Robert K. Selander

1927-2015

BIOGRAPHICAL *Memoirs*

A Biographical Memoir by
Howard Ochman

NATIONAL ACADEMY OF SCIENCES

ROBERT KEITH **SELANDER**

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By Howard Ochman

It has been many years since Robert Selander was a central figure in the study of the social behavior of birds, the genetic variation in animal populations, and the molecular evolution of microbial pathogens. He built a grand reputation in each of these fields, making abrupt changes in research direction and study system based on, from what I could gather, a combination of whim and ennui.

Born on July 21, 1927, in Garfield, Utah, Selander made his early mark as a naturalist and standout field biologist at the University of Utah, where he earned his bachelor's (1950) and master's (1951) degrees in zoology focusing on the biogeography and distribution of birds of the Great Basin. Well before the days when it became fashionable or was encouraged to include students on publications, his name appeared on multiple papers describing unusual sightings, range extensions, and the natural history of the avian fauna of Utah. Reading over some of these early accounts, one can perceive his signature writing style, though when asked decades later, he would deny any connection with those long hours in the field (except once, when admitting that it allowed him time to memorize the Latin binome of every species of bird in North America.)

Given his early passion for the natural world and his course of education, it seemed foregone that he would pursue a career in biology, but, in fact, he was also awarded a scholarship to attend Juilliard. He never divulged why he selected to study birds over Bud Powell, but throughout his life, he rarely strayed far from music. Sometimes it was marathon sessions of Wagner's operas, or long evenings as a pianist in a cocktail lounge or hotel lobby, or arranging and conducting jazz standards for the local ensembles and big bands. (He drolly conceded the difficulty of this last pursuit owing to the ageing band members, several of whom were losing their chops, and the inevitability that at least one would be absent on account of a hernia or pending prostate surgery.)

Whatever motivated his decision, he entered the Ph.D. program at the University of California, Berkeley (UCB) to work with the renowned ornithologist Alden H. Miller. Selander and Miller never co-authored a paper together, but from my reading of Miller's confidence, tenacity, drive (and musical prowess), it is clear that he met his match in Selander. Of his graduate student days, he spoke little, and little is known except what can be gleaned from his publications. From these papers, it might first seem that he simply expanded the range of his field observations with an auspicious shift to include California and Mexico. His dissertation, however, exposes hints about his scientific development—a tome on speciation in wrens (of the genus Campylorhynchus),[1,2] notable both for its comprehensiveness and for its deference to the evolutionist Ernst Mayr, whose work he had been reading extensively and had finally met. His dissertation extended far beyond cataloguing birds and makes evident that he had become much more curious about genetic features underlying their variation and social behavior.

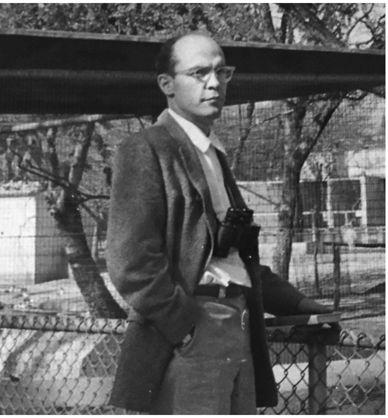

Figure 1: Robert K. Selander during his early years as an ornithologist, ca. 1961.

Upon earning his doctoral degree in 1956, he received a National Science Foundation (NSF) postdoctoral fellowship to work with Mayr, who had moved a few years prior to Harvard University from the American Museum of Natural History in New York. Harvard's vast collection of ornithological specimens would have advanced his studies on sexual dimorphism and species differentiation, but he was also offered a position as an instructor at the University of Texas at Austin, so he forfeited the postdoctoral opportunity (Figure 1). Given his tendencies, the urban confines of Boston and its distance to expansive field sites with native birds were the likely deciding factors—though nearly twenty-five years later, I heard him rationalize his decision to the baronial Mayr by offering ambiguous comments about job security. In reality, he did not need mentorship to add new dimensions to his research program, and his work expanded to incorporate aspects of behavior (sexual dimorphism and mating behavior of grackles, cowbirds and mockingbirds);[3-9] physiology (hormonal control of incubation patch development);[10-14] evolution (speciation in sparrows, grackles, and wrens);[15–20] and genetics (polymorphism in Mexican jays).[21]

On the surface, his publications from that period might still appear to be observational records, but their findings were far from prosaic, and two papers, in particular, have had a sustained impact. An oft-cited paper on woodpeckers offered a truly new outlook on the origin of size disparities between males and females.[22] Sexual dimorphism—differences in size, form or appearance between sexes of the same species—is typically thought to come about by two means: intrasexual selection (competition between males for mates) and intersexual selection (female choice). Selander, however, showed that dimorphism in woodpeckers is not the result of any form of sexual selection but rather has a purely ecological basis. It derives from males and females utilizing different resources and thereby minimizing intersexual competition for food.

