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IJEE Soapbox: A NEVER-ENDING STRUGGLE: BECOMING A BETTER ECOLOGIST AND EVOLUTIONARY BIOLOGIST

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> "The search for objective knowledge strikes me as a form of heroism.… To subjugate yourself to the objective truth is a humbling experience."
> *Rebecca Goldstein, on why a novelist should care about realism.*
> *An interview reported in Bly (2010)*

Rummaging through some files in my office, I came across a long-lost, hand-written letter to me from the renowned evolutionary biologist and ornithologist, Professor Ernst Mayr of Harvard University, a letter that I had despaired of ever finding again. He wrote it to me when he was in his late 90s (he lived to be 100, passing away in 2005), in response to a letter of my own. Explaining the genesis of this correspondence permits me to reflect on the theme of this special issue of the *Israel Journal of Ecology & Evolution*, which is trying to characterize elements of "good science". I will dwell on this topic with the concrete example of this truly fine scientist in front of my mind.

The fundamental goal of science, intellectually, is to increase human understanding of the universe – conceived as broadly as possible – using methods that attempt to be objective and interpersonal, in that they are repeatable and public. This social goal is achieved by individual scientists who are motivated by curiosity about the world, or by the desire to address practical problems, naturally interlaced with the desire to craft a fulfilling and meaningful career. Like kicking a soccer ball, or painting a portrait, or laying down a carpet, one can do science poorly, or well. All these activities have in common that their value depends in large measure on their social context; part of the worth of any given scientific study comes from how it builds on, refracts, and amplifies prior understanding, and then provides a fruitful springboard for future study. And as

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The IJEE Soapbox provides an informal forum for leading ecologists and evolutionary biologists to expound on issues that they find particularly exciting, thought provoking, and novel.

Robert D. Holt is our first invited ***IJEE Soapbox*** essayist. Bob is Professor of Biology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

with any human endeavor, at any stage in a scientific career, it is worthwhile stepping back from the daily routine to ask how one can improve one's efforts. For students starting out in a scientific career, honing self-awareness about the kind of patterns of life that one should deliberately cultivate to aim for excellence is particularly valuable, and indeed necessary.

The essays in this issue provide a variety of valuable perspectives on what constitutes "good science", encompassing several meanings of the word "good". One use of the word "good" is more or less synonymous with "high-quality". Another meaning of the word "good" refers to adherence to ethical standards in the conduct of science (see Nevo, 2011, this issue), which shades into issues of the social organization of science (Messer-Yaron, 2011, this issue). I will not deal directly with issues of the ethical dimension of science, but recognize their importance.

The thoughtful essay by Ray Huey (2011, this issue) (building on thoughts he and Steve Stearns put down on paper, many years ago; the earlier documents are available at http://faculty.washington.edu/hueyrb/prospective.php) provides to my eye a particularly insightful perspective on how scientists of any age can strive to improve their game. Like him, I am not entirely comfortable with laying down dicta about what constitutes "good science", but instead can hope to articulate a few ways we can aim to become *better* at doing the science we do, and in particular, to become more effective and insightful in our pursuit of understanding in ecology and evolutionary biology.

Let me start out with a general observation. As the philosopher George Santayana once said, "Science is nothing but developed perception, interpreted intent, common sense rounded out and minutely articulated" (Santayana, 1905). The basic point here I think is that there is nothing magical or mystical in the scientific enterprise, but rather, science builds on a sharpening and at times formalization of the perceptual and conceptual tools that all humans have at their disposal. Science is the ultimate democratic enterprise, in that in principle all individuals can participate in some fashion, and the end product is a body of communal understanding, a public good that should benefit all. The conceptual end product of the enterprise of course need not match what initially one considers to be "common sense", at all (think of the wonderful weirdness of quantum physics). Much of one's training as a scientist has to do with refining one's perceptions of the world, seen both through one's own eyes, and through those of the authors of scientific papers and books, and also with developing the appropriate "articulation" of one's common sense. The latter can include experimental methodologies, statistical tools (Saltz, 2011, this issue), careful qualitative reasoning, and mathematical and theoretical models.

When I try to characterize how one can aim at becoming a better scientist, it helps me to focus on concrete human beings whom I have admired as practitioners of science. Keep in mind that there are likely many different personal pathways towards excellence in science, and I am recounting aspects of one such pathway; there may be others, quite different from my choice here, which could be just as or even more compellingly argued. Ray Huey, towards the end of his essay, recounts his brief but illuminating encounter as a postdoc with Ernst Mayr, driving him to the airport. Their conversation had to do with advice on how to stay fresh as a scientist, and also the rueful recognition by Mayr himself that some of his views had become rather fixed (at that time he was in his 70s), maybe even shading into dogmatism. Reading Ray's essay reminded me of the letter mentioned above, which in turn brought up memories of my own graduate years, when I was fortunate to get to know Professor Mayr a bit, due to sheer dumb luck.

