



IN MEMORIAM: THOMAS RAYMOND HOWELL, 1924–2004

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In Memoriam



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IN MEMORIAM: ERNST MAYR, 1904–2005

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Ernst Walter Mayr was born on 5 July 1904 in Kempten in southern Bavaria, Germany, and passed away quietly and peacefully on 3 February 2005 in Bedford, Massachusetts. His two daughters were at his bedside during his last hours. At the time of his death, he was the oldest member of the AOU and one of its longest acting, having joined in 1929. He was elected a fellow in 1937 and served as president from 1957 to 1959.

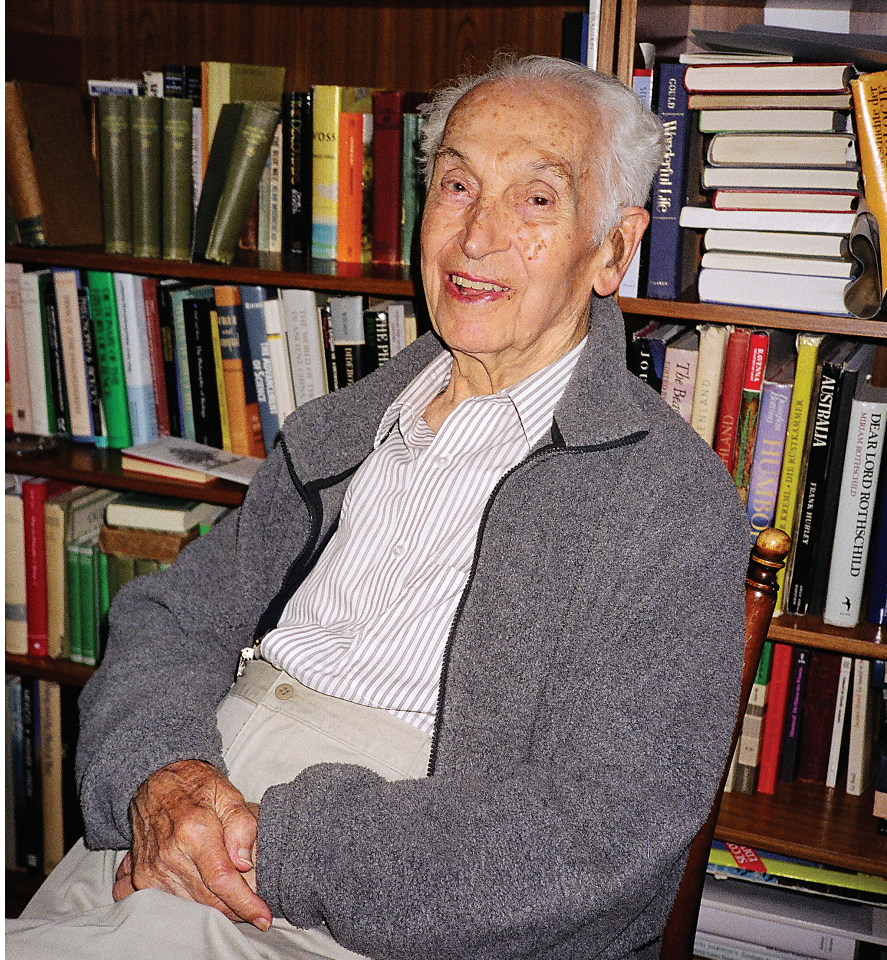
Inspired by his parents' interest in natural history, he became a naturalist at an early age and remained one throughout his life. By the time he was a teenager, Ernst could identify all of the local birds by sight as well as by call. Just after graduating from the Gymnasium in Dresden in 1923, he observed a pair of Red-crested Pochards, the first that had been seen in central Germany since 1846. Armed with a letter of introduction, Ernst interrupted his trip to the University of Greifswald and medical studies to visit Erwin Stresemann at the Natural History Museum in Berlin. Stresemann was convinced of Ernst's sighting of the ducks and, impressed with his enthusiasm for ornithology, invited Ernst to work in the museum during vacations. Soon Ernst became enmeshed in systematic ornithology. As he said many years later, this was as if he had entered paradise. Stresemann convinced Mayr to change from medical studies to zoology and ornithology, with a promise of an expedition to a tropical land once he completed his Ph.D. Before starting his studies with Stresemann, Mayr completed his basic medical courses at Greifswald, becoming a Candidate in Medicine, which would allow him to complete his medical training if his plans to become a zoologist did

not work out—a concern that proved unwarranted.