Also notable among his discoveries from this era is a report in *Science*[23] showing that the conspicuous variation in the color and size of house sparrows in North America was of the same magnitude as that observed across Europe—perhaps not surprising until one realizes that our house sparrows all stem from a release of a small number of birds into Central Park in 1852. The extent of phenotypic divergence was presumed to have required tens if not hundreds of thousands of years to manifest the races of European sparrows, and it occurred in a mere 100 years in North America. And given the cosmopolitan nature of the species, this work has been repeatedly interpreted as indicative of rapid, human-induced evolution.

His conduct at UT Austin has been as described as unstoppable (as well as some descriptors bearing less positive connotations). In fact, every adjective associated with a Type-A personality could be applied to Selander at that time. He ratcheted through the ranks from instructor to full professor at a fairly rapid pace, but even some of these promotions were the subject of spectacle. For example, several people mention, and some of us have seen, his letter to the dean refusing advancement to the rank of full professor. (Judiciously, the dean denied the request.)

Figure 2: Robert K. Selander.

It might, perhaps, seem surprising that after this highly productive decade at Texas, he published nothing beyond a couple of follow-ups during next two years. But this period marked a sea change in his research endeavors. Despite the attention and awards that his ornithological research garnered (Figure 2), he sensed that he would always be considered a “bird-watcher” when he compared himself to the molecular biologists who successes seemed to be infiltrating all fields of biology. So he made the abrupt decision to rid himself of everything pertaining to birds: books, literature, field notes, and even an Audubon print and stuffed specimens, were ferried into the hallway, and as word spread, graduate students and colleagues, some with lab-carts, "descended like vultures" on his vast collection.

Figure 3: Robert Selander standing behind Wilson Stone. (Image captured from a group photograph of the faculty in the Department of Zoology, University of Texas Austin), ca. 1967.

Selander's previous research had centered on variation within species—within local populations of a species, among geographic races of a species, between the two sexes of a species—and he had become frustrated that he could not make informative conclusions about genetic variation from the observed phenotypic variation.[24] That he would completely transform and confine his lab to the study molecular population genetics took courage, but it no doubt helped that his home department was then a hub of Drosophila genetics. Additionally, he was deeply respectful of and impressed by his forceful senior colleague, Wilson Stone (Figure 3). Just that year, Stone and colleagues had published a paper describing a way to survey genetic polymorphisms within populations by assaying proteins whose alleles were detectable as electrophoretic mobility variants.[25] Also that year was the coincident publication of two highly persuasive and influential papers that applied protein electrophoresis to measure levels of heterozygosity within populations,[26,27] which further bolstered his decision to abandon behavioral and observational research altogether.

At the start of these new endeavors, Selander somehow convinced his field-oriented graduate students that genetics and mice were more interesting than grackles or falcons.[28] He sent Grainger Hunt to Denmark to collect mice across a region where semi-species were known to hybridize, while he and Suh Yang developed protocols and fabricated the necessary lab equipment (noting that, at the time, power supplies were assembled Radio Shack kits and gel rigs were built from in-house designs). His new molecular lab was fashioned to exploit the methodologies applied by Stone (who died the following year), but the procedures were streamlined to maximize the number of starch gels that could be run each day. All available bench space, and often an idle desk or counter, was used to accommodate their gel rigs, leading to the processing and analysis of thousands of samples. Whereas several researchers at the time were applying these methods to resolve debates concerning the extent and maintenance of genetic variability—the so-called "classical vs. balance" or "selection vs. neutralist" controversies—Selander mostly ignored these issues and, given the volume of data his lab produced, became renowned for his use of electrophoretic markers to dissect the genetic structure of natural populations.

The ensuing years had a kid-in-the-candy-shop atmosphere as his lab surveyed protein polymorphisms in a wide assortment of species with the goal of uncovering the geographic scale at which genetic differentiation occurred. The initial studies on Danish mice reported a steep genetic gradient and large genetic disparity between the two interbreeding semi-species,[29] lending support to Mayr's theory that populations must accumulate a large number of genetic differences before they become completely separate species. Additionally, this study, which ultimately involved nearly 3,000 samples from 150 locations scored at forty loci, was of an unprecedented breadth and set a new standard of sampling for electrophoretic analyses.

