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WARDER ALLEE

1885—1955

A Biographical Memoir by

KARL PATTERSON SCHMIDT

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W. E. Allee

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THE APPALACHIAN FOREST, which once extended almost unbroken from New England to the Gulf of Mexico and westward to meet the sea of prairie in Illinois, remains one of the great forest regions of the world. This woodland dates from the Cretaceous age, when it was the home of towering dinosaurs and spanned the lands of the northern hemisphere. Some of its most conspicuous forest giants document that vast former reach, for sweet and sour gums, the tulip tree, the hickories, and the sassafras, which seem to us so distinctively eastern American, are to be found also in eastern Asia, and may be quite as distinctively Chinese. This mainly temperate forest has aspects of the tropical jungle, and often well represents the popular concept of "jungle," especially in the southern United States, where gigantic grapevines are the lianas that hang from the interlacing treetop canopy. The trunks of the trees are clothed with Virginia creeper and poison ivy, and bittersweet and cat brier form an almost impenetrable tangle in the undergrowth.

In such a forest there has been an evolution of complexity, combined with an almost unbelievable stability, through geologic ages; and such a forest exemplifies a kind of independent manifestation of life, at a level beyond that of individual, population, or species. Communities of plants and animals on so vast a scale presented to the maturing sciences of botany and zoology the kinds of problems that required for their attack and solution the establishment of ecology as an independent biological subscience. The forest had

challenged its European explorers to wrest it from the Indians; it had challenged the pioneers to create farms within it; and there remained for the present century the challenge to science to study it and to attempt the resolution of the all but inextricably tangled web of interrelations between living organisms and their physical environments, between plants and animals, and between plant and plant and animal and animal.

A remnant of that great eastern forest is preserved to this day on the Indiana farm on which Warder Clyde Allee was born. That remnant of original woodland charmed him as a boy and remained a special concern to the end of his life. Against the backdrop of the vast unresolved complex of the life of the Appalachian forest, Clyde Allee became one of the great pioneers of American ecology. That he could himself make only preliminary studies of the forest community was a concomitant of an internal personal environment molded by a series of tragic psychological and physical events.

His conquest of physical handicaps and his grim fortitude in facing personal tragedy relieve an otherwise almost unbearably saddening story. Calamities pouring in succession upon the head of a man of profound good-will recall only too evidently the theme of the Book of Job. His life was long. Throughout good and ill fortune we discern the helping hands of the "eternal womanly" that contributed to a radiant triumph of the human spirit. Throughout, the story discloses the thread of the personal salvation that comes through joining in that highest of human endeavors, the unending quest for truth.

Warder Clyde Allee was born on June 5, 1885, on a farm near Bloomingdale, Indiana. His father, John Wesley Allee, with names in his ancestry like Reed, Parkhurst, Warner, and Wesley, had been orphaned as a child, and grew up at the homes of various relatives in the Bloomingdale region. He was a Methodist, and joined the Society of Friends to marry Mary Emily Newlin, whose Quaker ancestry extended back to the seventeenth century in England and Ireland. The Newlin forebears formed a part of the

notable emigration of Quakers from the slaveholding southeastern states to the region north of the Ohio, an emigration that began in the late seventeen-hundreds and continued to the eve of the Civil War. It was this movement that established the Society of Friends in the southern half of Indiana, and provided the drive and the resources to establish a series of Quaker academies (preceding the era of the public high school), and to found Earlham College as a middle western counterpart of the eastern Quaker institutions of learning.

Clyde Allee attended a one-room country school, taught during several years by Mrs. Florence Rawlins Chapman, who was both teacher and friend of the family. Clyde led his class in scholarship, in spite of occasional interruptions for farm work. At Bloomingdale Academy he was again at the head of his graduating class and the winner of the oratorical contest. After his graduation, at the age of seventeen, he taught country school for a year and then the fifth and sixth grades in the Bloomingdale elementary school for another year. Then, at nineteen, he was drawn to Earlham College. This course of events was in wholly natural sequence, for the various Quaker academies were kept in extremely close relation with the college by a system of visitation from the Earlham staff for lectures and conferences, supplemented by appearances at the local Meeting House on First Day. At the turn of the century as much as half the graduating class at Bloomingdale Academy might go to Earlham College.

Four years at Earlham provided a sound and broad undergraduate education rounded out by active participation in college football, congenial to his athletic frame. An interest in the general field of biology brought with him from the farm was strengthened and confirmed. Upon his graduation in 1908, under the influence of David Worth Dennis, Professor of Biology at Earlham, Clyde Allee undertook advanced studies at the University of Chicago, where he received the degree of Ph.D., *summa cum laude,* in 1912.

