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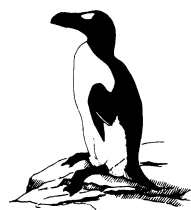
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PERSPECTIVES IN ORNITHOLOGY

ERNST MAYR AT 100: A LIFE INSIDE AND OUTSIDE OF ORNITHOLOGY

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LONG AGO—on 5 July 1904, just six months after the first powered flight by humans at Kittyhawk, North Carolina—a person was born in a small town in Bavaria, Germany, who was to make his name famous through study on another group of flying creatures. To put that date in proper perspective for ornithologists, it was the year before the 4th International Ornithological Congress in London and five years before the publication of the last volume of R. Bowler Sharpe's *A Hand-list of the Genera and Species of Birds*. And the American Ornithologists' Union (AOU) had just attained its majority, having reached its 21st year. I refer, of course, to Ernst Walter Mayr, whose 100th birthday is on 5 July 2004.

Many ornithologists have had long lives and others have reached the century mark, including Wilhelm Meise, another doctoral student of Professor Erwin Stresemann and a student colleague of Ernst Mayr in Berlin during the middle of the 1920s. Although Mayr turned to other areas of inquiry later in his career, he trained as an ornithologist, made his name as an ornithologist, and still is most interested in avian biology and in those who study birds. Other areas of study such as evolution, the history of biology, and the philosophy of biology

may also claim Ernst Mayr as one of their own, but ornithology retains his primary alliance.

Some years ago, while discussing several earlier workers, Mayr made the comment to me that Professor Erwin Stresemann never ventured outside of ornithology, a remark that I found very interesting. Upon further reflection, it was clear that Stresemann was similar to many other well-known students of avian biology. On the other hand, Mayr did go well beyond the boundaries of avian biology and was just as successful in those outside areas as he was in ornithology. It is this wandering outside of the area for which he was trained and in which he made his initial reputation that makes an examination of Mayr's career so fascinating—hence the title of this article.

A second aspect of Ernst Mayr's career worth examination is the series of accidental events that occurred to him, and the importance those accidental events have had to the success of his career. With due respect to Professor Mayr and to my students (to whom I insist that the following is a major error, because changes in one organism cannot be considered to be evolutionary), I would like to consider the development and success of his career in terms of the two basic sets of causes of organic evolution. These can be summarized as "accidental and design," to borrow the title of one of Mayr's papers (Mayr 1962); accidental when the origin

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of genetic-based phenotypic variation and other events are chance based (with respect to selective demands), and in which the action of selective demands can be considered as a “design” aspect of evolutionary change. Chance events, both good and bad, are common to all careers—for example, whether a desirable position becomes available just when one is able to fill it. Then one has to work to fulfill the promise of the chance event. Here, I describe the accidental events that happened to Ernst Mayr and, what is more important, how he responded to the “design aspects” that shaped his career. What is significant is the combination of accidental events and responses to them. The design responses are useless unless the proper accidental events precede them, as are the chance events if one cannot respond to them properly.

First, a personal note: because I grew up in New York City and because the Agriculture College at Cornell University still had a farm-practice requirement for male undergraduates at that time (of which two-thirds could be done away from farms for students in non-agricultural areas, such as the Department of Conservation), I spent several summers as a student volunteer working “on the range” in the collection rooms of the Department of Ornithology at the American Museum of Natural History (AMNH) during the first half of the 1950s. I had the chance to meet Ernst Mayr at the AMNH in August, 1953, just before he left for the Museum of Comparative Zoology (MCZ) at Harvard University and his new career as an Alexander Agassiz Professor of Zoology. At the end of the next summer, I saw him again in the AMNH and discussed graduate schools with him. Unexpectedly, Mayr suggested Harvard and the possibility of working with him—something that I had never thought of. Following his advice, I applied to Harvard, started my graduate studies in September 1955. I obtained my Ph.D. degree in 1959. Since then, I have maintained close contact with him. Therefore, much of the material in this history comes from personal contact with Ernst Mayr, and from an earlier article I wrote for a symposium honoring Mayr’s 90th birthday (Bock 1994), on his life as a naturalist and his contributions as a systematist and evolutionist (see also the entire symposium, Greene and Ruse 1994).

A major biography of Ernst Mayr is being prepared by Jürgen Haffer. It will appear in a

couple of years and will provide much additional detail.