This work was followed by the ongoing sampling and analysis of wild populations of house mice (Mus),[30–34] field mice (Peromyscus),[35-39] kangaroo rats (Dipodomys),[40] cotton rats (Sigmodon),[41] and other rodents across vast expanses of the Southeast, Texas, and California,[42,43] as well as some similarly comprehensive analyses of birds and lizards.[44–50] Overlayed on these studies were investigations of several non-vertebrates (snails, insects, and even plants) aimed at assessing the contribution of mating systems to genetic variability, which bore on evolutionists' favored topic—the evolution of sex.[51–54]

There were also some curiosity studies that considered populations presumed to have reduced variability, such as a species nearing extinction (elephant seals),[55] a species recently restricted to cave habitats (the Mexican tetra),[56] and a species of seemingly unchanged morphology since the Paleozoic (horseshoe crabs).[57] He generally avoided working on such systems—which he termed "disco" organisms due to their flashiness or popularity—but as a pioneer in the study of the genetic structure of natural population, he was continually solicited to survey the electrophoretic variation in someone's favored organisms.

The quality and comprehensiveness of his datasets lent themselves to in-depth comparative analyses of enzyme, organismal, and taxon variability and had numerous applications to the population genetic theories that were being developed by Motoo Kimura, Tomoko Ohta, and Masatoshi Nei. The standardization of methods, and the perceived ease and speed with which his lab could generate these data, probably helped prompt what was dismissively dubbed the "find 'em 'n' grind 'em" school of population genetics, insinuating an effortless and aimless examination of protein polymorphisms in any random organism. In actuality, few facilities rose to the standards, breadth, and proficiency instituted first by Suh Yang and later by Bob Hudson, who marshalled his lab during that period.

As a faculty member at the University of Texas, Selander's reputation grew—not only for his scientific awards and contributions, which were considerable, but on account of his antics, several of which have become exaggerated and implausible in the re-telling. He once provoked a regrettable confrontation with an officer that escalated to the point at which he was banned from parking either his personal car or field vehicle on campus. During a gala event several years later, he was cordially introduced to the president of the university, who sized him up and then remarked, "Ah…Professor Selander. We've almost forgotten about that parking incident." Gulp.

After nearly two decades at the University of Texas, Selander moved to the University of Rochester to chair of the Department of Biology, with the circumstances surrounding his relocation the subject of contradictory back-stories and speculation. His research was still devoted to examining the genetic variation within natural populations, but the impending publication of G. C. Williams' *Sex and Evolution* in 1975,[58] and the later appearance of Maynard Smith's transposably titled *The Evolution of Sex* in 1978,[59] added immediacy to his earlier work comparing genetic diversity under different breeding systems. Most literature on this topic was theoretical in nature and attempted to account for the maintenance of a sexual mode of reproduction, despite its obvious detriments, through some interplay of (and not limited to) mutational load, recombination, environmental heterogeneity, escape from parasites, population size, reproductive rate, sib competition, and dispersal. But there were few assessments of the standing genetic variation in sexual/recombining vs. asexual/clonal populations, or the genetic consequences of outcrossing, inbreeding, self-fertilization, and parthenogenesis. The new and varied taxa considered in these studies, including lizards, flies, cockroaches, worms, snails, slugs, frogs, fish, and even more plants, were often selected based on portrayals of their peculiar chromosome segregation systems in M. J. D. White's excellent (despite C. D. Darlington's hostile review)[60] treatise *Animal Cytology and Evolution*,[61] which served as a sort-of lab bible at the time. In addition to the stream of manuscripts spawned from these studies, Selander also became known for writing overviews that did not shy away from criticizing results he deemed as weak, unsound, or unwarranted—especially those claiming to show that selection was acting on molecular polymorphisms.

During this period, his lab hosted researchers at all career stages who wished to evaluate the genetic variation in their particular study systems. Prominent among these were ethologists who knew of Selander from his previous forays into bird behavior and who viewed protein electrophoresis as offering a new way of testing sociobiological theories concerning genetic relatedness and its consequences for social behavior. Allowing his lab and personnel to be exploited as a facility for these auxiliary research projects was a magnanimous gesture, more so because Selander refused to be included as an author on these studies. What was viewed as generosity was, in no small part, rooted in sensibility and selfishness—not one to merely add his name to an author list, he simply did not wish to invest the considerable amount of time he deemed necessary to produce manuscripts on topics in which he had scant interest and with authors he barely knew.

