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Grouse and Quails of North America — Frontmatter

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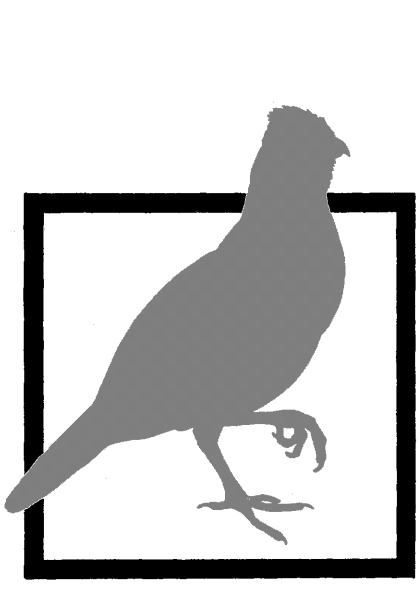

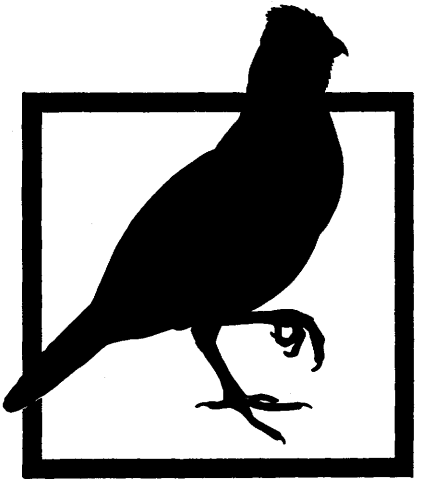

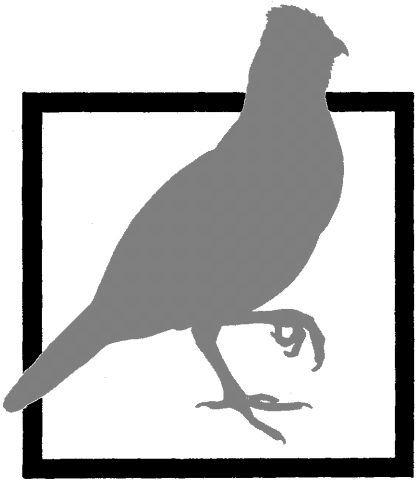

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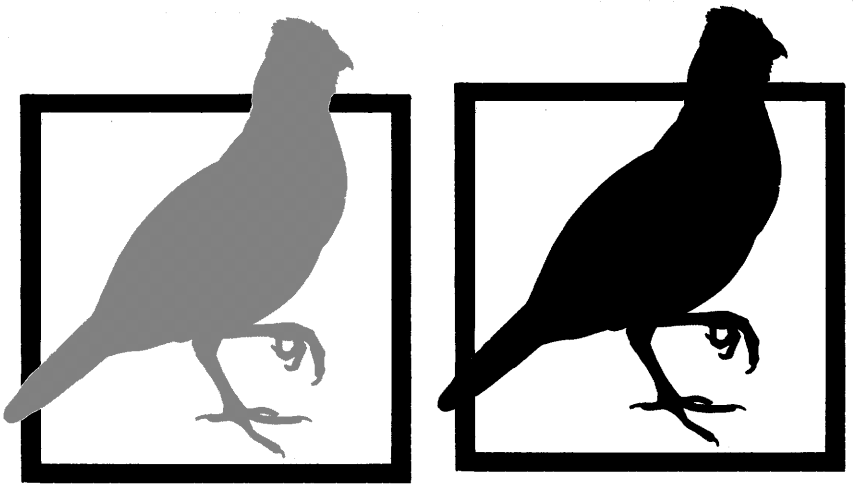

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To my children—Jay, Scott, Ann, and Karin—
in the sincere hope that they and their
children will be able to enjoy these
birds as much as I have

Table of Contents

List of Illustrations

PLATES

FIGURES

Tables

Preface

NEXT to the waterfowl, upland game birds have always occupied a special place in my heart. Some of my earliest memories are of riding along dusty North Dakota roads in the mid-thirties on pheasant and prairie chicken hunts with my father, long before I was able to carry a gun myself. My recognition of upland game as something other than exciting targets began during a 1952 tour of North Dakota game refuges while collecting waterfowl breeding records for an undergraduate special project. On one chilly May morning Merrill Hammond, biologist of the Lower Souris National Wildlife Refuge, drove me to a sharp-tailed grouse display ground. I watched the "dancing" of the grouse with fascination but, in retrospect, in virtual ignorance. At that time, terms like *sign stimuli, fixed action patterns,* and *isolating mechanisms* were foreign to me, and I was inclined to view the birds' behavior as a wonder of nature rather than as an intricately beautiful example of natural selection.

