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ALDEN HOLMES MILLER

*1906—1965*

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*A Biographical Memoir by*

ERNST MAYR

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*Biographical Memoir*

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*Alden H. Kistler*

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*February 4, 1906–October 9, 1965*

BY ERNST MAYR

ALDEN HOLMES MILLER was born at Los Angeles, California, February 4, 1906, and died of a heart attack at Clear Lake, California, on October 9, 1965. The most impressive aspect of his all-too-short life was the range of his activities. His premature death left a painful gap in the institutions which he had served with so much distinction and in the branch of biological science to which he had contributed so significantly.

It is no accident that Alden Miller became a naturalist. Loye Miller, his beloved father, "Padre" to his friends, was one of the enthusiastic group of California naturalists, and, even before he could walk, young Miller was forever out in the field with his parents. He did not escape the "pack rat affliction" of the young naturalist and made his mother's life miserable by trying to raise pollywogs in the bathroom sink and by converting a corner of his bedroom into a museum. How much Alden admired his father is obvious not only from the close contact he had with him all his life and the choice of his career, but also in the selection of specific lines of research (avian paleontology, anatomy, and vocalization). Both father and mother gave him a love for music which was heightened by the fact that he had "absolute pitch" and a fine voice. He was blessed being raised in a happy family, al-

though he tended to shyness and may well have occasionally felt overshadowed by the radiant personality of his universally popular father. He entered the University of California at Los Angeles, where his father was also teaching, in 1923 and earned his A. B. degree in 1927.

During this time he became engaged to Virginia Dove, a fellow student at UCLA, whom he married in August 1928. Their marriage was a very harmonious one, owing to a similarity of interests and their love and respect for each other. Alden was a kind and thoughtful father, guiding his three children in their education and leisure-time activities. The happy family life of the Millers was a joy and example to their many friends.

In college Alden Miller majored in zoology and chemistry, but he simultaneously studied music under John Smallman and developed a beautiful and well-trained voice. As a result, he became the baritone soloist in one of Los Angeles' largest churches, the First Congregational. Toward the end of his undergraduate days, he had to make a vital decision. Should he choose music as his profession, as he was strongly urged by his musician friends, or should he become a biologist? He finally decided that he would have a richer life if he became a scientist, and he enrolled as a graduate student with Joseph Grinnell in Berkeley. After this decision was made, his professional life was as straightforward and uncomplicated as any professional life can be in these complex and rapidly changing times. He remained associated with the Berkeley campus of the University of California until his death, and found it possible to develop his diverse interests and abilities within the framework of this one institution.

Miller soon became an enthusiastic, almost passionate Grinnellian. Grinnell's methods of field work, of data col-

lecting, and of presenting the results in subsequent scientific publications were unconsciously adopted by Miller, and much of this procedure was retained by him after his interests had outgrown Grinnell's traditional objectives. In the 1920s, Grinnell was a leader and pioneer. He was the first to develop some of the best-known concepts of ecology, such as the niche and competitive exclusion, and pioneered in various other areas of evolutionary biology, particularly the study of geographic variation in relation to climate and physical environment. Grinnell's ideal was to get away from the anecdotal approach of the traditional naturalist. His aim was to make natural history scientific by accuracy of recording, precision of description, and quantitative analysis of the data. Alas, this purely inductive method often overwhelms the investigator. Some of Grinnell's many students were rightly ridiculed for the publication of awesome mountains of undigested raw data. Alden Miller was far too good a scientist to go to such extremes, and yet, throughout his life, he had a tendency to give a greater amount of his strength and time to the gathering and presentation of data than they were worth. The systematist, using this word in the broadest possible sense, faces a genuine methodological dilemma. He cannot make any generalizations without the gathering of abundant comparative data, and yet, unless he is extremely careful, he may lose sight of the forest for the trees.