Ernst Mayr started his training in Berlin in March 1925 and completed his Ph.D. in June 1926, just before his 22nd birthday. He began an assistantship at the Berlin Museum on 1 July 1926. Several attempts at the promised tropical expedition failed until a combined expedition to New Guinea for Lord Rothschild at the Tring Museum and for the Berlin Museum (with additional support from the American Museum of Natural History [AMNH] and Dr. L. Sanford) was organized. The work in New Guinea was successful and before Ernst could return to Europe in 1929, he was invited to take part in the AMNH's Whitney South Sea Expedition to the Solomon Islands. Ernst finally returned to Germany in April 1930, having been away for over two years.

Mayr's work in the Solomon Islands greatly impressed Dr. Leonard C. Sanford, a patron of the AMNH Department of Ornithology, who urged Mayr's appointment to the department to work on the collections amassed by the Whitney South Sea Expedition. Mayr arrived in New York on 19 January 1931 for a one-year temporary appointment. With the acquisition of the Rothschild collection, Mayr was offered a permanent position at the AMNH. He stayed at the AMNH for the next two decades as the Whitney-Rothschild Curator, working on perhaps the best collection of birds that had ever existed for the analysis of geographic variation, speciation, and island biogeography.

During his time at the AMNH, Mayr published his *List of New Guinea Birds* (1941), which is still the basic reference on this avifauna, and *Systematics and the Origin of Species* (1942), which



ERNST MAYR, 1904–2005

(Ernst Mayr in his apartment in Carleton Willard Village, taken on 13 September 2004 by David O. Hill.)

propelled him into evolutionary biology and later into the history and philosophy of biology.

Ernst married Margarete Simon (1912–1990) in the spring of 1935; they had two daughters, Christa and Susanne. In 1937, they moved to Tenafly, New Jersey, where they lived until leaving for Cambridge, Massachusetts, in 1953.

In 1953, shortly after the death of Dr. Stanford, Mayr accepted an invitation to join the Museum of Comparative Zoology (MCZ) at Harvard University as an Alexander Agassiz Professor. This was a research position and did not entail work in the Bird Department at the MCZ or hold teaching responsibilities. Yet he

did both. Accepting the MCZ position meant that Ernst had to leave his beloved Whitney-Rothschild collection, and subsequently he did little empirical research. He did not leave ornithology, though, and he assumed the editorship of Peters's *Check-list of Birds of the World*, organizing and overseeing the publication of volumes 8–15 and the second edition of volume 1. He served as the president of the AOU (1957–59) and of the 13th International Ornithological Congress, in Ithaca, New York, in 1962.

Ernst went to Harvard to become more involved in teaching, which included teaching graduate students. His scholarly interests

turned first to evolutionary analyses (*Animal Species and Evolution*, 1963), then to the history of biology (*The Growth of Biological Thought*, 1982), and finally to the philosophy of biology (*Toward a New Philosophy of Biology*, 1988, and *What Makes Biology Unique*, 2004). Ernst retained his interest in ornithology to the end of his life and was always most happy to discuss avian biology with visitors.

The move to Harvard allowed Ernst to eliminate the hour-long commute between his home and the AMNH. He found an apartment within walking distance of the MCZ and, subsequently, a house even closer on Chauncey Street. His walk to and from the MCZ was an important part of his daily activity, as was an additional long walk later in the afternoon. It was always amusing that in his walk to and from the museum, Ernst took diagonals whenever possible, saying that it cut the distance he had to walk, which seemed illogical, given his longer, voluntary walks in the afternoon. Those walks, which he made into his last year of life, may well have had an important influence on his general health and long life.

