

PREFACE

The scientific discipline of ornithology is like a tree with new branches continually growing and reaching out. Unlike a tree, however, "The older it gets, the more vigorous its growth seems to be" (Mayr, 1983a). The revision of a textbook is at once a frustrating and a euphoric experience. It is frustrating in that the exponential growth of the discipline renders it impossible for authors to keep abreast of all new developments. It is a euphoric experience in that it affords us an opportunity to appreciate the vitality of the field and to absorb as many of the latest discoveries as we can. This done, we try to select the best and weave it into a coherent tapestry, and in the process correct errors and eliminate outdated material.

Early ornithologists wrote only for other ornithologists to read. Today, birds have been subjects of numerous studies contributing to the advancement of many areas of biology (see Foreword). A student of ornithology thus learns, sometimes incidentally, the principles of many biological disciplines.

The aim of this book remains that of the first edition: 1. To present, simply and straightforwardly, the basic facts of bird biology. 2. To arouse in the reader a lasting fascination for birds and for all the wonderful things they do. The book is directed towards the general student, not the specialist. Most of the chapters can be read and understood by the reader without special preparation.

Much of this book deals with natural history of birds. Good natural history is like good descriptive anatomy: when well done, both activities provide raw materials for experimentation and hypothesis-testing (Greene, 1986). Although much of this book consists of description, we tried to incorporate whenever possible good experiments testing biological principles. We try throughout to emphasize the fact that birds are products of natural selection, that selection operates on the individual, and that only individuals endowed with a certain complement of genes survive and reproduce to leave progeny. Here below we point out some of the highlights in our new edition.

Avian taxonomy is a dynamic field, and conclusions regarding relationships of birds are still not the final word in many cases. Most birds species have been discovered and described. However, adaptive radiation may mask true evolutionary relationships, and morphological convergences may lead taxonomists to erect phylogenies that may be erroneous. The field of avian taxonomy now calls upon techniques borrowed from sister disciplines such as biochemistry (DNA/DNA hybridization, electrophoresis), karyotypes, and ethology to help solve taxonomic problems. Recent advances in these areas are discussed in Chapter 2.

In Chapter 3 we bring together the latest studies on the secretory functions of the bird epidermis. The epidermis in birds has often been described as aglandular. Recent studies have shown, on the contrary, that the avian epidermis is very much living tissue capable of lipogenesis. One of the most exciting discoveries participated in by the junior author is that nestling Zebra Finches, *Poephila guttata*, are endowed with epidermal lipids organized into lamellar bodies which enable them to decrease cutaneous water loss and thus enable them to survive when heat-stressed. This is the first demonstration of how birds control transpiration through the skin.

Early texts also inform us that birds in general have a poor sense of smell and sense of taste. Only birds with large olfactory bulbs were thought to have a well-developed sense of smell. We bring together in Chapter 5 descriptive and experimental studies indicating that many birds may have good smell and taste capabilities. It has been suggested that large olfactory bulbs are not so

much indicative of greater olfactory sensitivity, as of greater discriminatory abilities. Experiments presented herein also indicate that birds may hear infrasounds and see into the near-ultraviolet.

In Chapter 6 we review some new literature on anatomical specializations adapting birds to certain dietary habits, e.g., grains, fruit, and conifer needles. We also introduce the student to the concept of "optimal foraging," one of the more active areas of ecological investigation today.

Chapter 7 deals primarily with physiological adaptations of birds to their environment or microenvironment. Oxygen consumption tends to increase when animals are exposed to high temperatures beyond the zone of thermal neutrality. Latest studies indicate that some hummingbirds do not conform to this principle. We review new literature showing that torpidity is utilized by small birds not only during emergencies but as a routine energy-saving device. We also discuss the latest literature and point out that the Greenwalt/Stein model of how syringes operate is not the last word and that different species vocalize in different ways.

Photoperiod is the primary trigger of gonadal growth in vertebrates. In Chapter 8 we bring together the latest experiments testing the synergistic role of avian vocalizations and photoperiod in effecting gonadal growth, and point out that extent of ovarian development may differ between adult hand-raised experimentals and those caught in the wild. Latest findings regarding other factors (e.g., food temperature, phytoestrogens) as triggers are also treated.