My next few years were spent intensively watching waterfowl, and through them I gradually gained insight into the significance of social behavior patterns in avian reproduction. Often while watching mallards displaying I would think back on the morning I watched sharp-tailed grouse, and ponder the parallels and differences between the lek displays of grouse and the social pair-forming displays of ducks. It wasn't until almost ten years later, in 1962, that I had an opportunity to renew my memories of grouse display. Then, in southeastern Nebraska, I spent an unforgettable April morning in the midst of a prairie chicken booming ground, and I became an immediate addict to grouse watching. As an ethologist, I could finally understand the evolutionary significance of these fantastic behavior patterns, and appreciate the marvelous opportunities that the grouse provided for behavioral studies under natural conditions.

Unfortunately, grouse do not readily adapt to captivity, nor can their

social behavior patterns be studied to advantage in such situations, thus I made no attempt to establish a captive flock. Instead, I decided that the New World quails provided a great potential for experimental behavioral studies and taxonomic research that had been largely overlooked by other investigators. Besides being relatively easy to keep and to breed in captivity, they exhibit a complex vocal repertoire that may readily be subjected to acoustical analysis. Further, the prior records of hybridization under natural conditions and in captivity suggested studies not only of possible genetic interest but also of potential taxonomic significance. Finally, the quails' ecological and behavioral adaptations provided such a striking contrast to those of their relatively close relatives, the grouse, that a comparison of the two and an evaluation of the possible reasons for these strong differences appeared warranted.

My plans for a comparative study of New World quails first took form in the fall of 1966, and were greatly facilitated by a National Science Foundation research grant (GB–7666X) awarded in the spring of 1967. This grant allowed me two summers of field work in Mexico during 1969 and 1970, where I traveled over ten thousand miles by car, establishing distributional limits and obtaining live specimens of various species of Mexican quails. In the winter of 1968–69 I first decided that a book-length summary of grouse and quail biology was worth undertaking, and during the academic year 1969–70 I began to actively collect references and wrote the first drafts of the early subject-heading chapters. I did not begin writing species accounts until the academic year 1970–71, during which I was granted a leave of absence by the University of Nebraska Research Council. Their financial assistance, and that provided by a Guggenheim Foundation fellowship during the spring and summer of 1971, allowed the completion of the manuscript.

The writing of a book on an assemblage such as the grouse or quails is greatly facilitated by the enormous body of technical literature that results from their importance as game birds. A useful work by Charles Crispens, Jr., *Quails and Partridges of North America: A Bibliography*, was published in 1960 and includes over two thousand references. No comparable bibliography exists for the North American grouse, but the Fish and Wildlife Service's *Wildlife Review* has abstracted over six hundred works published between 1935 and 1970 dealing with North American grouse species. Of these, 40 percent were concerned with the ruffed grouse, 18 percent with prairie chickens, about 10 percent each with sage grouse, blue grouse, sharp-tailed grouse, and ptarmigans, and 3 percent with the spruce grouse. During the same period nearly eight hundred publications on North American quail species were abstracted, of which approximately

80 percent dealt with the bobwhite, 10 percent with California quail, 6 percent with Gambel quail, and the remaining 4 percent concerned scaled, mountain, and harlequin quails. Far too many research studies on both grouse and quail have also been hidden in game agency reports that never are formally published and thus are, in effect, buried without benefit of epitaph. Except in a few necessary cases, where such information has been presented that was not otherwise available on a species, these sources were not used in this book. A recent index summary of published Pittman-Robertson research (Tait, 1968) provides a useful literature guide.

Far more interesting than digging through library stacks to obtain information have been my opportunities to see under natural conditions most of the species included in the book. Of the twenty-five included species, I have observed in life all of the nine species of grouse, both of the introduced partridges, and all but two of the fourteen species of quails. These birds have been observed in such diverse areas as the arctic tundra near Hooper Bay, Alaska, the lowland rain forests of Chiapas, and the Sonoran desert of Arizona. For example, during three memorable weeks in 1970 I waded in hip-deep snow along Trail Ridge of Rocky Mountain National Park while photographing white-tailed ptarmigan, climbed the humid and misty cloud forests of Hidalgo in search of bearded tree quail, and sweltered under a blistering Acapulco sun while trapping barred quail with mist nets. These great diversities in their ecology are one of the attractions of the grouse and quails; virtually every major community type in North America has been successfully occupied by one or more species of the group. As a result, every state and province in the United States and Canada supports at least one species of grouse or quail that may be legally hunted.