The move to Cambridge also permitted Ernst and Gretel to achieve another long-desired goal: a home in the countryside to be used on weekends and during the summers. They found a former farm with a badly rundown house, on a dirt road bordering a lake, in the shadow of Pack Momadnock Mountain in Wilton, New Hampshire. It had everything they wanted. "The Farm," as it was known, was purchased in 1954 and was improved over the years. The Mayrs were there every possible weekend from spring to Thanksgiving and every summer that they were not traveling. Ernst could continue his interests as a naturalist and entertain guests in a pleasant setting. Several research projects were carried out on The Farm, such as Hans Loehr's study of the Red-breasted Nuthatch and Ross Lein's thesis on warbler behavior.

Ernst was a disciplined, hardworking person with a critical, analytical mind. Many workers were awed and ill-at-ease in his presence, which he disliked. Once he remarked to me when I was a graduate student: "My bark is worse than my bite." He was also a dedicated teacher, and as such found it difficult to let an erroneous idea go uncorrected. Yet it was possible to argue with him, though one had to be certain of one's own position, and he would

readily change his position if it was shown to be wrong or indefensible. Mayr was very informal, a result of his years living in the United States, and asked younger colleagues and his students, once they obtained their Ph.D., to call him Ernst. This was a bit difficult at first, especially if one was raised to address one's elders formally, but he insisted, and after a while calling him Ernst came naturally. Ernst was fiercely loyal to his friends, with whom he corresponded throughout his life. One of the sad aspects of a long life, as he told me a number of times, was that so many of his old friends were gone. He was generous in discussing research projects with younger workers and reading the resulting manuscripts. Numerous visitors stayed with the Mayrs in their home in Tenafly, Cambridge, and at their rural retreat in New Hampshire. Ernst and Gretel played important roles in the AOU project that sent care packages to European ornithologists following World War II, as well as sending a large number of packages independently of this cooperative ornithological effort.

Detailed coverage of Mayr's work in systematics, evolution, and the history and philosophy of biology was published in honor of his 90th birthday (J. Greene and M. Ruse, "Special issue on Ernst Mayr at ninety" in *Biology and Philosophy* 9:263-435, 1994). A symposium presented at the 2004 AOU meeting in Quebec in honor of his 100th birthday, with a CD of an accompanying interview, will soon appear in the *Ornithological Monographs* series. A brief account of his life, "Ernst Mayr at 100," appeared last year (*Auk* 121:637-651, 2004). A book-length biography with the proposed title *Ornithology, Evolution and Philosophy. The Life and Science of Ernst Mayr (1904-2005) "Darwin of the 20th Century"* is being completed by Jürgen Haffer.

Ernst Mayr was arguably one of the greatest ornithologists and evolutionists of the 20th century, and an outstanding biologist. He was a leader in the history of biology and one of the driving forces behind the emergence of the philosophy of biology in the early 1960s. His long life provided a connection for many workers to what most of us would consider the dim past. He was well known to scholars around the world and will be missed by all. For me, he was a teacher, mentor, and close friend for more than 50 years.

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IN MEMORIAM: THOMAS RAYMOND HOWELL, 1924–2004

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Member of the AOU from 1948, Elective Member in 1953, and Fellow in 1959, Thomas Raymond Howell was a prominent figure in American ornithology during the second half of the 20th Century. He died quietly at the age of 80 on 14 December 2004 in North Chatham, Massachusetts, after several years of incapacitating illness. He will be remembered as an outstanding avian scientist and teacher and for his many services to the ornithological community.

Tom was born in New Orleans, Louisiana, on 17 June 1924. His father, W. Lyall Howell, was a self-taught chemist who became head of the analytical laboratory at the New Orleans Customs House. His mother, Frances Raymond Howell, taught mathematics in elementary school and had an avid interest in the sciences. With this intellectual home environment, Tom soon began to develop a strong interest in the out-of-doors and in animals. From the age of seven, there are childhood essays and drawings that reveal his interest in precisely observing living nature. At first he was fascinated by snakes, but by junior high school he had switched to birds, because he found them easier to observe and their behavior far more interesting.

From first grade through high school, Tom attended the Metairie Park Country Day School, a private institution on the outskirts of New Orleans, which was fortuitously surrounded by a park of oak trees rich in birdlife. His teachers nourished Tom's interest in natural history. The surrounding countryside, the shores of Lake Pontchartrain, and the Audubon Park Zoo were exciting places to observe birds. Tom became the leader of a group of schoolboys who were fascinated by birds, and they spent many weekends on fieldtrips to various local birding hotspots or visiting the zoo.