When I entered Harvard University as a beginning graduate student in 1973, I was ensconced in the Museum of Comparative Zoology (MCZ), and as in all museums (which after all tend to fill up with specimens), space was at a premium. It was unclear who my advisor would be, so in my first year, I was stuck in a former storage room which happened to be up in the bird range on the upper floor, next to Professor Mayr's office. He was quite near retirement, but still showed up regularly at the office. My temporary office was full of dust, battered Victorian office furniture, and generic clutter, so I tried to make it more habitable. Hidden away behind a tall piece of furniture, which I moved to improve the organization and lighting in the office, I found hung a small watercolor of the Cuban green woodpecker (*Xiphidiopicus percussus*) by none other than one John James Audubon! This was quite an improbable find, and I loved having this piece hang on my wall, but it also made me a bit nervous, so eventually I told Professor Mayr about it. The watercolor was soon whisked away to more secure quarters (this artwork still hangs somewhere in the MCZ).

Mayr appeared at my first encounter with him to be both formidable – after all, he was a towering figure in evolutionary biology – and kind. We had a chat which diverged into a discussion of bird-watching, and travel to exotic places. I have been a birder since childhood, and Mayr had himself been quite passionate about bird-watching and yearned to travel as a young man, so we had something in common. After his doctorate, he launched his career with dramatic expeditions to New Guinea and the Solomon Islands, and I was keen on the idea of spending time in the tropics, so we talked a bit about both birding as a hobby, and as an activity that could act as a spur and complement to serious science, and induce folks like ourselves to explore a range of habitats and environments. At the time, I had also started to read some of his classic works, in particular *Animal Species and Evolution* (Mayr, 1963), as part of a general program in my first two years of graduate study of reading through foundational books and papers in ecology and evolution. I was impressed by Mayr's emphasis on philosophical issues and the conceptual foundations of biology (which became a major theme in much of his later writing life, e.g., Mayr, 1988). So I mentioned that, and he suggested that I drop by and visit to talk about such issues from time to time.

I profited from and thoroughly enjoyed several informal chats scattered over time with Ernst Mayr about my own research interests, his own life, and different themes in evolution, ecology, and indeed beyond (e.g., philosophy of science). Here are some thoughts, drawn from memories of those encounters, about some of the elements required to become better as a scientist, in particular in the disciplines of ecology and evolution, using Mayr as a standard for an exemplary scientist.

STAY GROUNDED IN NATURAL HISTORY

One recollection I have from those conversations is that Mayr strongly felt that in order to do creative work in ecology and evolutionary biology, it was valuable (if not absolutely essential) to have some kind of grounding in natural history. He sustained this concern with natural history throughout his life (see his Academy of Achievement interview from 2001), for instance using the phrase "We naturalists…" in a late publication (Mayr, 2004). In a way, this issue of natural history has to do with providing a motivation for getting into the field (as it were) in the first place (e.g., because one simply enjoys learning about and experiencing animals, plants, and landscapes). Moreover, to understand ecology and evolution, one can only go so far mining databases and pouring over remotely sensed images; ultimately, nature has to be studied, in nature. But I think the issue here goes beyond these observations. An appreciation of natural history can lead to a kind of sharpening of our perceptions, including a recognition of questions latent even in commonplace observations. I recall talking to him about how when we just open our eyes, we can find numerous unanswered puzzles about nature, right around us. For instance, Mayr reflected on how little was known about the social lives of porcupines, even though this species was common (and at times a pest) on his New Hampshire farm and indeed throughout New England.

There is a growing concern about the lack of exposure many young persons have to natural environments. When teaching an undergraduate ecology course recently, I was shocked to learn how few of the students knew the names even of the commonest trees and birds on campus. It was as if they had blinders on, as they walked past live oaks draped in Spanish moss, and magnolias bursting with plate-size white blooms, and palmetto leaves rustling in the breeze, and mockingbirds singing their lungs out. Students in an ecology course are presumably a biased sample of the student populace, so the true level of ignorance must be even higher in the population at large. As Louv (2005) remarks, for newer generations, "nature is more abstraction than reality". There is increasing evidence that this pauperization of experience may impair psychological and physical health (Louv, 2005).