In Chapter 9, Behavior, we develop the themes put forward by Tinbergen as the ultimate goals of ethology, namely, evolution, ontogeny, causation, and function. We emphasize that there is a continuum between nature and nurture in the development of behaviors and bring together experiments indicating that learning may occur on the level of the single neuron. Although earlier texts have sometimes stated that tool-using in animals other than humans is a rare phenomenon, we discuss the literature indicating that tool-using and cultural traditions of various types are commonplace among birds and are often prime examples of the interplay of genome and environment in shaping behaviors.

In Chapter 10, Social Behavior, we bring up to date the concept of "imprinting" in birds. The early literature on imprinting is replete with studies on the "following" response but few studies on sexual imprinting. We develop Lorenz's four criteria pertaining to sexual imprinting, namely, the sensitive phase, supraindividuality, irreversibility, and manifestation later in life. We call attention to "contact" versus "distant" species in studying avian social behavior, and in the section on avian aggregations, we speculate on the costs and benefits of being the subordinate in a flock.

Modern instrumentation has permitted scientists to make great strides in the field of avian bioacoustics (Chapter 11). Songs appear to be characteristic of males of the species, and indeed females (e.g., of Zebra Finches) may not even have the neural equipment to store and produce songs. We review experiments on hormone manipulation which result in females developing male song centers in their brain and, with testosterone treatment, actually producing male-like songs. We also bring together experiments demonstrating various functions of bird song. In the section on song learning we develop the principles of "the early sensitive phase" and "stimulus filtering" showing that birds are much more plastic than early investigators have led us to believe. Again, the role of nature versus nurture in ontogeny is discussed. Finally, we discuss the controversial topic of assortative mating and avian song dialects.

In the chapter on territories (Chapter 12) we emphasize the fact that territories did not evolve for the purpose of limiting population density. Individuals compete for territories for their own benefit, with the consequence that density is often limited. We distinguish between territories and home ranges, show examples in which the two may or may not overlap, and point out that there may be geographical differences even within a species. We develop Huxley's idea of territory as an "elastic disc," and introduce the controversial concept of the "superterritory" as a manifestation of spiteful behavior.

The mating systems of birds (Chapter 13) comprise a very active area of ornithological research, especially in this age of "sociobiology." We give examples of the different mating systems, presenting them in the order of increasing male involvement: promiscuity, polygamy, monogamy, and polyandry. We discuss the evolution of various mating systems, and review some studies on the role of hormones in promoting polygyny.

Many species of birds are known to have helpers at their nests (Chapter 13). A superficial glance at these data suggests that this phenomenon is a manifestation of "altruism." Recent long-term studies indicate, however, that this phenomenon may be interpreted in terms of "selfishness" and selection

on the level of the individual. We also develop the concepts of outbreeding mechanisms, cuckoldry, and intra- versus intersexual selection *sensu* Darwin. We describe and discuss controlled experiments which have provided support of Darwin's idea on intersexual selection.

In Chapter 14, we develop the theme that a bird's nest is a product of natural selection—the shape of the nest, its placement in a particular microenvironment, its proximity to others of its kind—all these factors may effect the survival of the young. Birds may take advantage of local microclimates, so that there may be geographical variation within a species as to where nests are placed. We also discuss the role of nature versus nurture in the nest-building process.

The avian egg has also been the subject of much research in recent years (Chapter 15). We review studies of egg physiology which have advanced our knowledge of development of the egg, changes occurring in the egg during incubation (e.g., calcium absorption), and gaseous exchange through the shell. We also discuss correlations between life history strategies and size of yolk, number of pores in the shell, and clutch size. Finally, we consider the possible adaptive significance of larger clutch sizes at higher latitudes.

In Chapter 16 we review the recent literature on behavioral and physiological aspects of incubation. We bring together the latest studies on hormones and brood-patch production, point out differences in brood patch construction for different avian taxa and review recent literature on incubation patterns in birds. Modern instrumentation has permitted investigators to monitor egg temperatures, demonstrating that eggs survive large fluctuations in temperature range, and that in certain habitats and under certain conditions birds cover eggs to protect them from overheating rather than to raise their temperature. We review the latest literature on brood parasitism and develop the thesis that this breeding strategy evolved as an adaptive behavior for the parasite rather than as a result of deterioration and loss of the nest-building and incubation instincts, as some have previously suggested. We also discuss brood reduction in birds, a topic of much interest recently, and examine its possible adaptive significance.

