Commentary

The Contributions of Ornithology to Biology

Ernst Mayr

Molecular biology completely dominates today's biology. Viruses and bacteria are the organisms most frequently used in research, and someone familiar only with this segment of the literature is usually somewhat surprised when told of the massive contribution to knowledge and theory in biology made by other organisms, for instance birds. To be sure, birds also appeal to our aesthetic senses, as do orchids and butterflies, but few biologists realize to what great extent they have contributed to a better understanding of the world of life.

The study of birds is for many nothing but a hobby, and in the last century even professional ornithologists were rather uncertain as to where to draw the line between the hobby of bird watching and the scientific study of birds. This is reflected in a statement made in 1901 by the well-known American ornithologist Robert Ridgway in the introduction to his great work *The Birds of North and Middle America*. He said: "There are two essentially different kinds of ornithology: systematic or scientific, and popular. The former deals with the structure and classification of birds, their synonymies and technical descriptions. The latter treats of their habits, songs, nesting, and other facts pertaining to their life histories." In other words, he considered anything dealing with the living bird to be popular ornithology.

This commentary was the invitation lecture presented on the occasion of the celebration of the centennial of the American Ornithologists' Union in New York City, October 1983. Ernst Mayr is with the Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

When we read Ridgway's statement today we realize what an extraordinary change in our concept of scientific ornithology has occurred since 1901. This is well reflected in the subject matter of 900 theses submitted at American colleges for master's and Ph.D. degrees in ornithology during a recent five-year period (King and Bock 1978). Among these, 46% were in ecology, 23% in bird behavior, and only 4% in systematics. These figures illustrate dramatically the change in the concept of ornithology that has taken place since the founding of the American Ornithologists' Union in 1883 (also see Brush and Clark 1983, Stresemann 1975).

The history of ornithology from Frederick II's superb treatise *De arte venandi* (1250) to the present is a fascinating subject (Stresemann 1975). At first the study of birds was simply a part of general natural history and was conducted in the spirit of natural theology during the 18th and early 19th centuries. By the latter third of the 19th century, however, ornithology had become a self-contained science, although concerned primarily with problems of interest only to ornithologists and resulting in papers suitable only for ornithological journals. A look at the literature of that period reveals the dominant interest in collections, new species, migration, and faunistic records. Many factors can be cited as responsible for the dramatic change that has taken place in the last 75 years. Perhaps the most important was that a number of ornithologists became professors of zoology at leading universities and developed broadly educated students. Among these professors were Menzbier in Moscow, Palmgren in Helsinki, Stresemann in Berlin, David Lack at the Edward Grey Institute at Oxford, and Joseph Grinnell in California. Let us compare this with the present: In the US alone, 244 teachers of ornithology responded in 1975 to a questionnaire. They were teaching at 189 American institutions and 84 of them were directing the studies of 205 Ph.D. candidates, while 392 additional graduate students were working towards a masters degree (King and Bock 1978). These figures illuminate the massive basis on which the modern scientific study of birds rests. In 10 major textbooks in the fields of behavior, ecology, biogeography, and evolution, birds furnish more examples than do any other class of vertebrates.

Part of the reason for the extraordinary popularity of birds is that they are particularly advantageous for many scientific studies. There are two sets of properties of birds that make them exceptionally favorable material. Birds are conspicuous and easily observed by us because sight and hearing, the dominant senses of birds, are the same ones that are dominant in man. Therefore, the intraspecific signals of birds such as plumage displays and songs and calls are as easily perceived by man as by fellow members of the various bird species. As a result, the biology of birds can be studied without any elaborate apparatus. Furthermore, in contrast to many mammals, most birds are diurnal, live aboveground and outside water, all of which adds to the ease of observing them. Anyone who has been trying to observe mammals, fish, or insects appreciates these manifold advantages of birds.

Birds have another enormous advantage. They are more completely known than any other group of organisms. Whenever it is important to make generalizations and to arrive at statistically substantiated results, one is much safer with birds than with almost any other kind of organism. This is particularly true in speciation research and in faunistic-zoogeographic studies. Also for no other group of organisms has anywhere near as great a percentage of species been closely observed and their life histories worked out in detail.

