ERNST MAYR: SOME QUESTIONS ANSWERED

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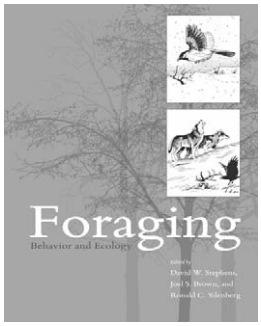
territoriality, and foraging, as well as for his work in the analysis of metabolic rate and population dynamics.

Writing a synthesis of foraging theory in the early 1980s may have been a rather straightforward task, given the small number of basic models and empirical investigations that characterized the field, but at the turn of the millennium, that task is completely different—and most likely daunting—because the field has exploded into a surprisingly diverse set of research programs and traditions.

So what should be included in such a new synthesis of contemporary foraging research? Clearly, the synthesis should present a greater integration of neural mechanisms and cognition into foraging behavior. It should also be clear that those physiological mechanisms of digestion and energy management that have long been ignored by foraging behavioral ecologists must be brought to the forefront. It would be unthinkable for such a book not to update certain problems of classic foraging theory without also dealing with more recently formulated social foraging questions. Finally, the long-unfulfilled promise must be met: the book must deal with the population-level phenomena that foraging theory was meant to address in the first place. *Foraging: Behavior and Ecology* does all of this in four parts.

To cover such a broad diversity of subjects would be nearly impossible for a single author, so Stephens, Brown, and Ydenberg invited a team of 27 contributors to help them achieve their goal. However, calling upon such a team of collaborators, which includes both senior and junior scientists, leads to a problem frequently found in edited volumes: the uneven depth of treatment of issues and the different writing styles turn the book, at least in some parts, into a quilt of topics rather than a unified whole. Most chapters were simply delightful to read, and I learned a great deal from them. A few, unfortunately, failed to capture my attention, as I kept wondering why I was being told what I was being told. The editors apparently worked very hard to overcome this unevenness by insisting that each chapter start with a clear, vivid natural history example of the topics the chapter would cover. These chapter openings are universally interesting.



The construction of *Foraging* is innovative. The editors asked some contributors to write full-length chapters, whereas others were invited to compose boxes for presentation within the chapters; the boxes provide either a review of a related topic, some introductory material, or more specialized accounts of specific topics. This innovation works well. The numerous halftones by Todd Telander give the book a pleasing visual quality (which reminded me of the illustrated adventure books of my childhood). In general, *Foraging* is a good piece of workmanship with an impressive bibliography and nice graphs, but I must point out that typographical glitches—Greek letters missing in the text and in the equations of chapter 2—marred my cloth edition. An errata sheet inserted in the paperback version took care of that problem, so if you buy a copy, make sure it comes with the errata sheet.

I highly recommend this book to all who study foraging. Graduate students will find a wide array of fascinating questions about foraging, from the neurological pathways of the ventral unpaired median neurons to cognitive maps, digestive physiology, impulsiveness foraging games, food hoarding and provisioning, the cycling of predators and prey populations, trophic cascades, isobars, and giving-up densities and conservation strategies, to name a few. Researchers and faculty members will find a convenient source of updated information on foraging theory and foraging behavior.

Reading *Foraging* will surely conjure up exciting discussion topics. For instance, as I read chapters on brains and foraging behavior, I wondered whether it could be possible for mechanisms to be of general interest, given that they so often seem specific to each of the extremely diverse set of taxa being studied. Perhaps the persistent calls for greater study of mechanisms in behavioral ecology are dangerous sirens luring behavioral ecology toward the same end that ethology met only a few decades before? At that time, many ethologists abandoned proximate questions of mechanisms to embrace a behavioral ecology that boasted a more general and exciting functional approach. Stephens, Brown, and Ydenberg have demonstrated that foraging is most certainly not a depleted research patch. It is rich, and offers a diverse set of questions moving into a wide range of research traditions. Make sure you read it.