In 1941 Tom enrolled at Louisiana State University (LSU), but his education was interrupted by service in the U.S. Army from 1943 to

1946. During part of his service, he remained at LSU in a special military educational program and received his undergraduate degree in 1946. Tom's mentor was Professor George H. Lowery, Jr., who strongly influenced Tom's future direction in ornithology, especially his foundation in taxonomy, systematics, and museum-based science.

Tom entered the University of California at Berkeley in 1946, receiving his M.S. (1949) and Ph.D. (1951) under the supervision of Professor Alden H. Miller at the Museum of Vertebrate Zoology (MVZ). His doctoral dissertation dealt with the natural history and geographic variation of the Yellow-bellied Sapsucker and involved both study of museum specimens and fieldwork in northern California and British Columbia. Howell demonstrated how habitat preferences, migratory behavior, and degree of difference in sexual dimorphism in color combined to keep gene exchange among distinctive subspecies at a very low rate in areas where their breeding populations meet. His work was very much in the MVZ Grinnell-Miller tradition and prepared him well for the comparative approach to biological research.

When A. J. van Rossem, curator of the Donald R. Dickey Collection at the University of California (UCLA), Los Angeles, died unexpectedly, the UCLA Zoology Department asked Alden Miller to recommend a finishing graduate student to function temporarily as curator until the university could decide what to do with the collection. Tom accepted the position. The university wisely decided to keep both the collection and Tom Howell; he became a full-time lecturer in 1951 and spent his entire academic career there, rising to the rank of Full Professor. He was chairman of the Biology Department from 1963 to 1966 and retired in 1986. His close working relationship with George A. Bartholomew lasted nearly 30 years.



THOMAS RAYMOND HOWELL, 1924–2004

(Photo courtesy of Don Bleitz.)

Tom and Bart shared connecting offices with a common laboratory and conference room between them, and their students intermingled freely. They taught a highly popular graduate seminar in vertebrate biology, held in the conference room, where aspiring students honed their analytical and reasoning skills against the hard questioning of their professors in discussions of current literature and biological theory. Sometimes the discussions became heated. On one occasion, two students got into an argument over some abstruse issue of evolutionary theory. They started shouting and calling each other names. Just when it looked like they would come to blows, they both suddenly jumped out of their chairs and shot each other across the table with water pistols. Needless to say, that ended the seminar for the day, but the incident says much about the camaraderie and trust that existed between the students and their professors.

Tom's courses in advanced ornithology and vertebrate biology were extremely popular and

always had waiting lists. His lectures were current, broad-ranging, and elegantly delivered in his soft, southern Louisiana accent.

Tom's research reflected his broad interests in avian biology, but most of his work falls into two categories: (1) behavioral and physiological ecology, particularly in relation to thermoregulation and energetics of birds living in harsh environments (some of this work was done in collaboration with Bartholomew and others); and (2) zoogeography, distribution, and systematics, especially of birds in Central America. His early work in the first category dealt with the adaptive significance of torpor in hummingbirds, swifts, and the Poor-Will. There followed a series of ground-breaking studies of seabird energetics, behavior, and reproduction on some 10 species nesting on Midway Atoll. This interest led to his study of the Gray Gull, which showed how and why this species nests far from the coast in the Atacama Desert of Chile, the driest place on Earth. A monograph on the Egyptian Plover, which nests in the extreme heat of southwestern

Ethiopia, is perhaps his most unique contribution to understanding how birds can adapt to hot environments. He thoroughly analyzed the regulation of nest temperature in this egg-burying species, which also carries water in its breast feathers to wet the sand around the eggs in the hottest part of the day. He collaborated in research on the thermal characteristics of the huge, communal, thatched nest of the Sociable Weaver in the Kalahari Desert of South Africa, showing how the nest's insulative properties, combined with changes in the seasonal grouping behavior of the birds, serve to maintain the temperature of the nesting and roosting cavities near thermoneutrality year-round.