Writing a paper with Selander was instructive, theatrical, and never easy—and the process lent insights into his personality and spectrum of bents. Firstly, he was obsessively confrontational and quick to attack the most minor of slip-ups. Secondly, he was side-splittingly funny with snippy railleries, unconcealed histrionics, and a satiric take on the absurd. Thirdly, he loved his commas. (I have a book from his library in which he re-punctuated a paragraph of an article from an author he considered substandard—11 inked-in commas!) To co-author with him was to endure deskbound hours with grammatical rules and rants that too often lamented the eventual collapse of Western civilization (all due to the improper use of em-dashes and semi-colons?). But they were also some of the most unrestrained and hilarious performances I've witnessed. I regret not recording his tirade about the polarics of adverb placement since it ranks among my favorite comic routines.

By lucky coincidence, Bruce Levin, then a professor at the University of Massachusetts Amherst who was investigating the ecology of bacterial accessory elements, tempted Selander with the idea of studying variation in *E. coli*. Selander found this proposal appealing for two reasons: The first was scholastic, in that there was ongoing debate about the extent of recombination and clonality—a topic of his sustained interest—in bacterial species at large. Joshua Lederberg had won a Nobel Prize for discovering that asexual bacteria could indeed exchange genes, and a prominent electrophoretic study of *E. coli* variation by Roger Milkman confirmed this for a large set of natural isolates.[62] However, the repeated recovery of certain pathogenic clones of *E. coli* gave indication that recombination was rare. The second reason was personal—Selander had regarded the quality of Milkman's gels and the number of loci examined as suboptimal and insufficient to address the issue, so he wanted to prove his point.

Selander's and Levin's examination of electrophoretic genotypes in a worldwide set of *E. coli* strains isolated from humans, animals, and environmental sources, including many of those originally characterized by Milkman, revealed that the species was clearly clonal.[63] Although *E. coli* harbored the highest known levels of allelic diversity, strains from unassociated and geographically separated hosts were indistinguishable, an impossible outcome if recombination had occurred at the levels envisioned by Milkman.

This study proved pivotal to the next stage in Selander's career. Protein electrophoresis had previously been applied to microorganisms, but never at this scale and never by researchers so adept in the application of evolutionary theory. To comfort those unfamiliar with these procedures and ease his way into the vernacular of microbiologists, he adopted the acronym MLEE (multi-locus enzyme electrophoresis) as the sole way to designate the approach, which helped launch the field of microbial population genetics.

The early work on *E. coli* attracted two exceptional postdoctoral fellows, Dominique Caugant and Tom Whittam, both of whom ended up devoting their entire careers to the study of bacterial populations, and it also fostered collaborations with researchers and epidemiologists who had amassed large strain collections. By some accounts, electrophoretic variation was assessed in 10,000 strains of *E. coli*, followed by nearly the same number of Salmonellae, whose taxonomy and degree of clonality was even more mysterious than that of *E. coli*.

Selander was never one to concentrate his efforts into one or two focal species, but his broad and rapid expansion into the forest of bacterial pathogens involved in human outbreaks was due largely to Jim Musser, then an M.D.-Ph.D. student at the University of Rochester. Their chance meeting led to a three-hour discussion that culminated in Selander saying, "Well, there's the laboratory, go discover something." Jim had the knack, connections, and interest to obtain large bacterial collections from international sources that seemed unobtainable, and he worked tirelessly on sample processing, analytics, and manuscripts, even while earning his medical degree. These efforts demonstrated the value of population genetics in medical microbiology and infectious disease research, and enhanced understanding of molecular pathogenesis—a key finding being that most infections, regardless of the bacterial species, were caused by a very limited number of clones harboring unique virulence genotypes.[64-67]

By his own admission, Selander did not take well to his position of department chair at Rochester: he could not be bothered by the daily minutiae that kept him away from research and piano arrangements, he knew of no polite way to get people to leave his office, and he most assuredly did not want input from faculty on departmental matters. On the other hand, he was uncharacteristically proud of the way that he overhauled the introductory biology curriculum, mostly because he inflicted a day-long field component involving plants, birds, and snails upon undergraduates who were, by and large, pre-med majors.

By the mid-1980s, following his election to the National Academy of Sciences in 1982, Selander's research was devoted entirely to studying the evolutionary genetics of bacterial pathogens, and he published about a paper each month on this topic for the next seven years. He had witnessed that "techniques" papers earned the highest numbers of citations—in fact, the original field-mouse article that contained gel-staining recipes[68] still garners his top spot—so he composed an analogous paper outlining electrophoretic methods for bacteria to boost his renown.[69] In 1987, he again relocated, this time to Pennsylvania State University, where his former postdoc Tom Whittam already had a position. With the advent of PCR, the sequencing revolution had begun, so they mothballed the protein-electrophoresis equipment and switched to studying nucleotide diversity in epidemic bacteria, which he continued until his retirement in 1999.