SYSTEMATICS

Developments in systematics at the species level and population systematics in the last 100 years were largely the work of ornithologists. They made major contributions to the theory and practice of recognizing polytypic species, to the critical evaluation of the meaning of subspecies, and to the application of the results of systematics to evolutionary theory. Ornithologists such as Hartert, Stresemann, Rensch, Alden Miller, and myself were among the leaders of the so-called new systematics. Ornithologists had the great advantage that nearly all species of birds were known, that their distribution was well mapped, and that even most of the subspecies had been described and geographically delimited. The results were such excellent studies as Lack's *Darwin's Finches* (1947).

EVOLUTIONARY BIOLOGY

Darwin's studies of the birds of the Galapagos Islands made a decisive contribution to his conversion to evolutionism. Ever since, ornithologists have been in the forefront of research in evolutionary biology. No one has fought more vigorously for the establishment of population thinking and the rejection of typological thinking than the ornithologists. As far back as the first half of the 19th century such ornithologists as Schlegel and Baird stressed the collecting of population samples or series to permit the study of individual and geographic variation.

Ornithologists, together with some entomologists like Edward Poulton and Karl Jordan, were responsible for the introduction of the biological species concept. They insisted that the reproductive gap between coexisting populations was the only truly objective criterion of species difference and that it was unnatural to recognize and delimit species on the basis of arbitrary morphological characters of specimens in collections. To be sure, one still uses morphological and other phenotypic criteria, but only as inference concerning the probability of reproduction isolation.

SPECIATION

By the time Darwin published the *Origin of Species* in 1859 he had adopted the belief that most speciation is sympatric. Leading biologists such as August Weismann adopted Darwin's conclusion. The ornithologists, however, from Seebohm to Hartert, Stresemann, and Mayr, insisted on the prevalence of allopatric speciation, and, although the last word has not yet been said, there is now no longer any question that the reorganization of the genotype necessary for the achievement of species status occurs almost invariably in a population that is geographically isolated. Furthermore, it is due to ornithological research that it has been made clear that there are two kinds of geographical isolation: the first is a secondary division of a previously continuous species range by a newly arisen geographical barrier, a phenomenon that happened frequently during the Pleistocene both in the temperate zone and in the tropics, and the second is the establishment of a founder population beyond the contiguous species range through primary isolation where it evolves into a separate species. On continents most often the first-mentioned secondary form of isolation leads to the origin of new species, as has been shown by Keast for Australia, by Haffer for South America, and by Moreau and Hall for Africa. In island regions speciation through the establishment of founder populations is the prevailing mode.

When Darwin in 1859 published his theory of common descent, his opponents ridiculed him, saying that if he were right, one should be able to find intermediates between the major groups of animals, but there were none. Again birds came to Darwin's rescue. Within two years, in 1861, *Archaeopteryx* was found, the perfect intermediate between reptiles and birds. It is ironical that only a few years ago two paleontologists denied the intermediacy of *Archaeopteryx*, but one of them claimed that it was nothing but a reptile, the other that it was a perfect bird. What better evidence could one find for the intermediacy of this fossil?

The sexual dimorphism of pheasants, birds of paradise, grouse, and other birds was one of the sources for Darwin's theory of sexual selection. What Darwin had claimed was that selection might favor an individual, not merely because it was superior in the general struggle for existence, as by superior utilization of food or a greater ability to cope with adverse climatic conditions, but that an individual could also leave more offspring simply because it had greater reproductive success, like a particularly colorful bird of paradise. At first, indeed for about 100 years, Darwin did not succeed in convincing many biologists of the existence of such sexual selection. The mathematical geneticists in particular had not much use for it. In recent years the importance of such "selfish" selection for reproductive success has finally been generally recognized, and it has become obvious that birds are particularly suitable for the study of mating systems, of parental investment, sibling rivalry, female choice, inclusive fitness, and other aspects of reproductive biology that are now in the center of the attention of students of breeding biology.