Family background, and the influence of Earlham College, with

Quaker staff and a mainly Quaker student body, served to confirm the Quaker mold in which Clyde Allee was cast. Even more important to his confirmation as a member of the Society of Friends was his marriage to Marjorie Hill, in 1912. Marjorie Hill had been a freshman student at Earlham when Clyde was a senior. She was interested especially in English literature and in writing, and transferred from Earlham to the University of Chicago at the end of her second year to finish her undergraduate work. Her competence as a writer was of the greatest value to her husband in the preparation of his books and scientific papers, for which she served as critic, as unobtrusive collaborator, and on occasion as joint author. In later years she established herself in her own right as an authoress, with a notable series of novels for girls.

During the last two years of graduate work at the University of Chicago, under Victor E. Shelford, Clyde Allee began (or resumed) his teaching career, as Assistant in the Department of Zoology. In the ten years after receiving his degree, his teaching experience was expanded into a firm foundation for his subsequent thirty years' continuous tenure at Chicago, 1921-1950. In 1912-1913 he was Instructor in Botany at the University of Illinois in Urbana; in 1913-1914 he was Instructor in Zoology at Williams College, in western Massachusetts; in 1914-1915 he was Assistant Professor of Zoology at the University of Oklahoma; and then for six years he served as Professor of Biology at Lake Forest College, north of Chicago, where he followed James G. Needham and Cornelius Betten. The foundations of my own long friendship with the Allees were laid at Lake Forest in their close relations with my father (Professor of German in the college) and with my younger brother F. J. W. Schmidt, who was later to become an ecologist in his own right in the quite different environment of the University of Wisconsin. I had at this time followed James G. Needham to Cornell University; but when the Allees returned to the University of Chicago in 1921 and I came to the Field Museum of Natural History in 1922, there was a long history of family friendship on which to build our own.

One of the most significant of the influences that molded Clyde Allee's interests and his research career grew out of the departmental relations at the University of Chicago. Frank R. Lillie, long head of the Department of Zoology at the University, was one of the founders of the Marine Biological Laboratory at Woods Hole, Massachusetts. Under the Lillie influence, from his graduate years on, Clyde spent summer after summer at that great research center (Summer Instructor, 1914-1921, Director, Invertebrate Course, 1918-1921; Trustee from 1932 to his death).

Subtle influences from the older culture of the Hill home in southern Indiana were gently and harmoniously infused into the Allee household when the family came to the University of Chicago. That household was long graced by Marjorie's mother, Anna Mary Hill, one of those women who grow more beautiful year by year. A son and two daughters were born—Warder Clyde, Junior, in 1913, Barbara Hill in 1918, and Mary Newlin in 1925. When help was needed, it was drawn either from the student body or from refugees in whom the Quakers had a concern. Those thus engaged immediately became family friends, envied by their fellows. The book-lined walls at home were matched at Clyde's office by his vast array of biological books and pamphlets. Instead of contrasting, the two collections served to emphasize the unity of literature and science. The unobtrusive but undisguised relation to the Society of Friends provided a spiritual and religious background for two distinguished personalities in a distinguished home. Homes like that of the Allees form one of the most significant of the educational influences at every university; they reach into the classroom and to the campus to mold the hearts and the fundamental attitudes of mind of the generations of students who come into them.

Clyde Allee's teaching was so intimately related to his research that to give an account of his researches and of the books and papers that embody its results is to give some account also of his teaching. Of 181 research papers, reviews, and popular articles, 70 were in joint authorship with students or colleagues; he joined with

colleagues in writing several of his books, ending with the massive *Principles of Animal Ecology* with five authors. He clearly made a conscious effort to exemplify in man, at the university level, the principle of cooperation among animals.

The research papers begin modestly in 1911, while he was still a graduate student, with "Seasonal Succession in Old Forest Ponds," a plainly ecological topic; there is then a long run of reports on the reactions of the isopod *Asellus* to currents, with experiments modified, significantly enough, as to chemical and physical and social factors. These papers exhibit the influence of Vicor E. Shelford, under whom he had taken the doctoral degree in the field of ecology. They reflect also the focus upon ecological succession at the University of Chicago resulting from the pioneer studies of H. C. Cowles on the history of the plant formations in the near-by Indiana dunes region, at the southern end of Lake Michigan.