Partly because they were written at different times, the two major sections of the book have slightly differing outlooks. The first nine chapters, which are generally comparative in nature, are written in a somewhat formal, technical fashion. The individual species accounts were written with the thought in mind that not only professional biologists but also hunters and bird watchers will perhaps be reading them, and some attempt has been made to make them less formidable than the earlier chapters. Purists may object to this dual philosophy. Yet, in looking back on my own development as a biologist, it was the sections on habits, life history, or life story in the classic ornithological references that first captured my attention, and only much later did technical aspects of ornithology appeal to me. Thus, it is hoped that the people who obtain this book to read the species accounts will perhaps take an occasional look at the earlier chapters, and that the theoretical ecologist or evolutionist will also admit that his data must be based on actual living birds that possess both esthetic and scientific beauty.

A word of explanation about the basis for inclusion of species might be in order. All native species of grouse and quail occurring north of the Mexico-Guatemala border are included in the species accounts. By extending the geographic coverage to Panama, it would have been necessary to include *Colinus cristatus* (or *"leucopogon"*), *Rhynchortyx cinctus*, and four additional species of *Odontophorus*. Virtually nothing is known of the ecology or reproductive biology of any of these species, thus their inclusion in this book would have no great value. On the other hand it was decided to include both the gray partridge and the chukar partridge, since these species are well established in North America and considerable research on their biology has been carried out. In addition, they provide an interesting comparison with the true New World quails in terms of their ecology and behavior. In contrast, the ring-necked pheasant was purposely excluded; it has been well described in several monographs and is apparently not as closely related to the native quails as are the two introduced partridges.

Although I have been actively involved in research on the grouse and quails for four years, I must honestly say that very little in the present book represents new and original information. Nearly all of the findings reported are those of others, and the most that I can claim is credit for bringing them together in a single volume. Lest the reader believe that little research is left to be done on North American grouse or quails, he need only read the accounts of such species as the elegant quail, the harlequin quail, or the Mexican tree quails. Even for such intensively studied species as the bobwhite and ruffed grouse much more research might be done; I hope one of the virtues of this book will be to point out some of the great gaps or weaknesses in our knowledge. When initiating my research on grouse and quail after so many years of studying waterfowl, I felt as if I were embarking on an uncharted ocean. Since then I have discovered no new continents or even any major islands, and at most have simply confirmed or remeasured the depths already plumbed by others. Yet, inasmuch as any new voyage is an exciting one, I hope that others will see fit to follow me.

No voyage of any length is normally undertaken alone, and I must here express my great appreciation to the persons and agencies that assisted me. Foremost among the agencies that have assisted me are the National Science Foundation, the J. S. Guggenheim Foundation, and the Research Council of the University of Nebraska, all of which provided financial support for this study. Other institutions that have provided data, lent specimens, or allowed me to utilize their collections, are the American Museum of Natural History, the United States National Museum, the Chicago Field Museum of Natural History, the University of California

Museum of Vertebrate Zoology, the Los Angeles County Museum, the Denver Museum of Natural History, the James Ford Bell Museum of Natural History in Minneapolis, and the Chicago Zoological Park. The Cornell University Laboratory of Ornithology very kindly allowed me to reproduce a previously unpublished painting by L.A. Fuertes, and in addition provided copies of several sound recordings. Nearly all of the United States and Canadian game and wildlife agencies provided me with information about hunting seasons and, in many cases, data on estimated upland game harvests. The Secretaría de Agricultura y Ganadería of Mexico and its director general, Dr. R. H. Corzo, facilitated my Mexican field work and provided the necessary permits for collecting specimens.

Among the individuals who have personally assisted me I am particularly indebted to C. G. ("Bud") Pritchard, who painstakingly prepared five of the color paintings included in the book, and whose meticulous attention to the smallest details of feather and soft-part characteristics unfortunately cannot be adequately reproduced by the printing process. Likewise, on short notice John O'Neill set aside his other obligations to produce two stunning paintings of Mexican quail species that testify both to his great artistic abilities and to his personal familiarity with these tropical forest birds. Without the splendid paintings by these artists the book would have much less value and attractiveness. Charles Hjelte of the Colorado Department of Natural Resources very kindly allowed me to reproduce three excellent paintings done for that department by Dexter Landau, for which I am most grateful.