EARLY BEGINNING

Ernst Mayr was the second son born to a well-educated, middle-class family in which *Bildung* (education and a general knowledge of culture) was important; books were a significant part of their life. His father was a successful judge in the Bavarian State system, with broad interests outside of jurisprudence. Most significantly, both of Mayr’s parents had general interest in natural history and took their three boys on frequent walks in the countryside. Emphasis was placed on the identification of local fauna and flora. By the time he was a teenager, Ernst had become a dedicated and proficient bird watcher, knowing all the local birds by call as well as sight. After the father’s death at an early age, Frau Mayr moved with the three boys to Dresden, where Ernst attended the Gymnasium from 1917 to 1923 and completed the examinations for his Abitur in March 1923. He was given a new pair of binoculars by his mother as a present for passing these examinations, and spent the next days bird-watching. On 23 March 1923, he observed a pair of Red-crested Pochards (*Netta rufina*) in Moritzburg, Sachsen; that species had not been reported in Germany since 1846. This was the first big, and perhaps the most important, accident in his life. Ernst was unable to show the pair of ducks to any of the older members of the local nature club, because the birds had disappeared by 25 March when some adult members were able to accompany him to Moritzburg. But one of the members knew Erwin Stresemann (who had started as an Assistant in the Zoological Museum in Berlin on 15 April 1921, having received his Ph.D. the previous year) and provided the young Ernst with a letter of introduction to Stresemann.

Following the tradition in the Mayr family in which the boys went into law or medicine, and with his older brother, Otto, having decided to become an engineer, Mayr chose a career in medicine. His younger brother, Hans, followed their father’s footsteps, went into law and became a public prosecutor (*Staatsanwalt*). Ernst decided to study at the University of Greifswald, located close to the southern coast of the Baltic Sea in northeastern Germany, almost directly north of Berlin. He had made that choice not



Ernst Mayr on his 67th birthday at his farm in Wilton, New Hampshire.
(Photo taken 5 July 1971 by M. Ross Lein.)

because the university had any outstanding reputation for the teaching of medicine, but because Greifswald was located in one of the more interesting regions of Germany ornithologically. And by good fortune, Berlin lay almost directly in the path of the train between Dresden and Greifswald. Armed with his letter of introduction, Mayr broke his journey in Berlin and visited Erwin Stresemann to report his sighting of the pair of Red-crested Pochards. Stresemann read Mayr's field notes carefully and quizzed him on the identity of other species of ducks, using specimens in the collection. He was satisfied with the sighting and, impressed with the enthusiasm of this young student, invited him to work as a volunteer at the Berlin Museum during his university holidays. Mayr accepted immediately. He remarked later that "It was as if someone had given me the key to heaven" (E. Mayr unpubl. manuscript). Stresemann also invited Mayr to publish his report on the Red-crested Pochard (Mayr 1923a) and must have written the manuscript himself, because the published date of 1922 is incorrect—the pair of ducks were observed in March of 1923. Mayr's second paper followed immediately, reporting observations he made soon after arriving in Greifswald on the Red-breasted Flycatcher (*Ficedula parva*) as a common breeding species in the beech forests near Eldena in the Greifswald region.

Mayr worked at the Berlin Museum a number of times during university holidays and must have impressed Stresemann favorably, because Stresemann urged Mayr to change his career goals from medicine to ornithology (see Mayr 1980 for his description of his university training and early career). The bait that Stresemann used was the promise that he would arrange an ornithological expedition to some tropical area for Mayr after he completed his degree. That was too much a temptation, and Mayr succumbed to this bribe. He completed his basic preclinical courses, passed the examination for candidate of medicine with all "1s" and became a "Candidate of Medicine," which meant that he could return to medical studies if his plans to become a zoologist did not materialize. Having changed his studies from medicine at Greifswald to zoology at Berlin, Mayr completing his Ph.D. in 16 months (in June 1926) at the age of 21 years, immediately before his 22nd birthday. The rest is history. Had it not been

for the chance observation of the pair of Red-crested Pochards in the spring of 1923, Mayr might well have had a career in medicine in Germany, unknown to all of us. But I should mention that he used his abilities and developed his meeting with Stresemann into an invitation to study in Berlin, and thereby had the possibility to change his career to ornithology.

THE NEXT STEPS

Mayr rushed to complete his degree in June 1926 (at the young age of 21) because there was a vacant assistantship at the museum that he could obtain only if he had been promoted and received his Ph.D. Positions were scarce in Germany at that time, a period of rampant inflation. Mayr started his work at the museum, including a cataloguing of journals with his fellow assistant, Wilhelm Meise (Mayr and Meise 1929), and he published his first major taxonomic paper (Mayr 1927) on the systematics of the "snow finches." But he was anxious to travel to a tropical area on an ornithological expedition as promised by Stresemann, who was working hard to find or organize an appropriate one.

The second major chance in Mayr's life stemmed from the close relationships between Stresemann (Berlin), Walter (Second Baron) Rothschild (Tring), Dr. Ernst Hartert (Tring), and Dr. Leonard C. Sanford (New Haven and active patron of the Department of Ornithology, AMNH). Those workers formed a major international axis in ornithological systematics in the early decades of the 20th century. As is well known, Walter Rothschild had been actively putting together the world's largest private collection of birds in Tring, the Rothschild family seat north of London. Leonard Sanford is less known, but as a trustee of the AMNH he can be considered the patron of its Department of Ornithology because he directed funds into the department to collect actively, to construct the present museum wing that houses the department, to purchase the Rothschild collection, and to bring Ernst Mayr to the museum in 1931. In many ways, Sanford is the knight in shining armor of this tale. A major factor in the background of Sanford's efforts was that he was in friendly competition with Professor Thomas Barbour, curator and later director of the Museum of Comparative Zoology, Harvard University, to develop the largest and most

complete ornithological collection in the United States. Both wished to have a specimen of every genus, if not every species, of bird in the world.