A contrasting area of profound ecological interest had opened up to Allee at the Atlantic seashore. As director of the invertebrate course at the Marine Biological Laboratory (1918-1921) he was thrown, at an early stage in his career, into intimate contact with the patterns of distribution of marine animals, and with the problems these patterns present. The facilities for experimentation at Woods Hole made possible the laboratory study of such problems. This made him in the best sense an experimental ecologist, subjecting the situations found in nature to experimental analysis and verifying clues from the laboratory in the vast evolutionary panorama presented in marine life. He thus became familiar with the organized and often sharply distinctive biotic communities in the sea. Their existence as social entities made a profound impression upon his still expanding mind, and prepared him for immediate and for long subsequent research.

With these varied interests, with a broad geographic acquaintance with North America, and with his establishment in the congenial environment of the University of Chicago, Warder Clyde Allee was on the threshold of his mature career as a productive scholar

in 1922. Then, in 1923, came the first of the tragic family calamities in the Allee history. The accidental death of the ten-year-old son, in a street accident, on his way to school with his younger sister, struck a mind-rocking blow to both father and mother. The boy, named for his father, was a charming child, whose combination of strong physique and brilliant and active mind forecast a useful life and gave hope of a happy one. The psychological blow fell hardest on the mother. She had been radiantly happy in her family; she now withdrew into herself: "To comforters she lent an ear apart, while pain sat ever closer to her heart." For some years her husband's major preoccupation was to comfort and strengthen her, almost to the exclusion of time for his own grief, second only to hers, if indeed less.

Now, more than ever, it was essential that the Allee undertakings should be joint ones, and that these should be of attention-commanding interest. A major diversion of both minds from their internal grief-fixation was presented by the opportunity to spend the winter of the year 1924 at the Barro Colorado Island Laboratory in the Panama Canal Zone. This experience with the tropical rain forest added a third dimension to Clyde's ecological background. Making his own ladder of iron spikes driven into the trunk of a forest giant, he was one of the first to climb to the tree-top canopy, and to engage in actual measurement of its environmental factors. This was long before the importance of the tree-top mosquitoes to the transmission of malaria and jungle yellow fever was recognized. It was thus also before the modern facilitation of such studies in the Guianas, in Trinidad, and in Colombia. Scientific papers about the Panama forest were written; more profoundly important was a little popular book about their experience, *Jungle Island,* written in the joint effort of Clyde and Marjorie Allee to master their consuming inward grief, and to turn outward and forward again. They returned to Chicago as changed but still profoundly sane members of the University circle.

A special phase of the Allee researches was inaugurated in 1923

by a little paper in the *Condor:* "Animal Aggregations. A request for Information." The experimental approach to the analysis of the causes that produced the phenomena of aggregation and to the study of the resulting effects upon the animals involved was already familiar. The new researches grew directly out of the early series of experiments with *Asellus,* the little crustacean found in the local fresh waters. By 1926 a long series of research papers under the general title *Animal Aggregation* had begun to appear; it continued as the main field of his own and of directed student research long after the appearance of his book, *Animal Aggregations,* in 1931. In brief, the principal results of this research program were the repeated and conclusive demonstration that there is an unconscious need for the presence of fellow individuals in many species among the lower animals, and in most of the higher; that there is, in effect, a deleterious effect from *under-crowding* as well as the more familiar one from *over-crowding.* The phenomenon of a better group-survival, as contrasted with individual survival, was tested against such artificial environmental factors as poisons, and against unfavorable natural factors such as oxygen or carbon dioxide deficiency. More important was the demonstration of the reality of an unconscious cooperation, which he referred to as *proto-cooperation,* in a wide diversity of animal forms. The further insight that *proto-cooperation* supplies the natural foundation for both unconscious and conscious cooperation among the higher animals, in their various levels of social and community organization, led to the next segment of the Allee research program.

Early in 1930 the first indications of a most disturbing paralysis of the lower limbs began to appear. The paralysis increased, and was diagnosed as a spinal tumor, one of those strange unpredictable embryonic inclusions to which the human body is in relatively rare cases subject. The problem was faced, and an operation was performed by the great neurosurgeon Dr. Percival Bailey. The second and third thoracic vertebrae, high in the spine, were sawn through, the spinal cord laid open, and the offending cells, so far