Howell's other main focus of research was on the zoogeography and geographic distribution of birds in Central America, particularly Nicaragua. He had always wanted to work in the Neotropics, and because of the large number of van Rossem's specimens from El Salvador in the Dickey Collection, adjacent and poorly studied Nicaragua seemed like a fruitful place to go. He made his first collecting trip in 1951 and returned over several years until 1967. In the field, Tom was a tireless worker, usually rising between 0400 and 0500 hours to be in the field before dawn, collecting birds and making observations until lunch, spending the afternoons preparing bird skins and writing notes, and continuing the latter activities after dinner, late into the night. Those trips resulted in the collection of numerous specimens and the description of several unusually small subspecies of temperate-zone birds geographically isolated in the lowland pine savanna of north-eastern Nicaragua.

Tom wrote the accounts for the subfamily *Carduelinae* in volume 14 (1968) of the *Peters's Check-list of Birds of the World*. He served for many years on the AOU Check-list Committee and was a co-author of the sixth and seventh editions of the Check-list (1983, 1998). He received the Elliott Coues Award of the AOU in 1985 for his "meticulous and many-faceted approach to significant research problems" (*Auk* 103:451, 1986) and a Lifetime Achievement Award in 1995 from the Pacific Seabird Group in recognition of his pioneering work on seabird ecology (B. Flint, *Pacific Seabirds* 22(2):18, 1995). He and 17 of his graduate students were listed in the Academic Family Tree for Loye and Alden Miller (F. A. Pitelka, *Condor* 95:1065–1067, 1993).

Tom served as President of the AOU (1982–1984) and of the Cooper Ornithological Society (1964–1967). He was made an Honorary Member of the latter, in recognition of his long service. He was for many years on the board of directors of the Western Foundation of Vertebrate Zoology.

Tom Howell married Marjorie Cade Caldwell in 1951, and they had one son, Thomas R. Howell, Jr., in 1954. She died in 1958. In 1959, Tom married Trudi H. Gubler; they had two daughters, Yvonne (1960) and Heidi (1963). Tom and Trudi divorced in 1970. In 1981, Tom married his third wife, Eleanor Standal Dammann, whom he had met on a trip to the Galapagos Islands. Tom is also survived by a brother, W. Lyall Howell, Jr.

After his retirement, Tom and Eleanor moved to a new home near Gualala, California, overlooking the Pacific. They spent several years traveling the world to various exotic places, especially to Australia and Southeast Asia, where Tom completed significant field research on several species of wood swallows (*Artamidae*), and to Christmas Island, where he discovered that the egg of the Blue Noddy is the largest of any bird in relation to body mass. He had plans in retirement to finish writing the results of his Nicaraguan studies and the new material on wood swallows, and to indulge his latent interest in creative writing. Unfortunately, he and Eleanor became seriously ill in the late 1990s and required intensive care at home. She died in 2000, and Tom moved to a care facility near his daughter, Heidi, in Massachusetts, where he continued to take pleasure in being outdoors to the very end.

Tom Howell will be remembered by his friends, students, and colleagues as a cultured gentleman with southern manners and a dry wit, eager to collaborate and share his enthusiasm for birds with others—a consummate professional who effectively bridged the older tradition of ornithology, with its eclectic background in taxonomy, systematics, classification, natural history, and evolution, and the current emphases in behavior, physiology, ecology, and molecular genetics. His correspondence, publications, field notebooks, and manuscripts are archived as UCLA Manuscript Collection 576 in the Department of Special Collections.

We thank Thomas R. Howell, Jr., for information about the early years of his father's life.

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IN MEMORIAM: GUNNAR SVÄRDSON, 1914–2004

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Gunnar Svärdson, Professor Emeritus at the Freshwater Laboratory, Drottningholm, Sweden, and Corresponding Fellow of the AOU, was born on 19 September 1914 in Stockholm. He celebrated his 90th birthday shortly before his unexpected death in Stockholm on 6 November 2004. He was one of Sweden's best known and most highly respected evolutionary biologists and ornithologists.