One of the major objectives of Grinnell's school was to determine the precise distribution of each species of terrestrial vertebrates in California and adjacent states and to specify its dependence on certain landscape types and climatic zones. A second objective was to analyze the impact of the distribution on the geographic variation of each species. The needed information was gathered on a multitude of field trips to all parts of California and adjacent states. The findings were

presented in two types of publication. One was a series of monographs on the vertebrates of specific areas, and Miller was co-author of two volumes in this series, *The Vertebrate Animals of the Providence Mountains* (1948) and *The Lives of Desert Animals in Joshua Tree National Monument* (1964). Two major summaries were the other outcome of this research. The massive data gathered during a lifetime of faunistic researches were published by Grinnell and Miller, in 1944, as *The Distribution of the Birds of California* (608 pages and 57 figures, mostly maps). This formed the basis of *An Analysis of the Distribution of the Birds of California*, published by Miller in 1951, carried out entirely in the classical terms of life zones and biotic provinces, and vegetational associations as distinguished by the plant ecologists. As in much of the early ecological work, there was rarely a rising above the purely descriptive level. Yet, it must not be overlooked that this type of work has established an excellent basis for the conservationist, for the geographer, for wildlife management departments, and for all those who conduct more ambitious work in the field of ecology.

Miller's bibliography contains a total of 258 papers. They range from a new locality record of the black-bellied plover, published when he was just eighteen years old, to work on mammals, fossils, anatomy, physiology, systematics, behavior, and various areas of environmental and evolutionary biology.

Miller's Ph.D. thesis (1931), a broad-gauge study of the American shrikes (*Lanius*), foreshadows many of the lines of his future research. The first part of this monograph is devoted to a painstaking description of geographic and individual variation of the two species, one of the first ornithological papers giving detailed statistics of differences in measurable characters of sexes, age groups, and geographic races.

The degree of precision pioneered in this monograph set new standards and had a lasting impact on American ornithology.

The second half of this monograph is devoted to a detailed study of the natural history of American shrikes, much of it based on Miller's own field work. The breadth of his interests is best indicated by some of the section headings, such as migration, habitats, territory, courtship, nest-building, eggs, incubation, growth of young (16 pages), second and third broods, food, foraging, impaling instinct, digestion, preening and bathing, modes of progression, vocal notes, causes of death, and age. Fifteen other papers in his bibliography are devoted to various aspects of avian biology dealing with personal observations of courtship display, territorial habits, parental care (including distraction displays), and stages of the life cycle.

A special part of his thesis dealt with an analysis of plumages and molts. Physiologists and particularly endocrinologists have long known that a close study of molts and the sequence of plumages reveals a great deal about the annual cycle of hormonal levels. The "geography" of feather tracts is important also as taxonomic character in birds, and, realizing this, Miller devoted much study to this subject, so much indeed that he became the outstanding American authority in this field. A foreign author recently wrote me plaintively, "No one in America is qualified to review my book on molts, now that Alden Miller has died."

In spite of the wealth of descriptive detail presented by Miller, what he was really interested in was questions of causation. He said of his studies of the molts of the Loggerhead Shrike that they "have demonstrated that a pronounced geographic variation in the completeness of the first fall molt exists within this species. The variation appears to be associated not only with migration and with length of summer sea-

son but also with the structural features that differentiate subspecies." In a later paper (1933), he writes, "Experimental methods have been open to criticism from the standpoint of the naturalist because of the artificiality of the conditions attending the experiments. It appears, however, that in the analysis of *Phainopepla* [desert bird] plumage there is an opportunity to observe a natural experiment which under perfectly normal conditions seems to corroborate certain of the principles discovered by the experimentalists in the laboratory. By studying a group of immature *Phainopeplas* which have been preserved at varying stages of the body molt and with varying appearance of black pigmentation, we have, in a sense, a continuous picture of the period when the testes is apparently attaining full hormone secreting function." These comments foreshadow Miller's later intensive population studies of the hormonal and environmental factors controlling reproduction in birds.

Some thirty of Miller's publications, including his *Lanius* and *Junco* monographs, are in the field of taxonomy. Miller was the first and soon the leading proponent of population systematics among American ornithologists. He argued convincingly at a time when he was almost alone in these views that species and subspecies should not be conceived in the classical typological manner but as variable populations. He concluded a lecture at the International Ornithological Congress at Oxford in 1934 with these words: "The illustrations which the genus *Junco* offers should serve to point an inquiring finger at the simplicity of concepts of species and subspecies still retained by many persons, and should induce the student of taxonomy to search more thoroughly for the true nature of species." In seven revisions, he studied the geographic variation of certain North American birds with whole population samples. In each case a careful statistical analysis was under-