It seemed that a lot of Selander's opinions and advice was dispensed for shock or comedic value, but over the decades, I came to tolerate, appreciate, and then treasure his candor and acumen. Among the things I heard during my very first year as his graduate student were: (1) "Every paper, letter and memo that comes out of our lab must be letter-perfect and grammatically correct. We don't want the people in the English Department to think that we're monkeys over here in Biology." (2) "Be suspect of any scientist who is described as 'nice.' Real scientists are driven, selfish and insecure.…They don't need to be nice. If you're not good, you'd better be nice!" In the years leading up to, and then into, his retirement, Selander and I corresponded more regularly. His emails elaborated on a wide range of topics: his hobbies (sailing and music) (Figure 4); the arts (movies and literature), and his beloved dogs (Charlotte and Emily) (Figure 5), but most were commentaries on the state of popular culture and academe.

Figure 4: About to embark on a sailing expedition.

His viewpoints and pronouncements did not soften much as he aged, but he was more outwardly prone towards self-deprecating humor and acceding his audience in his later years. Among the scores of e-mails that I received from him during this period was one under the subject heading "Significant Photo," which contained a photograph of himself seated at a desk (Figure 6) and bore the caption: "Howard: Here I am–working late into the night in an attempt, in my inadequate way, to understand in some small measure, the empirical complexities, evolutionary implications, and philosophical ramifications of your latest paper! For me, to approach your work is tantamount to making a pilgrimage to the cave where Shiva can be worshipped as a stalagmite. rks" (though it was obvious from the stationery that he is actually transcribing a musical arrangement). Although he was blunt and outspoken about academic and societal issues, and valued an audience, he remained a private person. It was decades before he let on to me that he had an identical twin(!), who was a professor(!), and a biologist(!), who studied systematics(!!). Of his first wife, Bonnie, and their children, David and Jennifer, he revealed little. The only personal relationship he ever mentioned was that with his partner and spouse, Pilar, whom he adored.

Figure 5: On a Fall birdwatching excursion with Emily (left) and Charlotte (right).

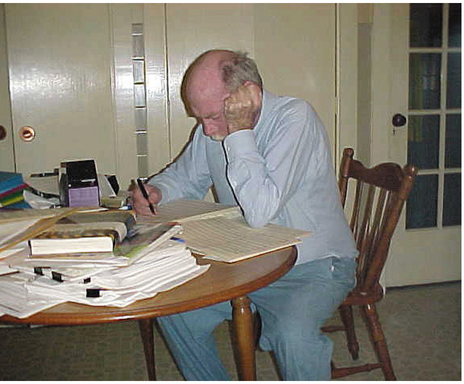

Figure 6: Working late at night (and into the morning) on a musical score.

Looking over our correspondence during the last years of his life, I was amazed at the insights, lucidity, and clarity with which he wrote about popular culture as well as the latest papers published in *Nature*, *Science*, and the *Proceedings of the National Academy of Sciences*. I asked him once how he managed to write so well at the age of 86, and his verbatim response was, "On the quality my writing, you are much too kind. I'll admit that some of it is fairly good, but only because I am able (and willing) to spend an ungodly amount of time and effort writing a single letter." Included in this email was an assortment of missives that he sent to authors of articles by which he was singularity impressed, and you can imagine the pyrotechnics he employed when he was writing to professional writers. He kept a list of well-turned phrases, sent to me appended with the comment: "God…I wish that I wrote that."

To put his scientific and creative output into perspective, he devoted the final pages of his twenty-nine-page academic CV to list his privately published songbooks, big band arrangements, original arrangements, adapted transcriptions, transcriptions, and eight-piece combo arrangements.

It is fitting to close with what he composed as the preamble of his own obituary, written on the day after he retired (and prior to going out birdwatching for the day). His alleged accomplishments aside, this is exactly how I wish to remember him:

> *Today, Prof. R. K. Selander passed on to what some have on occasion been wont to call "the great laboratory in the sky," where there is no teaching "load," all primers work, all grant applications are funded, all manuscripts are published (without revision), all graduate students speak idiomatic English, and both undergraduate evaluations and faculty meetings are forbidden.*
>
> *Early in his long—some would say, almost interminable—career, the goodly Professor attempted to study birds, first as a graduate student at the University of California, Berkeley and, then, as a faculty member at the University of Texas at Austin. In the ornithological community at large, he is to this day remembered for having been able (on the solid basis of specimen material) to extend the then known geographic breeding range of the Red-eyed Cowbird by fully 60 miles (from San Antonio to the outskirts of Austin).*

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