is, data that invalidate rather than support a popular hypothesis. A recent example of the tendency to denigrate field biology contributions is provided by the reception given to E. O. Wilson's (2012) book, *The Social Conquest of Earth*, where Wilson summarizes field data on human and social insect behavior that cannot be explained readily on the basis of individual or kin selection, and concludes that some form of group selection must be involved. This view is at odds with current theory and the majority of workers in the discipline of evolutionary

biology (e.g., Dawkins 2012, Mithen 2012). Nevertheless, it is based on a variety of excellent data from field studies for which, at present, there appears to be no better explanation.

Despite the obvious continued need for field studies, particularly in the case of migratory birds, there are serious issues concerning the formulation of hypothetical explanations based on field data. Indeed, these explanations have been criticized, often correctly, as the telling of "just so" stories, as in "How the leopard got its spots" (Kipling 1912), because the investigator essentially accepts an explanation for observations without testing among the alternatives. Admittedly, it is often difficult to construct an experiment that will provide the data necessary to evaluate competing hypothetical explanations in the natural world. For instance, whereas it is relatively easy to assess the effects of nitrogen on a particular crop by assigning different nitrogen treatments to a set of test plots, all of which are treated in exactly the same way except for the amounts of nitrogen given to them, it is a good deal less simple to test how a female Northern Pintail (*Anas acuta*) selects a mate, even under relatively controlled conditions (Sorenson and Derrickson 1994). Nevertheless, without some form of testing among alternatives, no hypothesis can be considered as properly vetted. A way out of this dilemma is through the presentation of testable predictions, at least in some cases. When one has gathered the data necessary to formulate a hypothesis or several alternative hypotheses, one can then put forward a set of testable predictions. These predictions allow for direct or indirect testing among the various alternatives, as long as the assumptions on which the study is based are valid. Where possible, I use this approach in an effort to make clear what is known as well as what remains to be done to understand the avian migrant, stimulate future research, and help resolve important issues.

A critical aspect of my examination of the avian migrant is consideration of what physiologic and behavioral characteristics of migration are precisely programmed (i.e., in the migrant's genome) versus what remains flexible within well-defined genetic parameters (i.e., "reaction norms") (van Noordwijk 1989; Schlichting and Pigliucci 1998; van Noordwijk et al. 2006). Although this move "beyond nature and nurture" (Pigliucci 2001; Piersma and van Gils 2011) has profoundly influenced thinking in field biology, some remain skeptical about the entire area of reaction norm investigation (Zink 2002). As I understand their criticism, concepts such as reaction norms lack meaning because they have no physical aspect that can be tested in a laboratory. In this, they are quite right: We are at present only beginning to understand how the same genetic structure can result in different behavioral or physiologic manifestations in different environments. In some ways, this debate is similar to earlier controversies. In fact, Darwin's (1859) theory of evolution by adaptation through natural selection has never lacked for critics since its first publication. Although often motivated by challenges posed to sacred beliefs, many of these critics had valid observations concerning the theory's deficiencies. The most obvious weakness, at least for the first few decades after its proposal, was the lack of a plausible mechanism allowing the passing of information concerning

the effects of natural selection from one generation to the next. Darwin's "gemmules" proffered a rather cumbersome but functional theoretical contraption to explain how natural selection might serve to use one generation to shape the next, just as Ptolemy's spheres worked for awhile to describe elliptical orbits for the planets. The work of Mendel, Hardy, Weinberg, Fisher, Watson, Crick, Mayr, E. O. Wilson, Dawkins, and many others built the foundation for the modern theory, placing it on much firmer functional ground. Nevertheless, the well-tested and studied principles of variation, heredity, differential reproduction, and mutation do not yet provide a complete explanation for how adaptation of populations occurs in the real world in general (Fodor and Piattelli-Palmarini 2009; Lewontin 2010) and in migratory bird behavior in particular (Helm et al. 2005; van Noordwijk et al. 2006; Piersma and van Gils 2011). Yet although the process may not be fully understood, the basic theory of adaptation through natural selection as proposed by Darwin remains the most powerful explanatory hypothesis we have for how organisms are shaped. Freeman Dyson (2003) wrote in response to critics of some of Isaac Newton's most profound thinking, "Newton was no fool." The same can be said for Darwin and for van Noordwijk as well.

Adaptations discussed for avian migrants in this book obviously are derived from natural selection, although some details of the mechanism remain to be clarified. Bird migration is one of the fields of biology where the concept of reaction norms appears to have its most obvious application. It may be that reaction norms are no more than another creaky contrivance, like gemmules, formulated to explain what at present cannot be explained by our modern theory of evolution. Nevertheless, they will serve my purposes well enough for the present, and I will use the concept to the best of my ability to emphasize those aspects of avian migration that make clear the fact that we do not yet have a complete understanding of how genes and environment interact to control the physiology and behavior of individuals.

The approach taken throughout the text has been to examine what is known versus what is hypothesized concerning the biology of the avian migrant. On occasion, this has resulted in detailed dissection of specific studies, a practice often referred to pejoratively (especially by those whose ideas have been subjected to such treatment) as setting up a "straw man" simply to knock it down. Although I sympathize wholeheartedly with the unhappy sensation caused by such treatment (having experienced it often enough myself), I disagree with the characterization. Those responsible for the hypotheses being parsed are giants in the field—straw is not the medium of which they or their ideas are constructed. Also, I am well aware of the fact that if my critique is flawed, I will receive a thunderous negative response in a variety of excruciatingly public venues. So be it. Progress in understanding is not achieved by blind acceptance or repetition. Failure to examine critically the assumptions on which important ideas are based or to consider alternative explanations are both serious disservices to science. Francis Bacon said, "If we begin with certainties, we will end in doubt, but if we begin with doubts and bear them patiently, we may end in certainty." This sentiment serves as the guiding

principle for this book in which critical interpretation of ideas rather than a summary of facts or accepted explanations is the focus. Inevitably, this approach will bring me into some level of disagreement with a fair number of my colleagues and predecessors in the field of migratory bird studies. For these differences, I express to them my sincere apologies. In no way do I wish to minimize the importance of their contributions. I am well aware of the immense amount of work and commitment involved in the conduct of field and laboratory research, and I deeply honor their contributions. Nevertheless, progress in understanding requires synthesis, and synthesis requires judgment. As I have said at the beginning of this preface, I am sticking my neck out and flying into the dark in the hope of building a clearer understanding of the avian migrant.