Stresemann was unsuccessful in his efforts to place Mayr on an expedition to Peru or the Cameroons. In 1927, he introduced Mayr to Lord Rothschild at the International Congress of Zoology in Budapest, and started arrangements for a joint expedition to Dutch New Guinea and to the former German Mandated New Guinea for the Berlin Museum, the Tring Museum, and AMNH (Hartert 1930; Mayr 1930, 1931a, 1932). Mayr left Berlin in February 1928 (23 years old) and his return was delayed to the end of April 1930 because, just before he was to leave New Guinea in 1929, he received a telegram asking him to join the Whitney South Sea Expedition, AMNH, to the Solomon Islands for approximately a year (Mayr 1943). This tripartite expedition to Dutch New Guinea, Papua New Guinea, and the Solomons, which lasted two and a half years, was the first and the last one in which Mayr participated. It was exceedingly successful. Perhaps the most important result was a negative one—Mayr failed to find five or six “species” of birds of paradise which were known only from trade skins. That failure provided Stresemann with the insight that there was something wrong with those species; he re-examined the specimens carefully and concluded that each was a hybrid between two well-known species of birds of paradise (Mayr 1981). Unfortunately, once Mayr reached AMNH, his work on the Whitney-Rothschild collection was too important for him to take part in other expeditions. He was chained to his desk, so to speak, and told that the department had storage case after storage case full of unstudied birds and that there was enough material for him to study for his entire lifetime; no more material was needed. He was frustrated at the time, but the decision of the museum proved to be to his advantage and certainly to ours. Mayr was a naturalist at heart and would have enjoyed further expeditions greatly, learning more about the life histories of the birds that he was studying. But that was not to be, and if he had participated in additional expeditions, he would not have added as enormously to our knowledge about the systematics and biogeography of South Pacific birds, which was essential for his later evolutionary analyses. It was only in the winter of 1959–1960, immediately before assuming his

duties as director of the MCZ, that Mayr was able to travel to an exotic country (one that he had not visited earlier), namely Australia.

But I have leaped ahead of my story. The third major chance-based event was actually a series of interconnected events. The first arose from the extreme slowness with which the vast collections made by the South Sea Expedition were being studied, because all of the members of the Bird Department were involved with other areas—Chapman with South American birds, Murphy with oceanic birds, deW. Miller with anatomical studies, and Chapin with African birds. The Whitneys, who provided the funds for those expeditions, were becoming impatient. Sanford, realizing this problem (and the danger that the Whitney funds could dry up if the collections from the South Sea Expedition remained unanalyzed), convinced the family that they should make funds available for a temporary or visiting curator (the vast sum of \$2,500 per year was provided). With that contribution in hand, Sanford went to Frank Chapman, demanding that he be allowed to locate someone to fill this position. Sanford had contacted his close colleagues, Rothschild, Hartert, and Stresemann, and already had a candidate in mind—Ernst Mayr, who did not have a permanent position in Germany. As usual, Chapman did not object to Sanford's plans. In reality, in those days the Bird Department of AMNH was divided into two informal units—New World birds and Old World birds—and Chapman was interested only in New World birds. Sanford could do what he wanted with respect to Old World birds as long as he raised the funds. And that he could do very well indeed. Not too long after he returned to Germany from the South Pacific, Mayr received an offer in October 1930 from the AMNH for a one-year position, which he accepted immediately. Mayr completed the essential work in Berlin and arrived at the AMNH as a Visiting Research Associate on 19 January 1931 (26 years old), only eight months after he returned to Berlin from his tripartite expedition, and just under eight years since the fateful sighting of the Red-crested Pochards in Moritzburg on 23 March 1923. A lot had happened during those years.

Typically for Mayr, before leaving Germany he had obtained the directions on how to reach the International House on Riverside Drive just opposite Grant's Tomb in Manhattan by subway

from the docks in Brooklyn, and further how to reach the AMNH the next day. He had reserved a room in the International House, which was established for foreign students and visitors. The next day, he reported to Chapman and asked for his assignment—on what project did Chapman as head of the Bird Department want him to start? As a former student and assistant in the Berlin Museum, Mayr was used to German procedures in which the boss tells the underlings exactly what to do. Chapman was used to different ways, and also was not deeply concerned with Old World birds. He indicated the collections with a wave of his hand and said in effect: “You came highly recommended as a specialist in South Pacific birds. Now get to work on whatever you consider most important and bring the completed manuscripts to me.” Mayr was surprised, but took Chapman at his word and went to work with terrific diligence. His first paper on the AMNH collection was published on 31 March 1931 (Mayr 1931b). Before the end of 1931, he completed 12 papers describing 12 new species and 68 new subspecies (peer reviews were not known in those days). But that effort made only a small dent in the available material from the South Sea Expedition. In total, Mayr has described 26 new species (Mayr 1991b, 2004; more than any other living ornithologist; he named a 27th species, but that species had been described a few days earlier by other workers) and 445 new subspecies of birds (J. Haffer pers. comm.), most during his tenure at the AMNH.