taken and an attempt made to correlate the observed variation in size, proportions, and coloration with the variation of the environment. His *Speciation in the Avian Genus Junco* (1941) was considered, at the time of its publication, "the finest study of this sort in the ornithological literature" and still deserves this evaluation. Unfortunately, Miller presented his findings in the Grinnellian tradition as a straightforward taxonomic revision, and some of his most interesting and novel evolutionary findings were recorded, in a fragmented way, under the heading of various junco subspecies. Consequently, this superb piece of research did not become nearly as widely known outside the small circle of specialists as it deserved. Its publication (1941) was timely, indeed, because it was at this period that Goldschmidt vigorously promoted the viewpoint that geographic variation and isolation were of no evolutionary consequence and had nothing to do with species formation. Miller proved conclusively that geographic races in juncos are incipient species, and show, indeed, such a perfect transition from local race to full species that to this date (1972) there is not yet unanimity among ornithologists as to which group of populations should be considered species and which others subspecies. Miller was quite justified in concluding that "the genus *Junco* contributes a rather complete exemplification of the stages and processes that lead to the first milepost in the evolutionary path, the full species."

His junco work foreshadows much that Miller continued to pursue during the ensuing ten or fifteen years. For instance, when geographic isolates among the juncos secondarily come into contact again, they show a lesser or greater amount of hybridization in this zone of contact regardless of the degree of morphological difference between the two populations. Miller was greatly interested in three aspects of this hybridization. First, to what extent the analysis of the hybrid flocks

sheds light on the amount of genetic divergence that had taken place in the parental population; particularly, which characters would seem to have an oligogenic basis and would show well-defined segregation and what other characters would seem to be polygenic and intergrade gradually. The second question he pursued was to what extent behavioral barriers had arisen during the preceding isolation that would prevent complete interbreeding of the populations. And finally, he was concerned in the role which differences in habitat selection (ecological preference) played in reenforcing the behavioral barriers between incipient species. He successfully reared hybrid juncos in the laboratory and came back to the problem of hybridization again and again in subsequent publications. His student C. G. Sibley, and in turn Sibley's students, have continued to study various aspects of hybridization between natural populations.

In the course of time, Miller became the outstanding authority on the taxonomy of the birds of western North America. Naturally, he was chosen by A. Wetmore to serve on the committee charged with the preparation of the fifth edition of the *Check-List of North American Birds* and to be responsible for the information relating to the birds of western North America. In this capacity, he had to do a great deal of *ad hoc* research, subsequently incorporated in about a dozen supplements to the previous Check-List. He had an even greater share in the *Distributional Check-List of the Birds of Mexico* and he also helped Peters in the *Check-List of Birds of the World*, co-authoring with John Davis the account of the family Mimidae (mockingbirds). All of this entailed painstaking critical work with museum specimens and in the library, and Miller's contribution was always thoroughly sound and completely reliable.

Loye Miller, Alden's father, was one of the pioneers in the study of the paleontology of American birds. It is only

natural that his son should have developed an interest in this formerly so-neglected area of ornithology. Even though birds have more species (8,600 recent species) than any other group of terrestrial vertebrates, they have been much neglected by paleontologists, bird fossils being generally of small size, lacking teeth, and possessing fragile bones. It requires real expertise to identify fossil bird bones, which is the reason that most work on avian paleontology is done by ornithologists. The first of Miller's twenty-seven publications on fossil birds was published when he was twenty-three years old; the last one posthumously. These publications fall rather clearly into two periods. In the earlier, covering the 1930s and early 1940s, he worked on the Tertiary and Pleistocene fauna of western North America. A second period began when he accompanied R. A. Stirton to Australia in 1961. His exciting discoveries of fossil flamingos and ratites in Australia are a major contribution, shared with Stirton. As a good naturalist, Miller was very much interested in the composition of fossil faunas and in the information they gave on the ecological conditions which prevailed at the time of the deposit. His paper on "An Avifauna from the Lower Miocene of South Dakota" (1944) well represents his approach.