The whole problem of group selection was raised seriously for the first time by an ornithologist, Wynne Edwards, and another ornithologist, David Lack, was the most active opponent of this theory. Wynne Edwards's theory, although now largely refuted, had a most stimulating impact on evolutionary theory. It focused attention on the importance of the question as to what is the target of natural selection, the gene, the individual, the kinship, or the population as a whole? And evidence from the study of birds has been crucial in much of the argumentation.

EVOLUTIONARY MORPHOLOGY

A comparative anatomist who is used to the great diversity of mammals (bats, monkeys, whales) or of reptiles (lizards, snakes, turtles, pterodactyls) might have little interest in a group that seems to him morphologically so uniform as birds. The capacity for flight imposes strong structural constraints, resulting in rather small body size, light bones, and a loss of heavy, hard teeth. These characteristics produce a fossil record that is much poorer than that of mammals or reptiles. Comparative anatomists in the classical tradition have for this reason always neglected birds. In A. S. Romer's textbook on fossil vertebrates only 16 pages are devoted to birds compared to 94 pages to reptiles and 216 pages to mammals.

The traditional method of comparative anatomy, which consists of reconstructing the common ancestor, has not been very rewarding as far as birds are concerned, in spite of much excellent descriptive work and the most careful determination of homologies by some morphologists. However, certain authors have found a far more exciting way of studying avian morphology. The more than 9000 species of living birds have entered a large number of different adaptive zones, and a study of the morphological transformations needed to become adapted to a novel niche is a fascinating occupation. How drastically does a bird have to be reconstructed in order to become a diver or a wading bird or a bird of prey? What makes this type of study particularly intriguing is that in most cases several unrelated groups of birds have made the same shift and have then secondarily become rather similar to each other, for example, hawks and owls, grebes and loons, auks and penguins, hummingbirds and sunbirds, swifts and swallows, or tyrant flycatchers and Old World flycatchers. Indeed, it has become very evident in the last 50 years that many previously accepted bird families like nuthatches *(Sitta, Daphoenositta, Hypositta)*, creepers *(Certhia, Climacteris, Rhabdornis)*, titmice *(Parus, Aegithalos, Remiz)*, Old World flycatchers *(Muscicapa, Monarcha, Petroica)*, thrushes, and several other avian families or subfamilies are converging assemblages of unrelated birds. Although this had been suspected for a long time, this conclusion has now been placed on a firm basis by the DNA hybridization analysis made by Charles Sibley and J. E. Ahlquist (1983).

These specific findings are of interest only to the ornithologist. However, such studies have led to an analysis of the causes of differences among taxa. The modern evolutionary morphologist asks why questions. Why did the descendants of a common ancestor become different? What induced them to enter different adaptive zones? What were the selection forces involved? Did changes in behavior serve as pacemaker in the evolutionary shift? An ornithologist, Walter Bock, has been a leader in posing such questions and in developing this new field.

BIOGEOGRAPHY

There is probably no other branch of biology as rich in controversies as biogeography. Why should this be the case? It is now becoming increasingly evident that it is largely because authors have based their conclusions on one particular group of organisms but that different organisms differ greatly from each other in their dispersal propensities and colonizing abilities. Darwin, more than 100 years ago, made the important discovery that mammals, except for bats, virtually never occur on true oceanic islands, and this is also true for primary freshwater fish, while such islands always have a rich bird fauna. Or, to give another example, mammals and birds of New Guinea resemble much more those of Australia than those of Southeast Asia. For plants, by contrast, the opposite is true. It is obvious then that biogeography deals with a highly heterogeneous subject matter, which makes it unwise to base sweeping conclusions on the study of a single group of organisms. The heterogeneity however goes even further. As Diamond (1975) has shown, 40% of the 321 lowland species of birds of New Guinea have been unable to colonize any island around New Guinea more than five miles distant from the mainland, even though other species of birds are known to have made colonization flights of more than 1000 miles, to New Zealand and to the Polynesian islands. Owing to this heterogeneity in the dispersal capacities of birds, ornithologists have been the first to emphasize the importance of ecological and behavioral factors in biogeography. It has helped them to avoid extreme biogeographic theories such as those of the land bridge builders of earlier times or the exclusive reliance on the movement of continental plates among some modern biogeographers. As I stated recently, ornithologists have come to the conclusion that "organisms are not like volcanic ashes or dust particles from the Sahara that are passively and indiscriminately dispersed. On the contrary, each species up to a point obeys its own specific rules of dispersal and colonization" (Mayr 1983, p. 14).