as possible, removed. Recovery was rapid, and Clyde Allee could resume his teaching and research; but only to have the too-familiar symptoms recur, so that by 1933 a second excision of the tumor was required. The prognosis of recovery from a second such operation is frighteningly small, but this hazard was again faced without hesitation. Then, after a second recovery, the tumor again slowly returned. Five years after the second operation, in March, 1938, conference with Dr. Bailey resulted in the decision to operate again, and this time to hesitate at nothing to remove the last trace of the offending tissue. The operation was again successful; the patient lived; but the damage to the thrice-operated spinal cord was permanent. For the rest of his life, Clyde Allee was confined to a wheel chair except as he learned to swing himself by his powerful arms from chair to car seat and from car seat to chair, or when (as often) he was carried over the shoulder by his student-attendant. The physical problems that face a man with lower abdomen and legs completely paralyzed are grave. Some hours of care were required every day to prepare the body of this undaunted teacher and researcher for the day's lectures, student conferences, committee meetings, discussion of departmental problems with colleagues, editorial work, and the occasional doctoral examination. It was characteristic that Clyde Allee refused to accept any consideration of his disability. He was particularly valued as a committee chairman, for he neither forced the proceedings nor let them drag. He carried a full teaching load, met every class, and continued to direct the research of devoted students.

The financial burden of the operations, each requiring months in the hospital, was providentially met by the success of Marjorie Allee's books for girls. There was romantic history in her Quaker background, and her intimate knowledge of the summer life at Woods Hole and the Indiana dunes, and of the University campus during the school year, afforded excellent and often novel background material, often enough with her husband (uncrippled in her imagination) as one of the older characters in the adventures of

a succession of children, teen-agers, and young women. Her version of a child's-eye view of the summer colony of professors and students at the great Marine Biological Laboratory was a notable success among the Woods Hole wives and mothers, not to mention fathers. The work of composition was an essential diversion from the overhanging shadow of the peril of the successive operations.

Studies of social organization by observation and experiment grew naturally enough out of the aggregation studies. The first title in this new research program, in 1934, was "The Social Order in Flocks of the Common Chicken and the Pigeon." With a strong overlap of studies from the previous period, it is the words *behavior* and *group behavior, social order* and *social organization,* and *leadership* and *dominance* that give the clues to the nature of the individual studies in this field. These lent themselves to the kind of professor-student relationship that became especially necessary, under the new physical handicap of the wheel chair.

For the distinguished series of Norman Wait Harris Lectures at Northwestern University in 1937 Professor Allee had to be carried to the stage by students. Once in his chair, as elsewhere, he was completely oblivious of his disability, and his audience became equally oblivious. The preparation of the lectures was a fortunate circumstance, for it forced him to put together into simple form the results of a quarter-century of active research. The chapter headings of the resulting book, *The Social Life of Animals,* outline this research, and again contain the seeds of the thoughts that dominated much of his later writing: I. Science versus metaphysics; II. History and natural history; III. Beginnings of cooperation; IV. Aggregations of higher animals; V. Group behavior; VI. Group organization; VII. Some human implications; VIII. Social transitions.

An illuminating light is thrown on this grafting of the interest in dominance and leadership upon the older one of the evolution of cooperation by Allee's statement in the 1952 paper "Dominance

and Hierarchy in Societies of Vertebrates." He writes:

"My reasons for working with social hierarchies came in part from my immediate amusement about certain superficial similarities between the peck-order in flocks of hens as described by Schjelderup-Ebbe and some human social hierarchies in which I was enmeshed, certain college faculties in the U. S. A., for example. Also, in research work at that time, we had been finding a large number of instances of apparent proto-cooperation, the existence of some of which had been overlooked or even denied by apparently competent investigators. I had been led by new evidence and by neglected reports in the literature to the conclusion that there is a basic far-reaching principle of cooperative tendencies underlying all group biology and forming a basis for general sociology. There was a possibility that we might be misjudging the evidence, and a probability that we needed to study other aspects of group biology. Hence we added to our program the study of aggressive behavior with particular respect to the active investigation of social hierarchies in non-human animals."

The synthesis of information in a given field into handbooks and larger treatises becomes a necessary outgrowth of research. Books and research papers and symposia, discussions of them, and first coordinations of their results crowd upon us, and it is essential to prepare the base from which new research, in new and fruitful directions, can be launched. *Animal Life and Social Growth* (1932) was such a synthesis of Clyde's own work and of his own thinking. Another handbook, *Ecological Animal Geography,* had meanwhile been growing as a joint product of the partnership between Clyde and myself.