The next part of this set of accidental events involved Lord Rothschild, who was facing serious financial problems. That was in large part because he was being blackmailed by the infamous (but still unknown) “titled lady” (Rothschild 1983). Although anonymous, she deserves special mention in the annals of systematics and evolutionary biology because she was an essential link leading to Mayr’s career in the United States and all of his contributions to ornithology, evolutionary theory, and the history and philosophy of biology. If Sanford was the shining knight in this tale, she was the dark lady, but just as important to the outcome of Mayr’s career. Because she drained Rothschild’s available funds, he was unable to continue his ornithological collecting and systematic studies.

When Ernst Hartert retired in 1930, Rothschild decided to offer the position of curator of birds at the Tring Museum to Mayr,

but had not so informed him. Had he been offered that position in 1930–1931, Mayr would have accepted it because it was the best one he could have obtained at that time. In that case, he might have spent his life in the pleasant small provincial town of Tring without an academic atmosphere, and at best he would have become a well-known systematic ornithologist.

Again, Sanford was on the alert; and as soon as he learned that the Rothschild bird collection might be available, he went to Gertrude Whitney, the widow of Harry Payne Whitney, and convinced her to provide funds to purchase the collection. He left immediately for England with a signed blank check and was successful in the negotiations; on 13 February 1932, ownership of the Rothschild collection was transferred to AMNH. The 280,000 specimens of birds filled 185 large wooden packing cases ($76 \times 76 \times 152$ cm), all of which arrived safely at AMNH in the summer of 1932. The Rothschild collection had been dumped into Mayr’s lap for integration into the main collection. Mayr resigned his position as an assistant in the Berlin Museum and was appointed Associate Curator of Birds of the AMNH in 1932; in 1935, he became the Whitney-Rothschild Curator.

Obtaining the Rothschild collection had several consequences. First, Sanford won his informal contest with Barbour and the MCZ because there was no way that the bird collection of the MCZ could surpass that of the AMNH without purchasing a large national collection. More importantly, Mayr obtained a permanent position at AMNH as the first and only Curator of the Whitney-Rothschild Collection. In this round-about way, he became the curator of the Rothschild collection, but not at Tring as originally hoped for by Rothschild. Not only could Mayr devote himself for the next 20 years to studying the systematics and biogeography of the superb material in the South Sea Expedition and the Rothschild collections, but he could do that in the United States and not in Germany. That was important not because of the political events in Germany and the subsequent war in Europe, but because Mayr was in the United States and hence out of direct interaction with Professor Stresemann. Mayr was able to remain good friends with Stresemann because they were on different continents and therefore were not in direct competition. Had he remained in Germany, no matter how good a position he

had, Mayr would have always remained under the domination of Stresemann, simply because of the nature of relationships between professor and student in German academics at that time. Moreover, it would have been impossible for Mayr to secure an outstanding position in Germany, again because of the nature of German academics. Although Stresemann had the title of Professor and is considered as the professor under which Mayr and many others studied, he was not an *Ordinarius* or *ordentliche Professor* (i.e. full university professor, or the C4 rank of the current system). In Berlin, it was a well-established tradition that museum people would not “*habilitieren*” but were given the right to teach and to direct students as *Doktoranden*; they were usually given the position of an *Honorarprofessor*. An *Honorarprofessor* is an *Universitätsprofessor*—but, of course, not of the status and rank usually connected with that word (which implies no formal status or ranking but is merely a word for a function or job). Mayr actually received his degree from Professor Carl Zimmer, who was director of the museum and the Professor of Zoology at the University of Berlin. It is the *ordentliche Professor* who counted in Germany and who had the influence to recommend persons for university positions. One only has to examine the careers of all of Stresemann’s students to appreciate the difficulties they had in establishing a career in the German university system. Simply stated, Mayr would have never been as successful in Germany as he was in the United States.

Dr. Sanford not only brought Mayr to AMNH, but became something of a mentor to him, almost like a father. For example, talking with Mayr in his office at AMNH one day in 1944, Sanford learned that Mayr was still not a full curator. Sanford got up and left without a word. Within an hour, Mayr received a telephone call from the museum director informing him that he had been promoted to the rank of full curator. That close relationship also meant that Mayr could not have left AMNH during Sanford’s lifetime, and he certainly could not have accepted a position at the Museum of Comparative Zoology at Harvard, as he did after Sanford’s death at the beginning of the 1950s.