From his father, Miller acquired also a considerable interest in anatomy, particularly functional anatomy, reflected in eight papers on the subject. Most of these are of little importance, dealing with such matters as his discovery of a buccal pouch in the Rosy Finch and the vocal apparatus of various species of owls. His most important contribution is a monograph on the structural modifications in the Hawaiian Goose (*Nesochen*), quite rightly called, in the subtitle, "A Study in Adaptive Evolution." This species, quite closely related to the North American Canada Goose, has become sedentary and largely terrestrial. In a superb functional anatomical analysis, Miller shows in how many different ways this

shift in the adaptive zone had affected the skeleton and muscles of the Hawaiian Goose, particularly its locomotory apparatus.

Miller was an enthusiastic field man. Although he did a lot of his research in the laboratory, his heart was in the outdoors. He had thoroughly accepted the Grinnellian view that the animal was part of nature and had to be studied as part of nature. We have no records of how many field trips he undertook with his father and as a student, but the field notebook which he kept after joining the Museum of Vertebrate Zoology contains records on 53 trips between 1930 and 1965. Most of these were undertaken to poorly known areas of California and adjacent states (Oregon, Nevada, Arizona, etc.), but from the 1940s on he visited also Mexico, Panama, Colombia, the Galapagos Islands, Australia, and New Guinea. He did not undertake these trips as a leisurely tourist but devoted every minute to making observations, recording these painstakingly, and adding to his collections. The last specimen collected by Alden Miller, catalogued in the Museum of Vertebrate Zoology, was a song sparrow collected on September 26, 1955, in Mendocino County. This brought the field number for specimens personally collected by him to 12,564. Only he who knows how much work it is to make up a bird skin and how far into the night one has to work to prepare the yield of a successful day will appreciate the significance of this figure. In the 1920s and up to World War II, a graduate student at the Museum of Vertebrate Zoology working for a Ph.D. degree had to take a summer field trip unless he was already an experienced hand. In those days, the end of the semester was a time of great excitement around the Museum, with field parties getting ready to leave for here, there, and everywhere, and envy on the part of the "unchosen" for those lucky enough to be participants. Of late, after the general

direction of the field had changed, the organization of official field parties was largely given up.

Miller himself was a superb field man. All of his students are unanimous in praising the acuity of his senses, his unerring ability to identify birds from even a fraction of song or call note (his outstanding musical ability was no doubt helpful), his determined planning, and his tireless dedication. One anecdote illustrates Miller's mastery in the field. On an overnight field trip to a waterfowl refuge in the Sacramento Valley, while supper was being prepared at dusk an anomalous bird call was heard and Miller said without the slightest hesitation, "Rock Wren." Since this camp, surrounded by tule marshes and ponds, was a totally unsuited locality for a rock inhabitant, the students were quite sure that their professor for once had goofed. Yet, next morning, they found the Rock Wren on a nearby lumber pile. The anecdote illustrates not only Miller's uncanny ability in identifying bird sounds but also his confidence in his ear. When he was sure of what he had heard, he would not say, "Sounds like a Rock Wren," but simply, "Rock Wren," no matter how unlikely the locality.

Seasonal phenomena are one of the most impressive aspects of animal life. Miller shared with other naturalists the excitement produced by William Rowan's discovery of photoperiodicity. This is evident from his review of Rowan's book in 1930 even though his own experimental researches on this problem did not begin until 1945. As an undergraduate at UCLA, he took courses with a well-known endocrinologist, Bennet Allen, who had made significant contributions to the understanding of the relationship between the pituitary body and amphibian pigmentation. Miller served as research assistant to Allen and learned to hypophysectomize amphibian embryos and larvae. He did more such work at Berkeley in Richard M. Eakin's laboratory in 1937, but never published his results. It was not

until Albert Wolfson did a Ph.D. thesis under Miller's guidance, dealing with aspects of photoperiodicity, that Miller himself entered this field. He was particularly concerned with the causation of the so-called "refractory period," a period after the breeding season during which birds fail to respond (with an increase of gonad size) to an increase in day length. The literature was quite confused, and different authors championed essentially three different causations (or various combinations). According to one, the refractory period was due to a specific environmental condition ("decreasing day length"). Miller demonstrated that this could not be correct. Added illumination, even when starting soon after the end of the previous breeding season and continued for almost an entire year, not only failed to induce a gonadal response but even prevented an increase of gonad size at the time when this took place in control birds. Nor could an internal rhythm be the entire answer. By keeping birds under midwinter light conditions for an entire year, he proved that there was a very slight increase (from one to four grams) in testis size owing to the internal rhythm, but nothing like the several hundredfold increase that occurred after added illumination. Obviously then a rather specific inhibition had to be involved.