Beyond this, a degradation of natural history is likely to impair the ecological sciences, for instance by contributing to the further decline of taxonomic expertise (Gotelli, 2004; Kim and Byrne, 2006). To address many important questions in ecology and evolution, including applied questions of critical importance to human health and well-being, requires the collection, wise interpretation, and utilization of natural history information (J. Tewksbury, pers. comm.). There is a widespread perception of a general loss of organismal biology in universities (e.g., Hoagland, 2004; McCarthy, 2012), and I wonder if this loss is fueled in part by a general decline in natural history in the populace at large. And for those students who do enter ecology or evolutionary biology in particular, a lack of natural history experience (and interest) may in a way literally impair their ability to perceive subtleties in the systems they study, constraining the range of questions they are likely to ask. Sewall (2011) has suggested that an interest in natural history can help mold neuroplastic responses, so that individuals can "see beyond the norm" in noting the reticulate details of natural systems. As science depends upon "developed perception", according to Santayana (1905), a lack of natural history might thereby quite literally reduce our capacity to "see" important questions or puzzles.

REMEMBER THAT EDUCATION IS NEVER-ENDING

Ray Huey remarks that Mayr's first bit of advice to him for remaining fresh as a creative scientist was "*go to seminars*". This is an excellent piece of academic wisdom (which could be broadened to include attending workshops, annual meetings of societies, reading broadly, and the like). After all, a good seminar speaker should be distilling years of work down to some key points, making a body of research much more vivid and alive than the impression one is likely to get from reading a pile of her papers. This can be particularly valuable on topics far from one's own research specialty. And Professor Mayr definitely practiced what he preached. I saw him at any number of departmental seminars. He even kindly came to the first semi-public talk I ever gave. This must have been in about 1975 or so, after I had developed my first ideas about apparent competition. The talk was to Richard Lewontin's lab group, and I was rather nervous about how my ideas would be received. As I recall, I presented some basic models with likely empirical examples drawn from the literature (all on hand-drawn overhead transparencies), and some general thoughts about indirect interactions. Much to my surprise, Professor Mayr and some other faculty showed up to listen to my ruminations, and had helpful questions for me afterwards. A few days later, I dropped by Professor Mayr's office, and remarked to him how infectious disease might lead to a form of apparent competition between hosts. He then shared with me and let me copy his own personal reprint of J.B.S. Haldane's (1949) brilliant but obscurely published essay on disease and evolution—which I likely would not have otherwise found at the time. Haldane suggested that "a non-specific pathogen to which partial immunity has been acquired is a powerful competitive weapon", and suggested as an example native ungulates in South Africa indirectly excluding domestic livestock via trypanosomes transmitted by the tsetse fly. I cited this paper in my dissertation, and later developed some first formal steps towards a theory of apparent competition due to shared pathogens (Holt and Pickering, 1985). There is now a considerable body of empirical evidence that infectious diseases can have a strong influence on the structure of ecological communities (Hatcher and Dunn, 2011).

KEEP SIGHT OF THE BROADER INTELLECTUAL LANDSCAPE

To succeed in a scientific career, an individual has to be a specialist, to some degree. As Ray Huey notes in his essay, some of the most effective scientists stay fresh in their work by shifting their domain of specialization from time to time.

But to carry out the best and most fertile scientific research, I also feel it is important to understand how any given specific piece of research fits into the broad sweep of science, and indeed intellectual life as a whole. One thing that impressed me as a student, and still impresses me to this day, was Ernst Mayr's breadth of knowledge of ecology and evolutionary biology (his immediately recalling that obscure paper of Haldane's is an example of this). As an indication of the breadth of his thinking, in the preface to *Animal Species and Evolution* he thanks an illustrious roster of prominent geneticists (J.F. Crow, Th. Dobzhansky, B. Wallace, and in particular Richard Lewontin), ecologists (R.H. MacArthur, F.A. Pitelka), wildlife biologists (J.J. Hickey, L.B. Keith), systematist/biogeographers (G.G. Simpson, E.O. Wilson) and a cytologist (M.J.D. White) for going over the chapters in his book. This list of names indicates the wide range of disciplines Mayr tried to link together to his central theme of species and speciation. Most of us cannot hope for the kind of intellectual breadth demonstrated by Ernst Mayr, but I think all ecologists and evolutionary biologists should strive to reach beyond their own specialties, so as to consider their disciplines more holistically, and in particular how these disciplines are related. Although historically often separated, ecology and evolution are today becoming increasingly interdependent. For instance, the traits of organisms and the structure of communities reflect historical, evolutionary processes, ranging from mutation to selection and speciation. Genetic and phylogenetic tools increasingly permit inference about population and community history, and the use of molecular tools is increasingly pervasive across both disciplines. In like manner, key drivers of evolution include ecological processes such as nutrient limitation, competition, and parasitism, and ecological perspectives in turn are essential to interpreting the flood of data emerging from genomics. There is increasing recognition that the time scales of ecological and evolutionary change overlap, including in many arenas of great concern for human welfare, such as the emergence of novel infectious diseases, the sustainable harvesting of natural resources, and the resilience of ecosystems to the looming threats of global climate change. Environmental management will increasingly need to include a dimension of applied evolutionary biology.

