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An Integrative Approach

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An Introduction to Animal Behavior

An Integrative Approach

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An Introduction to Animal Behavior
An Integrative Approach

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Front cover: The integrative nature and complexity of animal behavior studies are illustrated in this example of why birds sing, in this case a singing male oropendola, a member of the New World blackbird family. Data obtained (clockwise from top, left) from studies of the morphology of the syrinx that enables complex song production, the brain circuitry involved in song learning, a phylogeny of some oropendola taxa and sonograms of the song they produce, and a hypothetical relationship between male song repertoire size and the number of offspring sired are combined to provide an answer.

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*MJR dedicates this book to his daughters Emma and Lucy,
whose interest in and enthusiasm for the natural world
continues to fuel his own.*



*WW dedicates this book to Debbi Greene, who
continues to be his inspiration.*

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Preface

ANIMAL BEHAVIOR WEAVES ITSELF THROUGHOUT the tapestry of biology: It is sparked when neurons fire in response to stimuli in the external world, it forms the interactions that lead to reproduction and genetic propagation, and it enhances complex group function, even when it emerges from seemingly simple self-organizing principles. Animal behavior is the most integrative endeavor of biology—its practitioners vary from those interested in the molecular, hormonal, and neural control of behavior to those who concentrate on its adaptive significance, historical patterns, and ecological consequences. As such, animal behavior provides the interface between proximate and ultimate biology—the processes internal to the animal and the consequences external to it. As an example, an animal's sensory system is exquisitely designed to perceive and organize the details of its external world, and few would argue the potency of natural selection in bringing about such an adaptation. But selection does not act directly on a sensory system; it acts on the behaviors that emerge from the interaction between the sensory system and the world around it. Nor does behavior evolve directly; rather it comes about from heritable changes in its underlying mechanism. How can we hope to understand animal behavior, or more generally, the science of life, if we commit to the parochialism of proximate versus ultimate questions and the mantra that they have nothing to do with one another? A subtext of this book is that we welcome the demise of the old proximate–ultimate dichotomy and celebrate what we hope will become a seamless segue from molecules and neurons to adaptation and evolution in the quest to understand why animals behave the way they do.

Both of our research programs have benefited from continual discussion and interactions across the proximate–ultimate boundaries of animal behavior. Walter Wilczynski was a postdoctoral associate studying the neuroscience of auditory systems in the Section of Neurobiology and Behavior at Cornell University at the same time that Michael J. Ryan was completing a thesis on sexual selection and acoustic communication in the same department. We were both hired at the University of

Texas in the early 1980s, W.W. in the Department of Psychology and M.J.R. in what was then the Zoology Department (and later morphed into the Section of Integrative Biology). We quickly began a series of research collaborations on the mechanisms and evolution of acoustic communication in anurans that continues to this day. It was through these interactions that we both became convinced that integrative animal behavior consists of more than cataloging data at different levels of analysis but is most potent when it uses information at each level of analysis to inform research and interpretations at other levels. We also became convinced that this interaction is symmetric, with proximate details being as important to understanding ultimate processes as evolution is critical for understanding the precise design of mechanisms of animal behavior. It is in this spirit that we set out to present our view of integrative animal behavior.

Our book is not intended to be an exhaustive review of the field of animal behavior but instead an introduction from an integrative perspective. It is aimed at upper-level undergraduates, graduate students, and others wanting exposure to this particular approach to animal behavior. The field of integrative animal behavior is so vast that it is impossible to cover exhaustively. Our strategy was to discuss the areas of animal behavior that both were historically of great interest to the field and continue to receive considerable interest among researchers and students. Necessarily, some interesting areas were omitted or mentioned only briefly to keep the size of the book manageable: These neglected topics include aposematic coloration, plant–animal interactions, and many areas of great interest to comparative psychologists, such as animal learning and conditioning and the growing field of animal cognition. There is a dearth of behavioral development in this book, in part because the marriage of this historically important field and the current rages in “evo-devo” and “eco-devo” seem not yet to be consummated. In those areas of animal behavior we have covered, we hope to provide the reader with a sense of their basic ideas and research problems as well as examples of both classic and contemporary research. The references we provide for each chapter are meant to do the same. We aimed to provide a collection of classic papers, new research findings, and several review papers, chapters, and books that will afford the interested reader an entry into the field as well as credit those works that provide its foundation. Unavoidably, we neglected some important and interesting work, especially from the large amount of new research coming into the field every day. We apologize in advance for any oversights.