This still left quite uncertain what cause and target of the inhibition were, a puzzle that Miller also solved. A dramatic response of the testes during the refractory period to treatment with the pituitary hormone gonadotropin demonstrated that refractoriness is an inherent property not of the gonads but rather of the entire hormonal system governed by the pituitary. Miller, furthermore, provided new evidence that different species respond differently with respect to the length and intensity of their refractoriness and that caution is necessary in extrapolating from one species to another. What impressed Miller particularly in this research was the close

correlation between physiological phenomena and the climatic conditions under which each species and, in fact, each local population of each species lived and reproduced. Latitude and degree of migratoriness were accurately reflected in the photo-period response.

Miller's research so far had been done with North Temperate species and populations of the sparrow genus *Zonotrichia*. At this point, Miller had the brilliant idea of investigating the physiological control of breeding seasons at a locality where seasonal variation of day length is at a minimum, that is, directly on the equator. In 1949 and 1950 he began an extended project of studying periodicity in wild birds in Colombia at localities that are no more than  $3\frac{1}{2}^{\circ}$  latitude from the equator. Of ten species that were regularly sampled during three equally spaced periods of a year, eight showed no indication of a breeding season. Some breeding individuals were found in any period that was sampled. This finding corresponded closely to those in other tropical areas. But Miller was not satisfied with this. He asked himself, what happens to a given individual? Up to now his results had reflected the conditions as shown by the average of the species population. In his ensuing research he founded what constituted a new branch of biology, population endocrinology: he followed the endocrine cycle of an entire population of free-living bird individuals.

The planning and execution of the analysis of the breeding cycle in the Andean Sparrow (*Zonotrichia capensis*) is a model of its kind. In the course of a year 160 individuals of this species were captured in a restricted area and individually color-marked. The age of younger birds was determined by plumage condition and examination of the ossification of the skull. The breeding condition of males was determined by examination of testis size through laparotomy. These operations had to be

conducted so skillfully that the birds could be released at once and continue their normal activities. The operations caused no apparent debilitation of the birds, even though some birds were laparotomized three or four times. The results showed that each individual normally goes through two complete cycles each year averaging six months in duration. The breeding condition of males lasts about four months, while the intervening period of regression, rest, and recrudescence of the testes occupies two months. This research was rounded out and brought to completion by bringing a sample of living birds to Berkeley and exposing them to various light regimes, but was finally terminated by Miller's death.

An appreciation of Alden Miller would be incomplete that did not mention his substantial contribution as an academic administrator. The late J. B. S. Haldane always emphasized the benefits of human polymorphism without which our institutions could hardly function. Our universities are excellent testimony for this observation. We have a generous sprinkling of brilliant but often quite irresponsible individuals who do not possess the foggiest notion of how to translate their ideas into action and how to reconcile them with existing institutions. They could not keep a university functioning smoothly, considering that they are far too undisciplined to attend meetings regularly, to know how to draft an agenda, or to chair an orderly meeting. Fortunately, there is also a handful of efficient and selfless individuals at each of our universities who are more interested in the well-being of the university than in the promotion of their own egos. Alden H. Miller was such an individual, and yet, by his actions, he refuted everything that we usually say when slandering university administrators. Miller never sought an administrative career of any kind. In principle, he disliked administrative posts that were not directly connected with his scientific interests, and when accepting

such positions, he insisted on being relieved at the earliest opportunity. Nevertheless, he was unanimously praised as an excellent administrator. He saw his own involvement in the governance of the university, and that of his colleagues, as the logical and necessary extension of that faculty self-government of which Berkeley had always been proud. The epitome of this attitude is that if you are asked to perform a service, to fill an office, or to chair a committee, you have the responsibility to do so unless the task is physically impossible or is so extraneous to your experience that you honestly believe you could not discharge it properly.

Miller's full involvement with academic duties started in 1950, and in the last fifteen years of his life he served on no less than thirty committees of the University of California, of seven of which he was chairman. This service included committees on the college, campus, and state level. In the College of Letters and Science, he was Vice Chairman of the College Faculty and Chairman of its Executive Committee in 1961-1962. He was Chairman of the Budget Committee from 1957 to 1961. When Chancellor Glenn Seaborg went to Washington to head the AEC and Vice Chancellor for Academic Affairs Strong moved up, Miller became Vice Chancellor of Academic Affairs, 1961-1962 and 1963-1964. He served on promotion, curriculum, research, and publication committees. Yet, he steadfastly refused administrative appointments that would have made the continuation of his research career impossible.