His strong interest in natural history emerged early. After finishing school, he studied zoology, botany, and geography at the University of Stockholm. Like many biologists, he started out primarily as a bird watcher and had a lifelong passion for ornithology. Yet his best-known scientific contributions were based on studies of freshwater fish. In 1945 he presented his doctoral thesis, titled simply *Chromosome Studies on Salmonidae*. In his thesis, which is still cited, Svärdson focused on "a species" of whitefish (*Coregonus*) in Scandinavian freshwaters and demonstrated that it actually consisted of up to half a dozen genetically incompletely isolated populations, each adapted to a certain set of environmental circumstances. The "introgression" of genes into each of them from one or more of the others prevented their definite fission and kept them in a state of lasting incipency. Svärdson's work led to an entirely novel appreciation of the evolutionary history, genetics, and systematics of the genus *Coregonus*, and to this day it provides one of the most fascinating and intriguing examples of the dynamics of speciation in population groups. Svärdson applied an impressive array of methods and concepts, including cytology, biogeography, and behavior. A similar approach was later used by him to study other groups of salmonids and by other researchers for a great variety of other animal taxa. Moreover, in today's world of biotic globalization and violent anthropogenic perturbations of animal and plant communities, Svärdson's insights into the processes of species

formation and splitting have received increased attention. Hybridization is widely regarded as one of the theoretically and practically most important phenomena in population genetics, as well as in the struggle to preserve the world's biodiversity.

As the ideas of the "Modern Synthesis" reached Scandinavia during and after the war, Svärdson was one of the few who quickly realized the fundamental significance of this new way of thinking and became its leading proponent and defender in Sweden. Breaking as they did with the Linnaean tradition of systematics in Sweden, the new ideas aroused acrimonious feelings in wide and influential circles, and Svärdson was involved in many heated arguments. It is truly refreshing to read his crystal-clear contributions to this debate, and more than almost anything he published, those texts show him decades ahead of his time. Very little would have to be changed to make these publications reflect today's state of the art in evolutionary biology.

Another major contribution flowed from Svärdson's detailed familiarity with birds and bird communities in Scandinavian forests. In a comparatively brief paper in *Oikos* (1949), he presented an innovative model of the different evolutionary and ecological consequences of intraspecific and interspecific competition. Although based on bird work, the general applicability of the model was quickly realized in many quarters, and more than one of the most prominent (if aging) ecologists of the late 20th century have in conversations mentioned to me that "Svärdson 1949" was a major eye-opener for them and greatly influenced their own research in community ecology. Svärdson once related to me that this particular paper had been summarily rejected by the editor-in-chief of the new journal, with the argument that "this is not ecology." In those days, long before MacArthur, the attitude in Scandinavia was that

ecology consists solely of measuring “abiotic” factors and correlating them with the more-or-less poorly known local distributions of various animals. It was simply inconceivable to most ecologists in those days that competition could have an effect on patterns of distribution and composition of communities. Svårdson told me that the paper was grudgingly accepted only after he pointed out that he was, after all, one of the founding fathers of *Oikos* and therefore should be allowed to influence the scope of the new journal and, hence, what is inside and outside the field of ecology.

Gunnar Svårdson’s willingness to invest both time and energy in the service of ornithology is amply documented by the fact that he was one of the founders of the Swedish Ornithological Society in 1945 and of the Society’s bird station at Ottenby on the island of Öland, in the Baltic Sea off the southeastern Swedish coast. Immediately after World War II, Svårdson and some of his friends raised money for a bird station at Ottenby, and 1946 was its first year of operation. Today, after almost 60 years, it is as active as ever and plays a significant role both in ornithological research and in the Swedish program for environmental monitoring.

Svårdson and his family spent each summer in the late 1940s and early 1950s at Ottenby, and many of us young bird enthusiasts employed at the bird station to count the migrating birds or to ring them greatly enjoyed their company. Svårdson himself was a master of “enlightening conversation,” and we students used to look forward to the occasional day of foul weather that gave us some respite from the round-the-clock

field work and a little time for conversations with Gunnar about all matters evolutionary. I was certainly not the only one among those young bird enthusiasts to have had my professional life greatly influenced by what I learned during those discussions at Ottenby.