When I came to the then Field Museum of Natural History in 1922, the improvement and more formal organization of relations between the Museum and the University became a subject of interest to the two of us. When I approached Clyde as to the advisability, for myself, of taking a Ph.D. degree, our conversations resulted very much in the vein of William James's *The Ph.D.*

Octopus. We agreed that with firm tenure at the Museum, and with my own fields of research, quite different from anything then in vogue at the University of Chicago, I might better continue and expand my interest in the field of animal geography, as a natural outgrowth of my more special investigations of the distribution of reptiles. Professor Allee could not bring himself to recommend that I drop my preoccupation with the natural history of amphibians and reptiles and turn to the cutting up of flatworms to investigate the axial gradient, then one of the major preoccupations of the Department of Zoology at the University of Chicago under the regime of C. M. Child. With Dr. Allee's encouragement, I undertook, instead, the writing of a book on animal geography, envisaging something after the pattern of the works of Alfred Russel Wallace.

By 1925 I was actively engaged in gathering material for the projected book, when I encountered *Tiergeographie auf oekologischer Grundlage* by Richard Hesse, Professor of Zoology at the University of Berlin, which had appeared the year before. Hesse's point of view was radically different from that of zoogeographers of the older tradition; it was strictly ecological, and thus especially congenial to Clyde Allee. As a means of facilitating discussion of Hesse's text with him, I took to translating first one chapter and then another. Our discussions stimulated further translation, and the book went with me on a zoological expedition to South America in 1926. Two years later, on an expedition through the South Seas in Mr. Cornelius Crane's sailing yacht *Illyria,* with ample leisure for the first time available, I finished the long section on marine life. When I returned there was so little left to convert into English that the possibility of completion of the work came in sight. Professor Hesse had agreed to a revised American edition, and with this clear signal to go ahead we hastened our preparation of the text. We arranged for publication by an Illinois publisher, but to our dismay, after a fruitless two years of negotiation we discovered that our publisher would be unable to comply with

the terms of the agreement. We sadly canceled the contract. Then, to our great astonishment, we discovered that our revision had not been at all adequate, that many sentences remained in the inverted German style, and that there were still such traces of Lamarckism as would produce more than raised eyebrows among our colleagues. We felt that the failure of publication had been an extremely fortunate circumstance. By 1935 Clyde Allee had entered his long wheel-chair regime; again we sat across a table in his office, tore our manuscript to bits, and put it together again. It was much improved, and this time was placed in the competent hands of John Wiley and Sons, who brought out an American edition under the title *Ecological Animal Geography* in 1937. The book was by this time essentially our own work, but we took pleasure in retaining Richard Hesse as the senior author, by way of emphasizing his pioneer work in the field. My own book had long been lost sight of in the joint labor of producing *Ecological Animal Geography*. It was an extraordinarily agreeable occupation to us to examine in such detail a text of mutual interest, to subject it to the crossfire of critique from our quite diverse backgrounds, and to find that we could incorporate Clyde's data and views from the laboratory with mine from wide travels in the tropics. A final chapter in this history of an ecological book, prepared primarily as a service to our colleagues, was the welcome opportunity to sit again across the table in 1950 and again subject *Ecological Animal Geography* to a genuinely joint revision, for its second American edition (1951). This was much further altered from the German original; I have some reason to envisage a second German edition based on a back-translation from the latest American version.

Our joint work spanned the years from 1924 to 1937; it had begun when we could still plan joint field studies in the tropics. In mid-course, when I returned from the Pacific Islands, we had hoped for a visit to the Galapagos Islands together. At the end Clyde Allee was confined to his wheel chair and was facing the desperate gamble of the third operation on his spinal cord.

Learning to live in and from a wheel chair, Clyde had to adjust his research interests to that profoundly far-reaching circumscription. Research turned to experimentation of *Arbacia* and other invertebrates at Woods Hole, and the more important program at Chicago was more and more devoted to social organizations, and to the experimental modification of dominances and hierarchies in hens and mice at the Whitman Laboratory of Experimental Zoology.

As student and colleague of Victor E. Shelford, Clyde Allee could not entirely escape the oblique criticism of William Morton Wheeler anent the "silo and saleratus belt" ecologists, those Middle Western zoologists and botanists whose primary concern seemed to be with the physical environment, who occasionally joked among themselves about alternative careers as plumbers. Apparatus was an important interest in the early stages of the Allee research program. With the turn to the investigation of group physiology and the phenomena of aggregation, this aspect of his studies became chemical rather than physical, and then behavioral rather than physicochemical. In the end he was obviously interested in principles rather than in practice.