The fauna in any part of the world is the product of a long history. It is not sufficient merely to record what species occur where, as has been customary in regional zoogeography from Alfred Russel Wallace on. Darwin was not at all satisfied with such an essentially descriptive approach. Instead he asked how and why questions. And ornithologists have been among the leaders in this causal approach. Jared Diamond's analysis of the factors responsible for the distribution of birds on the islands around New Guinea is a superb example of such a causal analysis, superior to anything that exists for any other group of organisms. It was made possible by the extraordinary completeness of the knowledge of the bird faunas of these islands.

ECOLOGY

There has been an almost revolutionary advance in ecology in the last 50 years. What was at one time a basically descriptive science has evolved into a causal science dominated by how and why questions. Ecological problems are now dealt with in terms of selection forces, that is, under an evolutionary viewpoint. In almost all modern ecological researches a bridge is built to behavioral biology, as indicated by such subjects as habitat selection, foraging strategies, or resource partitioning. Furthermore, as in zoogeography, species and individuals can no longer be dealt with exclusively as so many items in a statistic or as inert particles, but their individuality must be duly considered. A populational rather than a typological approach must be applied consistently. In all these conceptual shifts, ornithologists have played an important and sometimes a leading role. Birds are excellent material for ecological studies, as recent work on the Galapagos and Hawaiian finches, on desert birds, and on montane species have shown. Accurate census data can be obtained for birds, which are easily observed while foraging and in intraspecific as well as interspecific encounters.

Except for Hutchinson's first seminal paper and some theoretical work by Preston and others, the modern study of species diversity is almost entirely based on ornithological research. It began with MacArthur's thesis on the distribution of warblers and is still being pursued actively. The role of competition and resource partitioning is still controversial, and I foresee an active continuation of these studies. I am not in this field myself, but it seems to me that one of the causes for this discord is that too much determinism was introduced into the models. There is a strong stochastic element in the interactions among organisms and in the effect of the physical environment on organisms. The range of variation is inevitably large, even where there is a more-or-less predictable mean value. One can confidently predict that ornithologists will continue to play a major role in the future development of this field.

POPULATION BIOLOGY

Birds offer unique advantages for the student of populations. Individuals can be marked by color bands so they can be observed without the need for recapturing. Population sizes are sufficiently small so that the total number of individuals of a local population can be studied simultaneously and the survivors identified in consecutive years. In many species there are sufficient differences between juveniles and adults and between males and females that the composition of the population according to sex and age can be determined by visual inspection. Finally, many species, particularly sea birds, nest in well-delimited and often widely separated breeding colonies.

Burkitt in 1924 was the pioneer in the study of an individually marked population, but it was Margaret Morse Nice who in her work on the song sparrow (1937), produced the classic of all time. More recently it has been discovered that there is great individuality in the songs of males of many species, and that records of these songs and their analysis in sonograms often permit the absolute identification of individuals.

As a result of the introduction of these techniques, it has been possible to provide precise analyses of local populations, including the determination of the longevity of individuals, the rate of population turnover, reproductive success, the size of the effective interbreeding local population, and other parameters. Such precise data are now available for scores of species and have in some cases been continued for dozens or scores of years. So far as I know, comparable data have not been obtained for any other kind of wild animals, although the study of lizard populations is rapidly catching up with ornithology.

BEHAVIOR

There is perhaps no other branch of biology in which ornithologists have so consistently displayed leadership as in the study of animal behavior. The founding of ethology is usually attributed to Konrad Lorenz and Niko Tinbergen, and as far as it is a well-organized branch of biology, this description is correct. Lorenz himself, however, designates Charles Otis Whitman and Oskar Heinroth as the real founders, thus pushing the beginnings of ethology about 30 years backward, both Heinroth and Whitman using birds as the observational basis of their theorizing. Yet when one studies the literature of the antecedent 150 years, one encounters a whole series of students of birds who laid a foundation for the subsequent scientific analyses. This begins with such names as Reimarus and Gilbert White in the 18th century, to the controversy in the 19th century between Alfred Brehm, who ascribed to birds the intellectual and emotional qualities of humans, and Bernard Altum, whose belief in instincts was remarkably similar to that of a modern ethologist, to naturalists like Edmund Selous, and many others. C. Lloyd Morgan's influential book *Habit and Instinct* (1896) largely used ornithological observations as the basis for his conclusions.