For most of his life, Svårdson was employed at the Freshwater Laboratory at Drottningholm and served as its director from 1963 to his retirement in 1980. According to his friends at the laboratory, there was no significant decline in the intensity of his research after 1980, and even in his last weeks he was busy preparing a major article in which he was to present a new view on certain puzzles he had discovered in the biogeography of Scandinavian salmonids. His scientific achievements were recognized in many ways. In 1966, the Swedish government conferred on him the rare honor of a Personal Professorship. He was elected Corresponding Fellow of the AOU in 1958, and a member of the Royal Swedish Academy of Sciences in 1975. He was given the Award of Excellence by the American Society of Fisheries in 1981.

Svårdson’s life was long and productive. His passion for science, the breadth and depth of his knowledge and experience, his openness to new ideas, and his willingness to share his insights with students and colleagues made him a model to many. His skill and ardor in defending curiosity-based research against its many enemies was renowned. Many of his ideas still stimulate research in different parts of the world and will no doubt continue to do so for a long time. He will be sorely missed as a respected colleague, teacher, and good friend.

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IN MEMORIAM: EBERHARD GWINNER, 1938–2004

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Eberhard Gwinner, founding director of the Max-Planck-Institut (MPI) für Ornithologie (Max Planck Research Center for Ornithology) and Corresponding Fellow of the AOU since 1975, passed away suddenly on 7 September 2004, after a brief battle with cancer. His pivotal studies provided the foundation on which our understanding of biological clocks and their role in organizing migration, breeding, and other life-history events are based. His energy, wit, and charming smile, along with his expansive warmth and generosity, will be deeply missed. He is survived by his wife, Helga, their three children, and four grandchildren.

Gwinner, fondly known as “Ebo,” was born in Stuttgart, Germany, on 26 December 1938 and attended schools in Ludwigsburg and Tübingen. His enthusiasm for the natural world began early, with his first scientific publication on birds at the age of 17. In 1964, he received the doctoral degree from the University of Tübingen for his work on ravens. His mentors, Gustav Kramer and Konrad Lorenz, served as cornerstones for Ebo’s work. He remained an enthusiastic field ornithologist throughout his life. An interest in biological clocks and his long association with MPI developed during post-doctoral study with Jürgen Aschoff, at the MPI für Verhaltensphysiologie at Andechs from 1964 to 1966. While working with Aschoff, Ebo began his quest to uncover the underlying processes of bird migration and breeding schedules. During 1965–1966, Ebo traveled to Zaire as a Fellow at the Institut pour la Recherche Scientifique en Afrique Centrale. In the tropics, unlike temperate areas, photoperiod and temperature provide less obvious cues for birds to coordinate their activities with the environment. Africa provided Ebo with the evidence that helped him unravel the complex nature of migratory behavior that results from interactions between

internal timing mechanisms and seasonally appropriate external cues. His ideas about internal control mechanisms continue to provide the framework for investigating the organization of key components of the annual cycle.

In 1967, Ebo provided the first empirical evidence of endogenous circannual rhythms in birds. Throughout most of those studies, he monitored key markers of annual cycle events, particularly the expression of migratory restlessness, termed *Zugunruhe*. He demonstrated that different populations of migrants had unique “signatures” or patterns of *Zugunruhe*; those observations led to his discovery that differences in migratory timing, intensity, and preferred orientation have a genetic basis.

The idea that an endogenous direction and distance program (vector navigation) guides first-time migrants toward their unknown wintering area was considered a cornerstone of bird migration theory. Yet throughout his career, Ebo felt that vector navigation was inadequate to account for the details of an individual’s first migration. This eventually led to important studies elucidating the interactions of endogenous components and environmental variables. The discovery of circannual rhythms led to an explosion of research into the endogenous nature of locomotor activity, migratory behavior, molt, and testicular cycles in a variety of species. From those studies, with colleagues that included Peter Berthold, Wolfgang Wiltsko, and John Dittami, came the groundbreaking idea that a steroid hormone, testosterone, could act as a key organizer for the synchronization of internal rhythms with photoperiod.