By inclination Miller was conservative rather than a great innovator. His contribution to administrative matters, in addition to his efficiency and integrity, was that he could analyze situations objectively, determine what was feasible and what was not, and provide a necessary balance to "weigh out" new ideas. His spirit of dedication was never more evident than at the time of crisis in the Department of Paleontology

(such as occurs so often in university departments), and the only solution seemed to be the dissolution of the department and reassignment of its faculty. Miller volunteered at this stage to assume acting chairmanship of the department for a year because he felt that the department was serving a useful purpose and should be continued. He soon worked out the source of the difficulties, proposed the needed actions, and turned a viable department back to the university at the end of his term. This was all done in a pure spirit of public service, since Miller himself derived no benefits from the assignment. Indeed, some of his associates have questioned whether he did not go too far in fulfilling this and other services to the community, since there was no doubt that he was constantly overburdened with administrative chores. There is, indeed, some evidence that his leadership as Director of the Museum of Vertebrate Zoology suffered from the harassment of his many-sided academic duties. There is much to indicate that his fatal heart condition might well have been brought about by these stresses.

It must not be forgotten that his work for the university was only one of his many administrative loads. Miller was very active in several of the national ornithological organizations, such as the Cooper Ornithological Society and the American Ornithologists' Union, and he served these organizations on their councils, as an officer, and in numerous other ways. He was President of the American Ornithologists' Union from 1953 to 1955 and Chairman of its Check-List Committee at the time of his death. From 1939 on, he served as the editor of *The Condor* and raised its standards to such a level of excellence that it was considered by many to be America's leading ornithological journal. Here again he displayed the virtues of unselfishness, conscientiousness, and integrity that distinguished all of his activities. One of his as-

sociates remembers that when they arrived late in the evening in Los Angeles after a tiring drive from Berkeley, Miller did not go to bed as his companion did but started editing proof of the current issue of *The Condor* and kept at it until nearly midnight. If he had not driven himself like this, the issue might have been late! Except for the German *Journal für Ornithologie*, all ornithological journals of that period were essentially devoted to faunistics and taxonomy. Miller sponsored a policy, by no means approved by the old-timers, to include manuscripts on experimental researches and to shift the balance from faunistics and systematics to ecology, physiology, and behavior. At one stage the new policies resulted in an actual rebellion of some of the older bird watching-avicultural members which required prompt and decisive action by Miller to prevent a dissolution of the Cooper Ornithological Society. It was a great source of satisfaction to him that in a subsequent vote his action was endorsed by about 98 percent of the membership.

His reputation as a person of efficiency and integrity and his ability as a troubleshooter resulted in his election as President of the International Commission for Zoological Nomenclature, a well-known hotbed of dissension. He had just started to exercise his talents in this new office when he was suddenly taken away.

Various ornithological societies honored him by election to offices and honorary memberships. In 1943 he was awarded the Brewster Medal of the American Ornithologists' Union, and his election to the National Academy of Sciences came in 1957.

In his personality and character, he displayed the usual contradictions. For instance, self-confidence and shyness would seem to be incompatible traits. Yet, what Miller wrote of his own teacher, Joseph Grinnell, was quite literally true of

himself also: "His self-confidence was not much revealed in public. An innate reserve and shyness and a distain for ostentation [concealed it]." Miller kept his feelings to himself, to such an extent that he appeared cold to those who did not really know him well. Yet, the example he set through his complete integrity and fairness, through the high standards he demanded, through his own hard work and his many-sided achievements, evoked a good deal of hero worship among his students. Even where they disagreed with him in certain scientific interpretations, they admired him as a human being and emulated him in many ways. He was dedicated to his family, but there were only a few of his students and colleagues who considered Miller a close personal friend. He had a quiet, almost shy humor, largely unknown except to his closest associates.