Chapter 17 covers the care and development of young birds. We discuss the stimuli eliciting the begging response in young hummingbirds: behavior of nestling hummingbirds differs from that in other birds in a number of ways. Altricial versus precocial young represent two ends of a continuum. In the first, much energy is invested by the parents in the care of the young after hatching. In the second, more energy is invested in the developing embryo, as the hatchling may care for itself to various degrees depending on the species.

Chapter 18 deals with population dynamics in birds. An important concept here is the inability of any organism to maximize all forms of reproductive investment simultaneously. Long-lived (K-selected) species tend to produce fewer young per effort than short-lived (r-selected) species, but they must invest more parental care in each offspring. Nestlings compete with each other for resources so that individuals in small broods weigh more than those in large broods. We also review studies indicating the selective advantage of colonial breeding. Finally, we discuss the phenomenon of "floaters" as an alternate strategy to "helpers" or independent breeders.

Ecology (Chapter 19) is an enormous topic, and indeed various aspects of ecology are scattered throughout the book, since ecology merges into other areas of biology such as foraging strategies and helpers. We discuss how birds have adapted to particular habits: as the extremely successful creatures that they are, birds have evolved different methods of surviving harsh environments or seasons. Thus, hummingbirds resort to torpidity to survive winters atop the Andes, jays and titmice cache seeds as food reserves in time of need, to cite some examples. We update the section on competition and competitive release, and stress the point, giving examples, that competitive exclusion cannot be assumed but must be *demonstrated* by removal experiments.

The subject of avian biogeography (Chapter 20) has benefitted greatly in recent years from studies of fossil and subfossil remains and from modern biochemical systematics. For example, recent DNA/DNA hybridization studies by Sibley and his colleagues indicate that several groups of birds thought to have invaded Australia from Asia have apparently evolved *in situ* along with the marsupials and eucalypts. The celebrated McArthur-Wilson model of island biogeography maintains that immigration balances extinction in island avifaunas. We call attention to studies by Olson and colleagues which advocate caution in computing turnover rates based on census of extant avifaunas, as hunting activities of prehistoric humans, predation by introduced predators, or changes in climate during the Pleistocene may cause extinction, which may result in distorted views of turnover rates.

Migration and orientation (Chapter 22) is another active field of research. We review the breeding hybridization studies by Bethold and his associates showing the heritability of wing-length, a feature associated with the migratory habit, and the heritability of the duration of *Zugunruhe*, which is positively correlated with distance of migration. There often is a differential migration distance between the sexes in birds: males tend to winter farther north than females in several passerines, the reverse being true in snowy owls. Several hypotheses put forth to explain the adaptive significance of this phenomenon are reviewed and discussed. We update the section on orientation and migration, reviewing recent studies on orientation using sun, stars, magnetic fields, and polarized light as cues.

In Chapter 23, *Origin and Evolution of Birds*, we discuss recent studies on *Archaeopteryx* and call attention to data indicating that, contrary to the opinion of earlier scholars, it was probably capable of flapping flight. We discuss the topic of domestication and remind readers of Charles Darwin's studies on this phenomenon which he considered an analog of the speciation process. We review recent taxonomic studies on the nature of isolating mechanisms, and discuss the fascinating story of disassortative mating in White-throated Sparrows and polymorphisms in their chromosomes, morphology, and behavior. The question of "kin selection" is treated and discussed in accordance with neo-Darwinian theories of selection on the level of the individual.

In Chapter 24, *Birds and Man*, we discuss various activities by humans resulting in environmental pollution and breeding failure in avian populations (e.g., air pollution, pesticides, and oil spills). Finally, we review the literature on conservation measures taken to save some of the more endangered avian species in the world. Some of these efforts have proved more successful than others, and we point out the factors needed for an effective conservation program.

In sum, we offer this new edition in the hope that it will stimulate the next generation of ornithologists to challenge and test the conclusions based on recent studies. Birds are creatures of wondrous beauty, both in themselves and as subjects of study in a diversity of disciplines. We hope that our efforts will satisfy readers who ask with Aristophanes,

*My question, answer in the fewest words,
What sort of life is it among the birds?*

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