THE FINAL STEPS

The last important chance event I will mention—the one that led directly to his career

in evolutionary biology—took place at the American Association for the Advancement of Science (AAAS) meeting in December 1939 (E. Mayr unpubl. manuscript). Mayr was asked to speak on his work on geographical variation and speciation in birds in a symposium on speciation arranged by the American Society of Naturalists and the Genetics Society of America (his first theoretical paper; Mayr 1940). He had the good fortune of speaking immediately after Sewall Wright, who was a terrible lecturer, and whose talk was a disaster, succeeding mainly in driving away much of the audience. Mayr observed this carefully, noting that the only microphone was at the podium, far away from the screen and the blackboard at the back of the stage. Wright had ended up at the blackboard writing equations and speaking to the blackboard rather than the audience; he droned on for over an hour and it is doubtful that anyone heard a thing. Mayr decided that the important points in his beautifully hand-colored slides would be perfectly clear to the audience, grabbed the sides of the podium firmly, and stayed at the microphone. His strategy worked completely, and his lecture was a great success—especially so because Professor L. C. Dunn of the Department of Zoology, Columbia University, approached Mayr immediately after the lecture, congratulated him, and asked if he would consider giving some of the Jesup Lectures in March 1941, together with the botanist Edgar Anderson. He did so, and was encouraged by Professor Dunn to expand his lectures into a book. Columbia University Press invited Mayr to submit a book manuscript based on his lectures, and one can spot the hand of Professor Dunn in that invitation, too—and hence, the publication of *Systematics and the Origin of Species* (Mayr 1942). With the publication of that book, Mayr’s position as a central figure in the evolutionary synthesis was assured. And I should point out that the book appeared just less than 20 years after the initial chance event that started Ernst Mayr on his career path. There were a number of important accidents, but of greater significance was the exceedingly hard and dedicated work done by Mayr in those years to reach the position he achieved in 1942.

Mayr continued at the AMNH for another decade during which time most of his work continued in avian systematics. Over the years,

in addition to his work on the bird collection, he was largely responsible for integrating the huge Rothschild Collection into that of the AMNH, which included estimating how much case space was needed for each family, arranging families in the various collection rooms, supervising the cataloging of the collection, and attending to all of the other details of curating a collection. That was a vast undertaking, one that can only be appreciated by the few persons who have been responsible for the total curation of a huge collection from the beginning. In addition, he was responsible for planning and supervising the new exhibition hall that covered the biology of birds and opened in the late 1940s (Mayr 1948). It was one of the first—if not the first—exhibition halls in a major museum presenting the manifold aspects in the life of a group of organisms.

At the beginning of the 1950s, Mayr was becoming more and more frustrated with his lack of contact with students. He accepted two single-term visiting professor positions—one at the University of Minnesota and the later one at the University of Washington. He was an adjunct professor in the Department of Zoology, Columbia University, but he could not direct graduate students, and daily contact was limited because of the 40 blocks separating the AMNH and Columbia; that distance in New York City is as if the two institutions were in different cities, if not different states. And he was getting tired of the hour-long commute from his home in Tenafly, New Jersey, and the museum. Moreover, his interests were drifting from systematic and biogeographic studies of birds to more purely evolutionary work. The invitation in 1953 to join the Museum of Comparative Zoology as an Alexander Agassiz Professor of Zoology came at just the right time. Going to the MCZ meant that he would have to leave behind the outstanding collection in the AMNH on which so much of his empirical work over the past two decades had been based. Although he had not exhausted the research possibilities of that collection, it was time for him to move on to other work largely outside ornithology.

But Mayr did not leave his original field completely. After arriving at Harvard, he was asked by James Greenway to join him as co-editor of the remaining volumes of the *Check-list of the Birds of the World*—basically the passerine birds. A few years earlier, after the death of James Lee

Peters, Greenway had been given the assignment by Professor Alfred S. Romer, then director of the MCZ, to assume responsibility for completing the *Check-list*. But Greenway did not feel confident to do the task alone and wanted Mayr to assist. Mayr agreed and assumed the lead role, organizing the arrangement of families into volumes, contacting many ornithologists around the world to write the text for those families, and helping to edit volumes. The task lasted for the following 30+ years, the result being a complete checklist of avian taxa down to subspecies (Bock 1990). But after his move to the MCZ, Mayr did little empirical research and published few papers on birds. Yet his interest in ornithology remained strong, and to this day he is still more enthusiastic in talking about ornithology than any of the other subjects that have occupied his time since leaving the AMNH in 1953—a half-century ago.

MAYR AS NATURALIST

Central to understanding Mayr's career is the appreciation that he has been, and remains to this day, a naturalist. As a boy, he went out with his parents on walks in southern Germany, observing the local plants and animals. He became an avid birdwatcher, which led to his observing the pair of Red-crested Pochards and his introduction to Professor Stresemann. His choice of the University of Greifswald for medical studies was because of its location in an ornithologically interesting area of Germany. And finally, his being a naturalist resulted in abandoning a certain career in medicine for a most uncertain one in ornithology amid the disastrous inflation of 1920s Germany.