A second synthetic work, in which cooperation of a group of authors was to become a major feature, was already in the offing. The first title in the Allee bibliography for 1939 is "Concerning Ecological Principles," a four-page statement in *Science* by himself and his colleague Thomas Park. This had already been presented to the "Ecology Group," and a digression is in order to explain what the Ecology Group was (and still is). During the years at Chicago, the custom had grown up for a meeting of the Ecology Seminar as a biweekly Monday evening event. The group was composed of members of the staff of the Department of Zoology; all interested students, many of whom were engaged in ecological research; and invited persons from other departments and from near-by institutions, like myself from the Natural History Museum, and Orlando Park, of Northwestern University. The dedication

of *The Social Life of Animals* (1938) reads: "This book is gratefully dedicated to the past and present members of our 'Ecology Group'; without their enthusiastic co-operation much of the underlying evidence could not have been collected during my lifetime, and without their critical attention the expression of these ideas would have been more faulty." The Ecology Group usually met in the Allee home; books and scientific publications of current interest were reviewed, current research was presented, often in preliminary form, for discussion and criticism, and the chapters of books in progress often provided series of programs. There was formal discussion, followed by refreshments and further informal discussion. The Ecology Group is of course in the familiar pattern of student groups in every field and at every university, varying only in detail from institution to institution.

Ecological principles became the preoccupation of Clyde Allee and Tom Park, and others were soon drawn in—Alfred E. Emerson and Ralph Buchsbaum, from the same department, Professor Orlando Park, of Northwestern University, one of Dr. Allee's distinguished former students, and myself, the least academic member of the group. Regular meetings of the authors began as early as May, 1939. The contract for a book was signed with the W. B. Saunders Company, of Philadelphia, in 1942. This was under the dynamic though tactful prodding of John A. Behnke, then connected with the Saunders firm. The title of the book was to be *Principles of Animal Ecology,* and Clyde Allee had agreed to continue the leadership in the project and the chairmanship of our meetings. Ralph Buchsbaum withdrew from the group on account of army duties in 1943. War or no war, the remaining five continued the composition of the various sections, with scheduled weekly meetings for discussion and rewriting of the manuscript as it accumulated. On account of difficulties presented by our crowded schedules, it became necessary for us to meet on Sundays, when this day was the only one on which we could all meet, there being the special complication that Orlando Park had to come from

Evanston, to the north, while I had to come from Homewood, to the south. The all-day Sunday absences became anathema to our wives. At best, composition and completion of manuscript dragged.

As the work on the book progressed, the interruptions implicit in multiple authorship delayed first one part of it and then another. John Behnke resigned his position with the Saunders Company. We had come to have a very high regard for his editorial ability and for his critical judgment in general, and missed him. Dr. Emerson made a trip to the Belgian Congo to collect and study termites. Thomas Park attended the 13th International Zoological Congress in Paris, and studied and conferred with colleagues in England. I attended the Sixth Pacific Science Congress in New Zealand.

The life of the indispensable leader and chairman was beset by further calamity, the most cruel blow of all—the death of Marjorie Hill Allee in 1945. The depth of Clyde's love for her could be appreciated only by his most intimate circle, and his need of her was inexpressible.

Cared for now by his daughters, when yet scarcely adjusted to the loss of his wife, an extraordinary accident befell him in February, 1946. It was his custom, after being delivered to his home by his student body-servant, and placed in his wheel chair inside the door, to wheel himself rapidly to the rear of the house, whirl the chair about to a right angle, and then, with his powerful arms, run the chair backward onto the platform of a home elevator, by which he could reach his room on the second floor. The elevator, by fixed family habit, was always in readiness for his arrival. On this occasion, the emergency of the arrival of a new student occupant of the attic room had interrupted the routine, and the elevator shaft stood open. Dr. Allee wheeled himself directly into the shaft and fell vertically eight feet, landing squarely on his head on the concrete floor. The crash was heard by the faithful Negro household maid, who called a neighbor and a physician and sent another neighbor in search of the daughters, who were momentarily

out of the house. When they and the physician arrived, their father had somehow been brought to the first floor and was seated on the living room sofa. Miraculously, Clyde Allee was partly but irrationally conscious, and was a difficult and stubborn patient. When the ambulance arrived to take him to the hospital, as the doctor had immediately advised, he quite refused to lie on the stretcher. It was necessary to put him in his familiar wheel chair, and he insisted that he was going to the laboratory for the afternoon's experiments. So, with hat and coat on, and clutching his brief case, the ambulance took him nevertheless to Billings Hospital, where arrangements had been made for his immediate admission. He remained conscious but irrational for some hours, and then lapsed into the coma suitable to a patient with a 180° skull fracture, and was again thought to be dying. His spinal surgeon, Dr. Percival Bailey, had meanwhile been summoned; in a momentary return of consciousness, Clyde remembered Dr. Bailey's firm voice saying, "Place the needle here," and remembered the feeling of confidence that he was in the best of hands as he drifted back into oblivion of pain and of the world.