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ERNST MAYR: SOME QUESTIONS ANSWERED

Ornithology, Evolution, and Philosophy: The Life and Science of Ernst Mayr 1904–2005. Jürgen Haffer. Springer, New York, 2008. 474 pp., illus. $59.95 (ISBN 9783540717782 paper).

Every evolutionary biologist has read something by Ernst Mayr, for he was one of the 20th century's great evolutionists. In *Ornithology, Evolution, and Philosophy,* Jürgen Haffer chronicles Mayr's life and his research. This is essentially a long obituary rather than a critical examination of Mayr's work, written by an obvious admirer. Haffer

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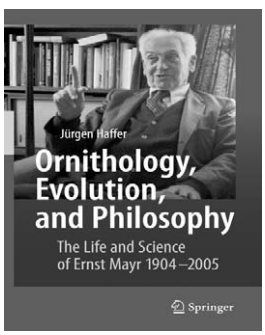
spent much time talking to Mayr and had access to letters and autobiographical notes. The book includes such details as pictures of Mayr's first car, his medical history, a list of his graduate students and their achievements, and histograms of Mayr's publications by field of study and date. Although a little repetitive and difficult to follow in places, the book will be useful not only to Mayr scholars but also to anyone wishing to understand the progress of evolutionary biology through the last century.

Ernst Mayr was born in Germany in 1904 and died in the United States in 2005. Between 1928 and 1930 he went on expeditions to New Guinea and, sequentially, to the smaller islands of the South Pacific. In 1931, Mayr moved to the United States to be a curator at the American Museum of Natural History in New York (Haffer notes that if he hadn't, he probably would not have survived World War II). He took up an appointment at Harvard in 1953, where he spent the rest of his career, including an active "retirement." During that time he wrote hundreds of papers and book reviews, and was author or coauthor of 22 books. He won the three major prizes in evolutionary biology—the Balzan, Japan's International Prize, and the Crafoord Prize—but not the Nobel Prize, which Haffer attributes to the fact that the Nobel is seldom awarded to evolutionists.

Haffer considers three main, overlapping periods in Mayr's career: his ornithological studies, his contributions to the so-called modern synthesis (the integration of population genetics into biological evolution), and his studies of the history and philosophy of biology. Of these, Mayr's midcareer syntheses on speciation are probably the most familiar to most of us. Through many writings he showed how the formation of new species could be studied through the documentation of geographical variation, which he emphasized could often be large. Mayr's 1942 book, *Systematics and the Origin of Species,* remains influential today. One of my former graduate students, Darren Irwin, developed his thesis after reading it and revisiting, with modern molecular and field studies, a pattern described therein.

It is probably fair to say that, unlike other major players in the modern synthesis, such as Dobzhansky (one of Mayr's closest associates), Fisher, Wright, and Haldane, Mayr is less well known for his original research than for his synthetic works (with the obvious exception of his brilliant book *Birds of Northern Melanesia,* coauthored with Jared Diamond, which was started in midcareer but published only in 2001). Mayr's main research through his early career was on the systematics of birds—he described 26 new species and 445 new subspecies—and museum based. Jürgen Haffer is an ornithologist, although he did not pursue an academic career, but rather worked in the oil industry. On the basis of field research in South America and, to a lesser extent, the Near East, he has written many important papers on the identification of historical barriers that might promote speciation. Perhaps because of Haffer's expertise, it is those chapters on Mayr's contributions to ornithological research and his early expeditions that were the most compelling for me.