When he arrived at the AMNH, Mayr immediately became active in the Linnaean Society, a bird-watching club that met at the AMNH. He became as well an honorary member of the Bronx County Bird Club, although a requirement for membership was that one was born in the Bronx; thus he learned North American birds. After moving, in the late 1930s, to the small town of Tenafly in Bergen County, New Jersey, he spent much of his spare time studying birds in that area. When they moved to Harvard and Cambridge, the first thing that Ernst and Gretel Mayr did was to purchase an old farm in Wilton, New Hampshire, where they spent most weekends from early spring

until Thanksgiving, and all summers. More important than just providing Mayr a quiet place to write, it gave him the chance to learn the local fauna and flora. Since moving to a retirement home in Bedford, Massachusetts, he has continued to walk and observe birds and learn the natural history of the area.

In the early 1990s, I took Ernst to Cape May, New Jersey, in the early fall. He had not visited Cape May for several decades. On that trip he was able to see his last life-bird, a Gull-billed Tern (*Sterna nilotica*). He remembered that sighting clearly when I told him that I had seen a flock of well over 100 Gull-billed Terns in the Jamaica Bay Wildlife Refuge, New York, in September 2003. In early fall of 2003, he arranged for a special trip to the Massachusetts Audubon Holly Tree Refuge on Cape Cod to see a flowering *Franklinia* tree, a species whose history he knew well, but which he had never seen alive. And while writing this article, I told him of a pair of Ravens (*Corvus corax*) nesting on the Palisades in Tenafly, New Jersey, last year and again this year. His interests were immediately aroused and he wanted to know exactly where, saying that when he lived in Tenafly, he had walked along the river path below the cliffs but never expected Ravens to be breeding there.

FIRST AND LAST INTERESTS

If asked about Mayr's major interests in ornithology, an ornithologist would answer immediately, "systematics and especially species systematics." However, that is not the case. His first and last interest in ornithology is biogeography, as indicated by his doctoral thesis (Mayr 1926) on the northern spread of the Serin (*Serinus serinus*) in Europe, and his masterful treatment of the historical biogeography of the birds in Northern Melanesia (Mayr and Diamond 2001). The latter is perhaps the most complete geographical analysis of a large group of organisms. His *List of New Guinea Birds* (Mayr 1941a) deals with the biogeography of those birds, as well as with their systematics and nomenclature. Over the years, he has provided the entire original formulation of "island biogeography" (Mayr 1941b, c), which was tested extensively in his analysis of the birds of the Northern Melanesian Islands (Mayr and Diamond 2001). In his treatment of the birds

of Timor (Mayr 1944a, b, c), he was one of the few ornithologists—if not the only one—to apply the (then) new ideas for analyzing the biogeography of birds that were advocated by Stresemann (1939). Although published over 60 years ago, Stresemann's "new" approach to historical biogeography still needs to be summarized and placed into proper context for zoologists. Using a faunistic rather than the traditional regional method, Mayr considered questions such as "What is a fauna?" (Mayr 1965), "What are the boundaries of a biogeographic region?" (Mayr 1944b), "What is the origin of the fauna of a region?" (Mayr 1944b, 1946a, 1972a), and "What are the factors influencing the history of a fauna?" (Mayr 1972b). Mayr's rejection (Mayr 1951) of the original theory of continental drift as Cenozoic connections across the South Atlantic, as proposed by Wegener, was entirely correct, because Wegener's original theory depended on a high rate of continental movement, not just that the continents moved horizontally over surface of the earth. Later theories of continental drift depended on plate tectonics; rates of movement of continents were not an integral part of those theories. Rather, one has to have rather precise information on the position and movements of the continents, the history of the groups of birds, and their abilities to disperse—resulting in continued difficulties to formulate and test historical theories of avian biogeography. In his more than 30 papers dealing with diverse aspects of biogeography, Mayr was able to demonstrate the superiority of the "new biogeographical method," which rapidly became the standard used today.

AVIAN SYSTEMATICS AND NOMENCLATURE

Clearly, the bulk of Mayr's empirical work was in avian systematics (mainly species-level work, including revisions of genera), but it also included revisions of families and a proposed classification of living birds (Mayr and Amadon 1951). By the time he completed most of his ornithological work, he had published over 250 papers, describing 26 new species; 445 new subspecies; numerous revisions of genera and families; and a thorough checklist of the birds of New Guinea (Mayr 1941a), which remains the basic work on the birds of that large island.

But he also went well outside ornithology in that part of his career, with his textbooks on systematics (Mayr et al. 1953, Mayr and Ashlock 1991) and his work as a member of the International Commission of Zoological Nomenclature. That began with his attending the Colloquium on Nomenclature in Copenhagen, immediately before the International Zoological Congress in 1953 (during which the set of rules for the new Code were debated intensively). Mayr continued as an active member of the International Commission on Zoological Nomenclature until 1979.