Emphasizing concepts and theory is, I think, an essential ingredient in striving for breadth in one's intellectual perspective, and an appreciation of mathematical theory can help achieve this goal. I have always greatly admired Professor Mayr's sustained emphasis on conceptual issues, and on the philosophical foundations of biology. Yet, he was famously skeptical of the uncritical use of mathematical models in evolution (Mayr, 1959). He himself admitted that he was not particularly good at mathematics (Academy of Achievement interview, 2001), and I do recall his discussing with me how some questions in ecology in particular might require, in some essential way, careful development of mathematical theory. Recent developments in genetics have reinforced the central value of mathematical and computational models in evolutionary biology, for instance in reconstructing phylogenies and population histories from genetic data (Crow, 2009). This may have been one arena where Mayr's admitted hint of dogmatism might be rather obvious. Indeed, some of his own ideas have not until recently been formalized, helping to characterize when the processes envisaged by him work, and when they do not.

One example is species' range limits. Mayr's personal focus was initially on avian biogeography and speciation, and he maintained an emphasis on the nature and generation of species throughout his career (e.g., Mayr and Diamond, 2001). His concept of the species as a metapopulation of lineages is still foundational, well beyond the usual formulations of the "biological species concept" (de Querioz, 2005). The species as a genealogical unit is of course fundamental to phylogenetic reconstructions of the history of life. If species are real units of biological organization, they must have a spatial extension. Mayr became keenly interested in the issue of species borders, and in particular understanding why species have limited geographical distributions, which can sometimes shift over time. His doctoral dissertation involved the controversial hypothesis that the serin (*Serinus serinus*) had recently spread across Europe, thus shifting its border, and tried to elucidate the ecological factors that led to that spread. He continued his interest in range limits in *Animal Species and Evolution* (1963, p. 61), where he surmised that the existence of generalized adaptive genes, which had "definite limits of tolerance", could underlie the determination of range limits. He further identified what he called "The Problem of the Species Border" as a puzzle in evolutionary biology, and remarked (Mayr, 1963, p. 524):

> The essential stability of the species border…would seem to contradict our belief in the power of natural selection. One would expect that a few individuals would survive in a zone immediately outside the species border and form a new local population which becomes gradually better adapted under the continuous shaping influence of local selection. One would expect the species range to grow by a process of annual accretion like the rings of a tree.

Mayr's own suggested solution to this puzzle was that local adaptation at the range margins would be disrupted by genes from the range interior. The issue of understanding species borders is still a fundamental question in both ecology and evolution (e.g., Case et al., 2005; Gerber, 2011). It took many years for theoretical biologists to address the detailed workings of Mayr's hypothesis about range limits (a start was made by myself in Holt, 1979, and Holt, 1983; a fully articulated model, however, awaited the treatment by Kirkpatrick and Barton, 1997). The latest work on the subject suggests that gene flow accounting for stable range limits requires that genetic variation itself be limited (Barton, 2001); gene flow is more likely to constrain range limits if selection is occurring on many characters simultaneously (Duputie et al., 2012) and if dispersal occurs across abrupt breaks in the environment leading to strong spatial asymmetries in demography (Bridle et al., 2010; Holt and Barfield, 2011). These theoretical investigations still await firm empirical testing (Gerber, 2011). But one thing has become very clear: a solution to the species border problem requires integration of knowledge across many different arenas of science, from genetics, to physiology, to demography, to community and even ecosystem ecology, and contingent knowledge of particular species in particular landscapes. In this sense, this important problem exemplifies the importance Ernst Mayr placed on synthesis across the biological sciences, and the grounding of ecology and evolution in natural history, as well as theory.