Whether it was hero worship for his father and for his teacher, Joseph Grinnell, or an innate tendency, there is no doubt that Miller was strongly inclined to be conservative. This tendency affected his judgment with respect to the strategy of scientific publishing, policy formation in the Museum of Vertebrate Zoology, planning of research, or other issues. He was never rude to anyone; indeed, an unflinching courtesy was one of his characteristic traits. He avoided arguments and unpleasantness as much as he possibly could, but when a conflict became inevitable, as happened two or three times in his life, he fought the issue with determination to a conclusive end. As he grew older, his personality became increasingly warmer. Quite evidently his former insecurity abated when he had proved himself so eminently successful in his chosen fields of endeavor.

Perhaps Miller's outstanding character trait was his tremendous drive to do research and fulfill his professional obligations. He would let nothing else interfere with these

aims. His capacity to organize work and make every minute count was quite extraordinary and was carried out without any fanfare. He always kept some minor tasks on his desk (such as proof to be read) to be done in the few minutes between appointments. His ability to compartmentalize was almost proverbial. A few minutes after a very emotional and controversial meeting had broken up, one might find Miller calmly working on a manuscript.

He was quite Spartan in his ability to endure privations and physical pain without a word of complaint. Some fifteen years before his death he had an extremely painful bone condition in his foot, later corrected by surgery, but this did not prevent him from continuing in his daily routine. And although he limped badly and sometimes had to use a cane, he even went on a field trip to Mexico with some associates. As one of them wrote me, "His foot hurt like hell, but he hobbled around, putting up his 15 bird skins a day without complaint. On one occasion, he got out of the Museum truck and put the sore foot right into a squirrel hole, twisting it badly. He righted himself, said 'Damn!' and stomped off."

On his field trips, he was able to do with a minimum of comfort and it was lucky that his wife was equally able to cope with such an austere life. Indeed, much of the credit for the achievements of his collecting trips should go to her, for she was at his side in the field as often as possible, and always after the children were grown. Whether it was in the rain forests of Colombia or in the fly-infested desert of Central Australia, she served as a field assistant, doing her share in preparing specimens and taking care of the camp chores, always cheerful even under the most adverse conditions. The Millers were often teased because they went camping as if they were gypsies, with virtually no equipment except for sleeping bags, a food box, and a couple of old car-spring

leaves to be used as fire irons over a camp fire. As his wife wrote, "Alden never complained about heat, cold, flies, or any physical discomfort, and by his example, taught me and all the children not to complain but to accept things as they are."

Miller had a considerable impact on American science. He exercised his influence in three capacities, as a scientist (through his published work), as an academic administrator, and as an educator, in the broadest sense of this word. He, more than anyone else, was responsible for the transformation of American ornithology from what might be called "glorified bird watching" to a legitimate branch of biology. He and his students were interested not only in birds as such but also in birds as suitable material for the study of challenging biological problems. By the breadth and quality of his work, he set new standards of excellence which have had a lasting impact. Berkeley became the training center of students to be raised in this new image of ornithology, "The MVZ School of Ornithology" as it was often called. No less than thirty-one graduate students took their Ph.D. degree with him, and in view of the fact that so many of them now occupy prominent positions in American universities, it would seem worthwhile to list them in the chronological order of their degree: T. H. Eaton, Jr. (1933), W. L. Engels (1937), E. T. Hooper (1939), F. Richardson (1939), F. H. Test (1940), H. I. Fisher (1942), A. Wolfson (1942), C. A. Reed (1943), A. S. Leopold (1944), F. A. Pitelka (1946), J. T. Marshall, Jr. (1948), C. G. Sibley (1948), R. W. Storer (1949), C. B. Koford (1950), J. Davis (1950), T. R. Howell (1951), G. W. Salt (1951), K. L. Dixon (1953), T. L. Rodgers (1953), D. E. Bowers (1954), D. W. Johnston (1954), R. A. Norris (1954), R. F. Johnston (1955), R. K. Selander (1956), R. I. Bowman (1957), J. Mary Taylor (1959), R. C. Banks (1961),

G. F. Fisler (1961), N. K. Johnson (1961), R. B. Payne (1965), and E. O. Willis (1965). Miller was always available for consultation if the student wanted to discuss his thesis with him, but he left it up to the student to take the initiative. He felt that the student would learn more if he had to find his own way than if the professor supervised him at every step. The great variety of thesis projects indicates how much freedom he gave to his students. The lack of domination is also indicated by how rarely Miller appears as a co-author in any of the papers done by students. Virtually the only exceptions are where he employed students as research assistants in his own research. He had a way of encouraging his students when they were doing well. His great innate courtesy expressed itself in the fact that he seemed to lean over backwards to avoid being critical. He thought the student could learn most by watching others at work, and this is one of the reasons why he set such an outstanding example of dedicated work and efficiency.