It was not only the great amount of work that Mayr did in avian systematics that was important, but the context within which he did that work. He was able to combine the training he received in Germany with the far greater flexibility of doing research at the AMNH, outstanding access to the literature of the world, easy contacts with several major universities, and the freedom with which a young investigator could interact with senior researchers in the North American academic system. He was completely free to work on whatever projects he chose (as long as they dealt with the collections in the Ornithology Department, AMNH) and he was free to think about his results. Yet almost a full decade passed before Mayr ventured outside of ornithology, in terms of publishing, with his first theoretical paper dealing with speciation (Mayr 1940). That was followed by papers on island biogeography based on the birds of Polynesia (Mayr 1941b, c) and *Systematics and the Origin of Species* (Mayr 1942). Even after that, most of his papers were within ornithology until he left AMNH for the Museum of Comparative Zoology at Harvard University in September 1953. For the next five to six years, Mayr completed publication of papers on his earlier empirical research on species of birds that had disappeared almost entirely after 1960. After that, virtually all his ornithological papers were those associated with *Peters' Check-list*, general reviews, obituaries, and reviews of books. Clearly, the change of Mayr's career from one within ornithology to one outside of ornithology occurred slowly, and the active period of change took about a decade—it was not a revolution. His later work, largely in the history and philosophy of biology, was grounded firmly on his earlier work in avian systematics, biogeography, and natural history.

EVOLUTION AND THE HISTORY AND PHILOSOPHY OF BIOLOGY

Mayr's move into evolution and the history and philosophy of biology was not an accident. He had long been interested in those fields, as demonstrated by his early paper on Bernard Altum's contribution to the concept of territory in the life of birds (Mayr 1935), and in the central implications of evolutionary theory (e.g. populational thinking) on the philosophy of science. His ornithological work led him directly into analysis of the species concept and the process of speciation, and hence to his 1942 book *Systematics and the Origin of Species*. With the publication of that book, Mayr was thrust into the center of the group dedicated to forming a society devoted to studying evolutionary biology (Cain 1994). He became the founding editor of the journal *Evolution* in 1947 and was elected as the president of the Society for the Study of Evolution at their annual meeting in 1949.

There were other indications that Mayr was considering new areas of research. In the second half of the 1940s, the Mayr family spent a large part of most summers at the Cold Spring Harbor Laboratory on Long Island, New York, where Mayr—in connection with his close colleague Theodosius Dobzhansky—carried out a series of studies on the courtship of *Drosophila* (see Mayr 1950). Furthermore, he was thinking of working on the individual and geographic variation of some invertebrate species to see whether the concepts applicable to birds also held for other groups, which led to an analysis of the snail genus *Cerion* in the Bahamas (Mayr and Rosen 1956). Clearly, he was getting restless and was considering other areas of research.

Since the end of the 1940s, Mayr had been contributing to symposium volumes and organizing major book-writing projects that took some years to complete—hence the gap between his leaving the AMNH in 1953 and the appearance of his major publications “outside of ornithology.” I should also note that one could take the year 1953 and Mayr's move to Harvard University as the major watershed between his career in empirical research in ornithology and his career in non-ornithological fields; that is not to say that he did nothing more in ornithology after 1953. Mayr was the driving force behind the completion of *Peters' Check-List*, organizing the remaining eight volumes, deciding to redo volume I,

and making the sensible decision to publish the volumes as they were completed rather than according to the decided taxonomic sequence (Bock 1990). Volume IX appeared in 1960, and the final volume XI in 1986, well after his formal retirement; his inscription in my copy was "At last the millstone is off my neck." He was the president of the AOU in the mid-1950s and the president of the 13th International Ornithological Congress in Ithaca, New York, in 1962.

After the appearance of his 1942 book, Mayr contributed more and more chapters to symposium volumes, developing his ideas on evolution and speciation in important early papers (Mayr 1947, 1949, 1954, 1957, 1959a, 1962). That series of studies terminated in his major book on the evolution of species (Mayr 1963, and the abridgement [really a major revision] of 1970).

Mayr turned increasingly to work in the history and philosophy of biology, areas of long-standing interest to him as shown by his early papers on Altum (Mayr 1935) and Leidy (Mayr 1946b). Those were followed by his analysis of Karl Jordan's contribution to the species concept (Mayr 1955; Jordan was Rothschild's curator for butterflies) and two papers on Darwin and evolutionary theory (Mayr 1959a, b; Mayr listed the latter paper as his first one in the history of biology, but he must have overlooked earlier ones). Less known are his historical introduction to a facsimile edition of the first edition of Darwin's *On the Origin of Species* (Mayr 1964) and an analysis of Lamarck's contributions (Mayr 1972c). Perhaps the most important of Mayr's studies of the history of evolutionary biology is his still little-appreciated analysis (Mayr 1985a) on the fact that Darwin advocated five independent theories about evolution in his *On the Origin of Species* in 1859—not just a single theory, as Darwin himself claimed, and which almost all subsequent biologists, historians, and philosophers have accepted. Four of those theories are nomological, and only one is historical (Bock 2004). As Mayr showed, those theories had very different histories of acceptance in the decades after Darwin. I regard Mayr's paper on the five theories of Darwin as the most important single paper in the history of evolutionary studies.