The important point I want to emphasize is that comparatively simple natural history observations can often become the basis for broad generalizations and the formation of new theories and concepts, which are then applicable to other organisms and even to man. Birds have become particularly important in recent years for shedding light on that problem of problems in the study of behavior, the relative share of inherited and acquired information. The vocalization of birds is superbly suitable for such studies. It began by raising birds in soundproof chambers, as was done by Franz Sauer and others, and by exposing them at various ages to conspecifics and to other sounds. Perhaps most interesting is the enormous difference among different species of birds concerning the degree to which inherited information determines adult vocalization. The number of new questions raised by the study of avian vocalization is legion. Martin Moynihan has attempted to determine the size of the repertory of vocalizations of a given species while W. John Smith is concentrating on avian semiotics, the relation between signals and messages.

Perhaps the most interesting modern development is the contribution birds are making to developments in neurophysiology. I refer to the names of Konishi and Nottebohm. I am not enough of an expert in this area to venture an interpretation of the exciting findings of these authors. The latest development seems to be that the asymmetry of the avian brain is apparently more easily accessible to experimentation than that of the human brain, and that the study of this asymmetry in birds may ultimately shed light on aspects of human speech. Again I want to emphasize the rich series of problems that birds offer us, and that it was ornithologists more than anyone else who have pioneered in the major scientific progress that has been made.

PHYSIOLOGY

Birds and ornithologists have made major contributions even to such a technical field as physiology. Birds with their high body temperatures, their long annual migrations, their adaptations to the hottest deserts and the coldest polar regions, are able to meet physiological challenges like almost no other organism. All these aspects have been studied intensively in recent years with the results splendidly recorded in the volumes of Farner, King, and Parkes (1971–1983). Invariably such researches start with simple natural history observations and are then followed up to an elucidation of a physiological causation.

MIGRATION

Every naturalist in the temperate zones, as far back as there is any recorded natural history, has been aware of the coming and going of birds with the seasons. Even today, for some bird watchers, the spring migration or the fall migration, are just about the only active times of the year. There is an excitement in seeing the first individual of a species one had not seen since last year. Or even more so, when it is an individual of a species that normally does not occur in one's district. Even a 50-year veteran of bird watching in New England is pleased if not thrilled by seeing a Cape May warbler, a cerulean warbler, or a prothonotary warbler making a fleeting appearance on some May morning.

Massive efforts were made in the last century to provide as accurate a description of the times and places where individuals of the various species of birds appeared in all parts of Europe and North America. But that was only the beginning. For the perceptive student every fact raised new questions. Do birds migrate on a broad front or on definite migratory highways? Where do they winter? It was soon found that, up to a point, the answer was somewhat different for each species. Further research raised new questions. How do birds find their winter quarters and, on their return migration, the breeding area?

Navigation became a major scientific problem. Not surprisingly, ornithologists soon led the field of animal orientation. Gustav Kramer (simultaneously with von Frisch for bees) developed the theory of the sun compass and the internal clock. Merkel provided the first proof for magnetic orientation, a field further developed by Wiltschko, Keeton, and J. Gould, but it is clear that we still have only a very inadequate explanation of orientation and a large number of investigators in eight or nine countries continue to make new discoveries, some of them quite unexpected.

The energetics of migration are another area of research, greatly stimulated by the questions ornithologists have asked. What resources permit a small hummingbird to cross the Gulf of Mexico? Can blackpoll warblers really fly from New England to the coast of South America in a single flight? Or, in the Old World, how do migratory birds conquer the successive barriers of the Alps, the Mediterranean, the Atlas Mountains, and the vast Sahara?