The needle was inserted into the cavities of the brain, fluid was drawn off, and the pressures were relieved. Clyde Allee again returned to consecutive consciousness. Then he slowly improved, at first with speech painfully slowed, and with large segments of memory and other faculties blocked out; then with gradual further improvement, to the astonishment of friends and surgical staff alike, he recovered. A remark to Alfred Emerson, when his speech was at the rate of only one word at a time, at intervals of several seconds, is on record. Dr. Emerson said to him: "Clyde, I think you are like a cat, with nine lives," and he replied: "Yes . . . and . . . I . . . think . . . I . . . must . . . have . . . used . . . up . . . five . . . of . . . them."

The shock of the accident to the other four co-authors of the *Principles of Animal Ecology* was compounded by concern as to the fate of the work, in which we all had an investment of some

years of effort. Under this stimulus we took up the lagging work with much renewed vigor. The acceleration of our writing was maintained; for while our chairman gradually regained his mental faculties completely, recovery was delayed in some small part of the brain that controlled temper. For the first time in our experience with him, Clyde Allee became driver as well as leader. He would bitterly excoriate any one of us who failed to bring a promised quota of manuscript to the renewed all-day Sunday meetings.

The work on *Principles of Animal Ecology* was finished in 1948 and the book was published late in 1949. It had a favorable reception in the ecological world. Charles Elton, our eminent British colleague, wrote in his review:

"Francis Bacon wrote that 'Some Books are to be Tasted, Others to be Swallowed, and Some Few to be Chewed and Digested.' This book belongs to the last class. It is by far the most important general treatise on the subject that has ever been published, and one which should . . . be in every ecologist's library (whether he be a botanist, zoologist, or general naturalist). To any serious working ecologist, and above all to the teacher on the subject, it is above price. The amount of sheer hard reading and analytical thought and writing that have gone into its making fills one with admiration and respect. . . . Anyone who takes the trouble to master this great treatise will find himself as well educated in animal ecology as anyone can be from a book. . . . I can hardly believe that anyone who really took in the range and depth of what is put into this book could remain narrow-minded."

Some further emphasis of the teaching career of one whose preference among titles was for "Professor" is essential to the present account of the life of Clyde Allee. His teaching began in the one-room country school familiar throughout the United States at the turn of the century. It included high school classes during his undergraduate years, a student assistantship during his graduate studies at the University of Chicago, and then the nine years of undergraduate teaching before he returned to Chicago.

At the University of Chicago he took part in the early survey course "The Nature of the World and of Man"; taught elementary zoology; gave the general course on invertebrates and in field zoology; and then later established his own courses in the fields of his major interests, Animal Aggregation, Animal Geography, and Animal Behavior. He seems to have been a hard taskmaster in both classroom and laboratory. Perhaps the innate character and the external events that made him drive himself made him also a driver of others. Occasionally the qualities that had made him a superb football player in his undergraduate years, and the coach of the winning team in basketball at the Hammond High School in 1908, came to the surface in student and sometimes in departmental relations in Chicago.

It was in the graduate school that his teaching was preeminent. At the research level he made lifelong friends of his students, and displayed more than ordinary interest in their careers after they left the University. This relation was often carried beyond interest to effective aid.

Another long-term segment of the Allee career was his active interest in the professional scientific societies to which he belonged. He was fellow of the American Association for the Advancement of Science, Vice-President in 1942; a member of the American Society of Zoologists, which he served as Secretary from 1918 to 1924, and as President in 1936; a member of the American Society of Naturalists; a member of the Entomological Society of America; and was member or fellow in many other organizations. He was a charter member of the Ecological Society of America, of which he was President in 1929. In this Society, he was influential in the establishment of *Ecological Monographs,* designed for longer papers than could be published in the Society's quarterly *Ecology.* His example of active participation in scientific societies was a further influence on his students, whom he steadily recruited into membership. In later years he was elected to membership

in the American Academy of Arts and Sciences and to the National Academy of Sciences.