Apart from enjoying interesting anecdotes—for example, Mayr probably ate more Birds of Paradise, his favorite group of birds, than any other ornithologist, and he once had to maneuver deftly to avoid becoming married to a village girl in New Guinea—we learn what it takes to become a successful scientist: hard work and ambition are two of the main ingredients. We also learn how new species were discovered and described in the early part of the 20th century: by staring at a series of skins for long periods. Haffer quotes a letter from Mayr concerning his studies of *Collocalia* swiftlets: "On some days… I sat there for 3–4 hours comparing a single specimen of *hirundicea* with a single specimen of *vanikornensis*.... Eventually I had developed such a clear mental picture of them that the classification of the other forms became much easier" (p. 152). This approach emphasizes the importance of identifying traits shared by all individuals of a species, so-called diagnostic traits. Mayr was very proud of introducing "population thinking" into systematics (i.e., emphasizing that, despite shared traits, all individuals of a species differ from one another, something that is so obvious as to be trivial to the geneticist). Passages such as the one about the swiftlets make it clear why this was such an important advance for systematists, because they continually try to "look beyond" the variation within species.

The "taxonomic species concept" that Mayr employed to describe species is quite different from his operational definition used to study the process of speciation ("the biological species concept": a species is a group of interbreeding populations reproductively isolated from other such groups). Haffer notes that the two or three species concepts Mayr used are generally obvious from the context, but it was only later in his career that Mayr acknowledged the alternative concepts that permeated his earlier work.

Something else I learned about Mayr's career, which Haffer highlights well, is that he made a large contribution to the development of science, especially organismal biology. Mayr founded the journal *Evolution,* and was a selfless editor. One famous incident concerns Mayr's visit at Cambridge University with Sir Ronald A. Fisher, a renowned population geneticist described by Richard Dawkins as "the greatest of Darwin's successors." At one point in the meeting, Fisher turned his back on Mayr. Folklore has it that Fisher did that because he disdained Mayr's rather unsophisticated understanding of population genetics; in fact, as Haffer outlines, it was most likely because Mayr

had rejected a paper Fisher had submitted to *Evolution*. Editors have a thankless task, but Mayr took on that job and many other administrative duties with good humor.

In an obituary for a second major figure of 20th-century evolutionary biology, W. D. Hamilton, Marlene Zuk wrote that it was not so much the number of correct ideas, but rather the sheer number of ideas, that made Hamilton exceptional. Reading Haffer's book, I was struck by how much this applies to Mayr, too. Mayr has often been wrong, which should encourage us all: He began his career as a Lamarckian, adhering to the discredited idea that traits acquired during one's lifetime can be passed on through the germline; and, although it is unclear that he rejected the theory of continental drift when it was first proposed, he does say in his 1982 book, *The Growth of Biological Thought,* that biogeographers were right to resist it, given the evidence of the time. He clearly—and notoriously—did not lack confidence. Even today, Mayr is credited with a model of founder-effect speciation described in a paper in 1954, one that he considered at the end of his career to be "one of the most important papers I have written." The model is accepted uncritically by some, but it has little theoretical justification and no empirical support.

In my view, Mayr's lasting major contribution was his precise formulation of the biological species concept, and I had always wondered why he did not spend more time investigating reproductive isolating mechanisms (the factors that prevent an individual of one species from mating with an individual from another, or if they do mate, those factors that cause the hybrids to be unviable or sterile). We learn here that he did try, first with caged birds, and again in a series of papers written with Dobzhansky on *Drosophila*. But he never connected his documentation of the often large geographical variation in plumage with the development of reproductive isolation. Why, when he was staring at those skins of similar swiftlets, did he not ask how it can be that "acquisition of reproductive isolation and morphological divergence are not closely correlated" (quoted from Mayr and Gilliard, "Altitudinal Hybridization in New Guinea Honeyeaters," *The Condor* 54: 325–337)? It seems to me this is one of many unanswered questions that emerge from Mayr's work that has great ramifications for our still rudimentary understanding of the process of speciation. *Ornithology, Evolution, and Philosophy* makes it clear that much remains to be learned about Mayr's thinking, which, once understood, may enlighten many problems in evolutionary biology. Mayr's legacy will continue to shape the field for the foreseeable future.

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