Other persons who personally helped me are too numerous to mention individually, but I cannot neglect Andrew Prieto or Edmund Sallee, who accompanied me on my Mexican trips, or Clait Braun, James Inder, and John Lewis, who assisted me with my field work in the United States and Canada. Dr. Starker Leopold gave me valuable advice and information; were it not for the groundwork provided by his research in Mexico my own work there would have been much more difficult and time-consuming. Many persons provided photographs, and although not all of them could be used, I wish to extend my thanks to David Allen, George Allen, Clait Braun, Edward Brigham, Glenn Chambers, Don Domenick, Kenneth Fink, Sean Furniss, Harvey Gunderson, C. G. Hampson, Joseph Jehl, K. C. Lint, Stewart MacDonald, M. Martinelli, Alan Nelson, Raphael Payne, Bruce Porter, C. W. Schwartz, Roger Sharpe, Charles Shick, Robert Starr, and Mary Tremaine. In particular, I appreciate Ken Fink's generous donation of his outstanding collection of grouse and quail photographs for my use.

Dr. Ingemar Hjorth very kindly allowed me the use of two of his published illustrations, for which I am very grateful. Many persons assisted me by

allowing me to observe or photograph birds in their collections, providing me with valuable specimens, or supplying me with information. Among these are F. E. Strange, William Huey, William Lemburg, and Glen Smart.

The use of the facilities of the Department of Zoology of the University of Nebraska has been of great benefit to me, and I must acknowledge the work of several of my graduate students, especially Daniel Hatch and Calvin Cink, in caring for birds and in maintaining incubation and rearing records. I owe a special debt of gratitude to Viki Peterson and Mrs. Janette Olander, who as departmental secretaries often neglected more pressing duties to type or retype a section of the manuscript without the slightest hint of complaint.

Finally, and most importantly, I must thank my wife, Lois, for patiently enduring too many summers alone, and for lovingly accepting too little gratitude in return.

Introduction

NEARLY all of the gallinaceous birds that are native to North America are included in two taxonomic groups, the grouse-like species of the subfamily Tetraoninae, and the quail-like species of the subfamily Odontophorinae. The former represent a temperate and subarctic group of about sixteen species which collectively have a widespread distribution in the Northern Hemisphere, and over half of which are found in North America. The latter group is a strictly Western Hemisphere assemblage that collectively includes about thirty species, almost half of which occur north of the Mexico-Guatemala border. Most of the remaining quails are tropical forest birds of northern and western South America about which very little is known. Thus, evidence suggests that North America was originally doubly colonized by early gallinaceous stock; from the south by basically tropical-forest-adapted birds that have evolved into the present array of quail species, and from the north by relatively arctic-adapted forms that have given rise to the present species of ptarmigans and grouse. Convergent evolution of these two separate but related stocks has since allowed much of North America to become inhabited by birds having similar ecological adaptations and in some cases overlapping distributions.

Within each of the two ancestral groups, evolutionary radiation has developed an interesting spectrum of anatomical variations, ecological adaptations, and behavioral specializations. These latter two aspects—adaptational niche variations associated with habitat differences, and behavioral variations associated with maximal reproductive efficiencies under varied climates, habitats and contacts with associated species—are the primary subjects of this book. Anatomical and physiological considerations will be given some attention in the early chapters, but the primary focus will be on the living bird in its natural environment.

In the species accounts, the summaries of the ranges are in general derived from *The American Ornithologists Union Check-list of North American Birds* (1957), modified as necessary to take recent changes and new information into account. This will be referred to as the *"A.O.U. Check-list."* Likewise, the ranges of the strictly Mexican species are generally based on the *Distributional Check-list of the Birds of Mexico* (1950) by Friedmann, Griscom, and Moore (referred to as the *"Check-list of the Birds of Mexico").* In cases where subspecies have been described since the publication of these books, they are listed but are identified as not yet verified. In a very few instances, subspecies described earlier but not recognized by the A.O.U. by 1957 have been recognized here. Also, contrary to current A.O.U. practice, most of the accepted subspecies have been given vernacular English names. However, such subspecies have normally been designated by simply adding a descriptive term to the species' vernacular name, so that confusion in species identification may be avoided. This usage of special vernacular names was felt desirable in view of the rather broad species concept employed in this book and the proposed merging of certain forms that have usually been recognized as separate species. In a few instances this has forced a deviation from vernacular names of American species as used by the *A.O.U. Check-list.* I have avoided possessives in English vernacular names, using for example Gambel quail rather than Gambel's quail. For strictly Mexican species I have in general followed the vernacular terminology used by A. S. Leopold in *Wildlife of Mexico: The Game Birds and Mammals.* Measurements indicated for each species were largely derived from those appearing in *The Birds of North and Middle America,* part 10, by R. Ridgway and H. Friedmann. Unless otherwise indicated, measurements for the folded wing represent unflattened wings, and tail measurements are from the tip of the tail to the point of insertion.