A study of the entire migratory route as well as the winter quarters has destroyed the concept that a migratory bird is a temperate zone species, considering that it actually stays in its breeding range only for three or four months of the year. Survival during migration and in the winter quarters may actually be more important for the maintenance of the species than the breeding range. It began to be realized that the limited range of the Kirtland warbler cannot be explained entirely in terms of the vegetation types of Michigan and adjacent states. The discovery of its winter quarters in the Bahamas and the realization that the islands, where it winters, are only a small remnant of the vast Grand Bahamas Bank of the Pleistocene, have opened up entirely new questions. The catastrophic decline of many birds in Europe during the 1950s and 1960s seemed quite inexplicable in terms of the environmental changes in their breeding quarters. The fact that some of the decline was most precipitous in species like shrikes, which feed on grasshoppers on migration and in their winter quarters, suggested that the massive application in Africa of pesticides for grasshopper control might have been a major factor in the decline of certain species. Here, again, we have to realize that north and south, east and west, are "one world."

The timing of migration led to another set of questions. Why does one species leave for its winter quarters in August, another not until October, whereas a third does not migrate at all? They all live in exactly the same environment, let us say an orchard in northern New York State. Questions like these, together with questions concerning the time of arrival in the breeding area, the beginning of song in resident species, and other aspects of the annual cycle of birds, led to an analysis of the underlying physiology. William Rowan was the pioneer in this area, and the study of the interaction between environmental factors, like day length, and various endocrine glands—the pituitary, the thyroid, the pineal, and the gonads—has been an extraordinarily productive area of research in which ornithologists have consistently been among the leaders. (Farner, King, and Parkes 1971–1983).

Studies of the internal clock (circadian rhythms) were eventually expanded to the highly controversial problem of the existence of annual rhythms. The first definite proof of their existence was provided by J. Marshall and Dom Serventy (1959) on the basis of a year-long study of caged shearwaters. Independently it was established by Pengelley and Fisher for ground squirrels (1963) and then again by Gwinner (1968) for European warblers.

I refer to these developments merely to illustrate again that such a familiar phenomenon as bird migration, watched with undiminished enthusiasm by birders all over the world, has been the starting point for some of the most interesting developments in general biology, with ornithologists having made some of the most important contributions.

CONSERVATION

Ornithologists, or at least birds, have also made numerous contributions to applied biology. I shall single out only one single area, conservation. In the early phase of conservation, all measures were prohibitions, such as the prohibition of collecting and selling the plumes of egrets and birds of paradise or the prohibition of shooting water fowl outside an ever-shorter open season or of shooting or collecting most other birds any time or anywhere. Soon it became apparent that such negative measures were insufficient; they were unable to halt the decline of certain rare and vanishing species. In some cases, as in that of the Hawaiian goose *Nene*, the solution was supplementing the wild stock by captive-bred releases. In most other cases it became evident that a study of the native habitat was a prerequisite for the adoption of sound conservation measures. Every species is a component of an ecosytem, and its health depends on the health of the other components of this system. Ornithologists have pioneered in pointing out that certain species require a minimal amount of area in order to persist in a sanctuary. Its size seems to vary from species to species, and the whole subject is still somewhat controversial. Nevertheless, conservation research is again an area in which ornithologists have been pioneering.

INTELLECTUAL LEADERSHIP

I hope I have by now established the fact that ornithologists have played an important role as pioneers in new researches throughout the history of biology. This has led not only to important biological discoveries but in some respects to a rethinking of basic biological or even philosophical concepts. I have already mentioned the important role ornithologists have played in introducing population thinking. To mention another conceptual shift: there was a period not so long ago, as I showed in my recent book (Mayr 1982), where the experiment was proclaimed as the only method of science. Ornithologists were the ones who refuted this claim by showing that observation, scientifically conducted and carefully controlled, is a method of equal importance. Ethology, evolutionary biology, and population biology have supplied abundant proof for the validity of this assertion. To mention a third conceptual shift, it was through ornithological research conducted by John Baker, David Lack, and myself that it was clearly shown that there are two entirely different causations for every biological phenomenon or process. These being, to use John Baker's terminology, proximate or physiological, and ultimate or evolutionary, causations. To make this distinction has greatly clarified the interpretation of many phenomena concerning which there had previously been much controversy.

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