The role of melatonin, the pineal gland hormone, in the circadian and circannual cycles of birds received attention for many years. Ebo demonstrated that melatonin synchronized and entrained circadian rhythms and developed a



EBERHARD GWINNER, 1938–2004

(Photo courtesy of Dieter Schmidl.)

multiple-oscillator model of circadian organization that remains viable and important today. Along with his colleagues, he demonstrated that the tissue producing rhythms of melatonin production, even when isolated in culture, can “remember” information about day length (and thus season) long after they have been transferred to constant darkness. Other studies revealed differences in pineal biology between long-distance migrants and nonmigrants, which suggested that changes in clock behavior may enable migrants to accommodate nocturnal migration, large longitudinal displacements, and other aspects of a life on the move. Ebo also performed innovative studies on differences in cognitive abilities and brain structure (especially of the hippocampus) in long-distance migrants. He returned to Africa whenever possible, and eventually developed a long-term comparative study on endogenous timing mechanisms in temperate- and tropical-breeding Stonechats.

Although established early as a leader in the field of bird migration, Gwinner continued to expand his skills and explore new areas. He learned about reproductive endocrinology with Donald Farner at the University of Washington

(1969–1970), and spent 1970–1971 studying circadian rhythms with Colin Pittendrigh at Stanford University. Before returning to the MPI in 1979, he studied at the Ludwig-Maximilians-Universität in Munich where he received the prestigious Erwin Stresemann Award from the Deutsche Ornithologen Gesellschaft (German Ornithological Society). He would later receive the Irving Scholander Award from the University of Alaska in 2001. In 1979, Ebo became head of the Vogelwarte Radolfzell at the MPI für Verhaltensphysiologie for two years. He was appointed the institute’s Director in 1991 and served as the head of the Vogelwarte Radolfzell until 1998. In 1998, he founded and became director of the Max Planck Research Center for Ornithology at Andechs, a position he held at the time of his death.

Ebo chaired a Gordon Research Conference on Chronobiology in 1999 and served on the editorial or advisory boards of several prestigious journals, including *Behavioral Ecology and Sociobiology*, *Hormones and Behavior*, and *Journal für Ornithologie*. He was an officer in several organizations, including the Society for the Study of Biological Rhythms, Society

for Behavioral Neuroendocrinology, German Ornithological Society, and International Ornithological Committee. Ebo was a member of the Max-Planck Society and an elected foreign member of the Italian Academia Nazionale dei Lincei. He served on the board of trustees for the Institut für Vogelforschung and the Konrad Lorenz Institute of Comparative Behavioral Research and, at the time of his death, was serving on the European Science Foundation's Coordination Committee.

Ebo published more than 230 publications in such journals as *Science* (including his recent "Chronobiology: Life's Daily Beat," *Science* 304:1906–1907, 2004), *Nature*, *Journal of Comparative Physiology*, *Oecologia*, *Journal für Ornithologie*, *Naturwissenschaften*, *Physiological Zoology*, *Journal of Biological Rhythms*, *Behavioral Ecology and Sociobiology*, *Scientific American*, and *The Auk*. He wrote numerous book chapters on endocrinology, endogenous clocks, and migration. With Michaela Hau, a former student, he wrote the chapter on pineal gland activity, circadian rhythms, and photoperiodism for Sturkie's *Avian Physiology*. Ebo's books, *Circannual Rhythms* (1986, Springer-Verlag, Berlin), *Biological Clocks and Environmental*

Time (coauthored with S. Daan in 1989, Guilford Press, New York), and *Bird Migration, Physiology and Ecophysiology* (1990, Springer-Verlag, Berlin) remain required reading for today's students of migration. Ebo worked almost exclusively on Old World taxa, but his discoveries and ideas are applicable to birds (and other major taxa) throughout the world. He organized many symposia, such as the first Symposium of the Physiological and Ecophysiological Aspects of Bird Migration (Tützing, Germany, 1988), a format in which young scientists, in particular, were encouraged to participate and share their ideas with the current leaders of the day. Ebo's stimulating ideas, his infectious passion for his work, and his great warmth and willingness to involve others have been passed on to another generation of researchers. His many colleagues will miss his leadership and his outgoing personality. Ebo once said that he came up with his best ideas while working in his garden. We don't know whether that plot produced good crops of vegetables. But for the field of avian biology, it was very fertile ground indeed.

A brief obituary appeared in *Nature* 432:687 (2004).