STRETCH ONE'S MIND BEYOND ECOLOGY AND EVOLUTION

I had a further insight into Ernst Mayr's intellectual breadth due to a fluke of timing in my graduate education. After he retired, Mayr felt he needed to have some contact with graduate students and younger faculty, so for several years he would organize informal evening sessions at his home. His wife Gretel served tea and cookies, and then we would have a discussion on a question Professor Mayr had chosen for the evening. These ranged widely. One evening the topic was: "Is there intelligent life with sophisticated technology on other planets?" All of the graduate students were convinced there likely was, but Mayr was quite skeptical; had anyone been judging our debate, it would have surely come out at best a draw, he versus the gang of the rest of us. The question was not whether or not life was elsewhere; we all thought this was quite likely. Mayr kept coming back to the observation that so far as one could tell from the fossil record, technologically sophisticated intelligent life had arisen just once in the near countless number of evolutionary experiments that had occurred, so as a contingent fact of evolution, it should be considered improbable, a priori. This issue continued as an occasional theme in Mayr's career for years afterward (see Mayr, 1995, for a celebrated exchange between Ernst Mayr and Carl Sagan on the likelihood of extraterrestrial intelligent life). We still of course do not know the true answer to this question (as an aside, reading the political news makes me sometimes wonder "Is there intelligent life on Earth?"; that quip is surely not original with me!). Mayr's stance in this debate brings up several other dimensions of what counts as "good science". First, good science is not determined by majority opinion. Second, one has to take risks in posing questions to tackle, since many ideas are likely to fail; experiments and observational studies can fail for many reasons, and perfectly plausible hypotheses can fail empirical test (a point Ray Huey makes quite nicely in his essay). All it will take will be one counterexample of observing extraterrestrial intelligence, for Mayr to be proven wrong. I am sure he would be amazed at the occurrence (as would we all), but were he still alive, he (and we) would doubtless get up and carry on. As Samuel Beckett once astringently quipped, "Ever tried. Ever failed. No matter. Try again. Fail better." (Beckett, 1984; this quintessential modernist playwright of the absurd may himself have been influenced by philosophical ideas about science in some of his writings (Ackerley, 2010; C. Ackerley, pers. comm.).

This quote from Beckett reminds me that Professor Mayr had been trained to some extent in philosophy, and he viewed evolutionary biology as in many ways more akin to the humanities, in particular history, than say to physics, and he viewed a grounding in the history of biology to be essential for a full understanding of the subject (p. vi in Mayr, 1963). My final observation about the need to maintain intellectual breadth is that engaging with disciplines outside of science, such as philosophy, history, and literature, can indirectly facilitate one's abilities within the discipline. This is more of a hunch than a crisply articulated line of argument. At the very least, wide reading might help one become a more supple writer, and as Ray Huey notes, the most important skill one may have as a scientist is that of communicator—to one's peers, granting agencies, and ultimately the public. Ernst Mayr was a most effective communicator, in person and in his writings.

And this brings me back to the issue of why there was a correspondence between Professor Mayr and myself in the first place. I moved to the University of Florida in 2001, and gradually unpacked my boxes of books and put them on the shelves in my lab library, with some attempt at order. A substantial part of one shelf was devoted to books by Ernst Mayr. Noting this, I started thinking back to my graduate school days, and a memory of those warm and intellectually invigorating evenings at his home bubbled up in my mind. I knew he was in his 90s, but still by all reports mentally vigorous. So I wrote him a letter, in effect thanking him for those evenings. And he quite rapidly wrote me back, a warm and thoughtful reply. I was really touched by this.

So, in conclusion, as one strives to carry out "good science", as a general rule it might be particularly useful to keep in mind examples of unquestionably fine scientists one knows, such as Ernst Mayr.

ACKNOWLEDGMENTS

This essay has in effect been a way to say another "Thank you" to Professor Mayr. My reflections above draw on a mélange of more or less distinct memories from my graduate student days; memory we all know can be flawed, but I hope in this case it is reasonably reliable (I have no contemporaneous notes). I could have equally written essays lauding, and thanking, the other fine scientists it has been my good fortune to know and be influenced by, first as an undergraduate at Princeton (e.g., Robert MacArthur, John Bonner, John Terborgh, Henry Horn, and Egbert Leigh) and then later in graduate school (e.g., Ernest Williams, William Bossert, Stephen Jay Gould, Richard Lewontin, Robert Trivers) and beyond (e.g., John Lawton, Mike Rosenzweig, Jim Brown, Si Levin), who exemplify the many different ways individuals can carry out "good science". A few sentences in this essay have been drawn from a report I (chairing a panel) prepared for the Academy of Finland this past year (2012). I thank Chris Ackerley for information about Beckett, the editors for their patience, and the University of Florida Foundation for its support.

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