In preparing this book, we drew heavily on others that are more specialized and provide a greater depth on aspects of behavior, neuroscience, and behavioral endocrinology. Most are included in the references in various chapters where they were most helpful, but we feel it important to express our appreciation and mention those here, as they would be excellent resources for readers who want more depth in various areas covered in our book. Every biologist who thinks herself educated should have read Darwin's *On the Origin of Species*. If interested in behavior, she should add *The Descent of Man, and Selection in Relation to Sex*, as well as *The Expression of the Emotions in Man and Animals*. The nine editions of John Alcock's *Animal Behavior, An Evolutionary Approach* have schooled many generations of behaviorists

over the last 35 years, and the textbook *An Introduction to Behavioral Ecology* and the collected writings, *Behavioral Ecology, An Evolutionary Approach*, by John Krebs and Nick Davies, have performed a similar task for the subdiscipline of behavioral ecology. Few textbooks combine both the excitement of animal behavior and concise and critical analyses of theory and data as do those of Alcock and of Krebs and Davies. A new set of textbooks has recently updated the field and they fill a role similar to that of the old “Krebs and Davies.” On the more mechanistic end of the animal behavior spectrum, Ralph Greenspan’s *An Introduction to Nervous Systems* and Gunther Zupanc’s *Behavioral Neurobiology* are complementary in providing excellent introductions to neuroscience as well as to neural mechanisms of behavior and neuroethology. Several books were especially helpful in providing background on the endocrinology of behavior: Randy Nelson’s textbook *An Introduction to Behavioral Endocrinology*, Elizabeth Adkins-Regan’s *Hormones and Animal Social Behavior*, the edited book *Behavioral Endocrinology*, by Jill Becker and colleagues, as well as the five-volume work *Hormones, Brain and Behavior*, edited by Donald Pfaff and colleagues. The latter is a major reference in the field of behavioral and neural endocrinology.

We also were greatly aided by numerous colleagues who provided comments and criticism of the chapters, shared unpublished data and background information, and engaged in discussions that clarified numerous issues. In particular, we would like to thank Karin Akre, Kim Hoke, and Deborah Lutterschmidt for their insightful reviews of the entire manuscript, and the Cold Spring Harbor Laboratory Press editor Judy Cuddihy for her exquisite attention to both detail and organization. In addition, we thank Elliott Albers, Greg Ball, Robert Bridges, David Cannatella, Lars Chittka, David Crews, Steve Emlen, Matthew Grober, Kim Huhman, Jonathon Losos, Robert Mason, Michael Meany, Kirsten E. Nicholson, Steve Nowicki, John Phillips, Joan Strassman, Greg Sword, David Quellar, and the late Jerry Waldvogel. They have all helped improve the quality of this work. We would also like to acknowledge the support we have been fortunate to receive for our research. Mike Ryan’s work has received support from the National Science Foundation, the Smithsonian Tropical Research Institute, and the Clark Hubbs Professorship in Zoology. His department also provided a semester faculty leave to work on the book. Walt Wilczynski’s research has been supported by the National Science Foundation, the National Institute of Mental Health, the Smithsonian Tropical Research Institute, and the Center for Behavioral Neuroscience, a Science and Technology Center established with funding by the National Science Foundation with continuing support from Georgia State University. We would also like to thank the past and present members of our own labs, who drove our research and our intellectual engagement with animal behavior and all the areas of science that connect to it. It is not inappropriate to thank in advance our future students and colleagues as well, for helping us explore areas of animal behavior yet to come.

M.J. Ryan
W. Wilczynski