Two other important projects dealt with topics close to Mayr's heart. The first was a history of the evolutionary synthesis, 1937–1948 (or 1950, depending on one's views), based on two conferences held in the late 1970s in Boston,

Massachusetts, and on questionnaires sent to a number of evolutionists active during that period (Mayr and Provine 1980). That project recorded the events of the evolutionary synthesis while a number of the major players were still alive. The second project was Mayr's (1982) massive *The Growth of Biological Thought*, which deals with evolutionary biology and is still the most important history covering that part of biology. He had planned a second volume dealing with functional biology, but that did not materialize. These two volumes by themselves would ensure a strong international reputation for any historian of science.

Mayr mentions his paper with the vague title "Discussion: Footnotes on the philosophy of biology" (Mayr 1969) as his first contribution to the philosophy of biology, though a number of his earlier papers on systematics and evolution have a direct and important bearing on the philosophy of biology. Moreover he had published some comments on the philosophy of biology earlier (Mayr 1965), such as his early stated position against typological essentialism and in favor of populational thinking. But in the 1970s, he started to work on a number of topics in the philosophy of science, such as teleology (Mayr 1974), ethics (Mayr 1984, 1988a, 2001a), the nature of classifications (Mayr and Bock 1994, 2002), species as individuals (Mayr 1988b, 1996a), philosophical meanings of evolutionary theory (Mayr 1959b), dual causation (Mayr 1961), reductionism versus analysis (Mayr 2004), the autonomy of biology as a science (Mayr 1985b, 1996b), and so on. Those papers are scattered in a diversity of journals and symposium volumes, which makes them rather inaccessible. Fortunately, almost of all of those writings on the philosophy of science have been collected into several volumes (Mayr 1976, 1988a, 1991, 1997, 2001b, 2004; these citations show that Mayr spent the past decade publishing as if he were a young assistant professor worrying about promotion and tenure, rather than a professor emeritus—although he has strong views against the institution of tenure; Mayr 1978).

As a body of work, Mayr's writings on the philosophy of science center around several major interrelated themes of populational thinking, dual causation, and the autonomy of biology as a science. In all of those papers he compares and contrasts the approaches needed in biology, and especially in historical analyses, with those used in the physical sciences. Mayr

concludes that the methods used in studies of the physical sciences, as summarized by most philosophers of science, are simply not completely adequate for all studies in biological sciences, especially if one desires full explanations. The major problem lies in the existence of biological historical-narrative explanations that do not exist in the physical sciences, but also in some of the nomological-deductive functional explanations in biology, such as the Hardy-Weinberg equilibrium, and in ecological relationships such as competition (see also Bock 2000, 2004). Whether one agrees or disagrees with Mayr's conclusions on the philosophy of biology or with the reasons behind some of his conclusions, what is certain is that he has presented a unified philosophy of biology based on a lifetime of empirical research in biology. The latter is exactly what is lacking in the analyses of most philosophers of biology. Again, Mayr's several volumes of collected essays (Mayr 1976, 1988a, 2004) by themselves are sufficient to guarantee him a strong international reputation among philosophers of science.

EPILOGUE

It is fortunate that Ernst Mayr has enjoyed such a long life, because he had to fit at least four major careers into it—that of an avian systematist, an evolutionist, a historian of biology, and a philosopher of science. And he was successful in all of those careers, inside and outside ornithology. The questions of major interest are the mutual influence of ornithology on the non-ornithological areas and vice versa, and whether one could become an outstanding ornithologist without going outside of avian biology. The answer to the second question is quite easy—certainly one can become a great ornithologist without ever working outside of the field. There are many excellent examples, starting with Erwin Stresemann and including many notable North American ornithologists. Moreover, simply venturing outside of ornithology will not necessarily make a person a better student of bird biology. Yet, I feel that it is almost axiomatic that going outside of ornithology and applying what one has learned in other fields to the study of birds will improve the latter work. It appears certain that this is exactly what happened in the course of Mayr's earliest career as an avian systematist, in that he must have been

thinking about the historical and philosophical implications of his taxonomic work from the very beginning, even if he was not publishing in those other areas. That is certainly what happened with respect to his thinking about evolutionary ideas, such as the species concept and speciation, when he was working on the birds of the Southwest Pacific.

The influence of ornithology on Mayr's contributions to evolutionary theory, the history of biology, and the philosophy of science is not only clear, but of major significance. He would not have been able to make the important contributions in those fields without the extensive empirical work he did in avian biology. Here I should emphasize Mayr's broad interest and observations in many areas of avian life—he was a true naturalist well before he completed the *Gymnasium*. He was able to solve questions that eluded specialists in the history and philosophy of science because he was a broadly trained biologist. I need mention only his analysis of Darwin's five theories. A biologist can do well in these episcientific fields, if one is a broadly trained biologist. It is exactly here where a background in ornithology or any of the other specialities based on a group of organisms has its greatest value. A thorough knowledge of the biology of birds, or mammals, or spiders, or ferns provides the best possible foundation on which to delve into evolutionary biology or the overarching areas of the history and philosophy of biology. Hence, we should not only urge our students to think about the broader implications of their studies in ornithology, but to acquire as deep a training in avian biology as possible.

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