Miller was only thirty-four years old when, in 1940, he took over the directorship of the Museum of Vertebrate Zoology after the premature death of Joseph Grinnell. He served as the director of this important university museum for a period of twenty-six years. In spite of certain innovations, it is evident that Miller considered it his task to maintain the Grinnellian tradition. Field work remained the key activity. The delimitation of biotic districts and the determination of intraspecific geographic variation were considered major tasks. He deviated from tradition in one respect, by enlarging the geographic framework beyond the western states to include Mexico and South America and eventually even the Australian region. Also his interests were broader than those of Grinnell, as indicated not only by his work in paleontology and anatomy but particularly by his research in reproductive

physiology. Indeed, he felt that an ornithologist should be interested in all biological aspects of birds, rather than becoming a narrow specialist. Consequently he frowned on the idea of establishing a separate physiological and behavior group in the Museum. With the Grinnellian tradition so well established, he considered it his role as director to serve as chief administrator rather than as team leader. Combined with his conservatism, all this tended to favor the status quo. This tendency was reenforced by the Museum's appointment policy. As long as the emphasis of the research in the Museum was on California, it seemed natural that positions should be filled by young vertebrate biologists trained in California, preferably in the Museum itself. The result was extreme inbreeding of the staff of the Museum (and of the attached Hastings Reservation). Seth Benson, Frank Pitelka, Starker Leopold, Ned Johnson, Jean Linsdale, and John Davis were all home products. This did not encourage pioneering in new directions.

Whether it was because Miller was conservative by nature or whether it was his great sense of loyalty to Joseph Grinnell, the fact is that Miller continued many of the old traditions of the Grinnell School long after the law of diminishing returns had taken its toll. His determination to continue collecting trips and the publication of faunistic reports were symptoms of his attitude. The fact of the matter is that developments in evolutionary biology were faster than the changes in Miller himself. Science thrives on breakthroughs and controversies. When the battle over the cause of evolution was won, when the polytypic species had been adopted by vertebrate taxonomists, when the role of the environment as chief factor of selection had been universally acknowledged, a change in the interests of students occurred. They lost interest in field trips, and recruitment into verte-

brate zoology became more difficult. The excitement of the 1930s and 1940s in the new systematics, culminating in a crop of nine Ph.D.'s in the Museum of Vertebrate Zoology in the early 1950s, declined quite noticeably. By this time, Miller's own energy and attention were largely occupied with his crushing burden of academic administration, and the criticism that the Museum no longer had the aura of excitement of former decades was heard increasingly often. Perhaps it is asking too much that one center should display continuous leadership, particularly after some of its outstanding students had established flourishing new centers at other universities. This is a familiar phenomenon in academic life.

By inclination and as a follower of Grinnell, Miller was committed to the inductive method. Yet, it is not altogether true, as has sometimes been stated, that he was uninterested in generalizations. Not only is an appreciable section of his junco monograph devoted to generalizations but Miller published six smaller essays which deal with generalizations and theoretical issues. Each of them is still worth reading and some of them had a considerable impact when first published, such as that on habitat selection (1942), on population size in birds (1947), on the role of key adjustments in the origin of higher taxa (1950), and on the role of ecological factors in the rate of speciation (1956). Nevertheless, Miller was more of a particularist than a synthesizer. He never published a major book dealing with any of the topics with which he was most familiar. This is why he was best known to those who worked in the same field and with the same material. It is unquestionably in ornithology that he had his greatest impact and where his loss is felt most acutely.

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## KEY TO ABBREVIATIONS

Audubon Mag. = Audubon Magazine

J. Mammal. = Journal of Mammalogy

Proc. Biol. Soc. Wash. = Proceedings of the Biological Society of Washington

Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences

Record S. Australian Mus. = Record of the South Australian Museum

Univ. Calif. Publ. Geol. Sci. = University of California Publications in Geological Sciences

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