One more long-continued activity remains to be mentioned—his nearly twenty years of editorship of *Physiological Zoology*. This journal was founded as an enterprise of the University of Chicago Press in 1928, during the chairmanship of the Department of Zoology of Professor C. M. Child, who served as its first editor. The subject matter envisioned was broad—"The physiological aspects of all fields of zoology"; this meant more particularly the physiology of embryonic and reconstitutional development and of relation to environment in general; physiology of the cell and of protoplasm; physiology of the nervous system and behavior in the stricter sense; hormones and other features of chemical correlation; sex in its physiological aspects; and the physiological phases of genetics. Clyde Allee was a member of the editorial board from the first and became managing editor on the retirement of Professor Child in 1935. He continued this service through 1954; it was perhaps one of the most effective of his contributions to the scholarship of his generation.

Clyde Allee was a profoundly religious person and lived his life within the framework of an organized religious group, the Society of Friends, commonly known as the Quakers. He was brought up in a Quaker home, educated in a Quaker academy, and graduated from a Quaker college. His services to the Friends included active participation in the 57th Street Meeting, in Chicago; and chairmanship of the Chicago office of the American Friends Service Committee. Beyond this, he served as Trustee of Earlham College from 1925 to 1939; when his paralysis became confirmed, and made attendance of the annual meetings difficult, he gave up this congenial duty.

Within the Society of Friends he represented the extreme of liberalism with the minimum of preoccupation with theology. There is no record available of the evolution of the boy's expanding mind as he passed from the naturalist's outlook on the farm and in his

academy days, through the give-and-take of student discussion at Earlham College, and through the maturation of his outlook upon religion as he became a professing and an acknowledged scientist at the University of Chicago. I first knew Clyde Allee when he was 37, much more sure of himself than I, and without visible evidences of the emotional conflict that may result from the impact of the world of science on a religious personality. That Marjorie Hill had aided in that adjustment is evident; that it was complete and forthright appears in his religious confession of faith in 1943, when he was fifty-eight, in the essay "Where Angels Fear to Tread," in which he writes:

"Religion has much to learn from science in objectivity, in willingness and courage to follow evidence fearlessly, and even in judging what constitutes valid evidence. . . . In short, religion can profit by becoming intellectually more sound without losing for a moment its proper emphasis on the deep emotions of man. . . . Religion is ill-served by past and present emphasis on mystical and supernatural improbabilities. To me 'God' is a possibly permissible personification of all the best that the human race has been able to think and do and of all the beauty we have created, together with all the natural beauty we can appreciate. Such a conception transcends tradition and mere emotion and has both power and dignity. . . . Science has much to learn from . . . a religion characterized by unselfish living and honest thinking combined with propaganda of the deed. . . .

"We scientists can profit by a frank admission of our awe and admiration for the pervading beauty of the phenomena we study, the charm of which often escapes us because of our preoccupation with details. We will profit by being less certain that the more unpalatable the interpretation, the closer the approach to truth. . . . Science, and mankind too, will profit by scientists who live closer to the ideals expressed and practised by the more devoted men of science or of religion."

The directions of much of Clyde Allee's research and thought,

especially in his later years, exhibit the impact of his scientific outlook upon his personal religious history. He became preoccupied with the problem of the evolution of human ethics out of the crude struggle for existence, envisaged often in terms of individual combat. He deplored the conclusions of Thomas Henry Huxley and Herbert Spencer, who saw no escape from the inexorable struggle, from a background of nature envisaged as dominated by the values of "the ape and the tiger." In the short step back to Darwin, Allee found the clear recognition of the survival value of *cooperation* in natural selection. His attention was caught by the work, among others, of Espinas, *Des Sociétés Animales* (1877), and by Kropotkin's *Mutual Aid a Factor in Evolution* (1902); and he found congenial colleagues in Alfred E. Emerson, in his own department, and in Ralph W. Gerard, the physiologist. It is not surprising then that he was repeatedly asked to contribute to or take part in such meetings as the Fifth Conference on Science, Philosophy, and Religion (1945), and the Colloques Internationaux du Centre National de la Recherche Scientifique (in Paris, in 1950). For this last, on the subject of the structure and physiology of animal societies, he was accompanied by Alfred Emerson. The opportunity to travel to Europe enabled him to visit his younger daughter, married to Fredrik Barth, a young Norwegian ethnologist in Oslo, surely a happy interlude in his now much too solitary life. The conjunct dedication of a new science building and a new Friends meetinghouse at Earlham College in 1952 was appropriately made the occasion for a week's convocation to discuss "The Contribution of Religion and Science to a Free Society." To this meeting Dr. Allee was invited, and with other distinguished alumni, and it was my privilege to accompany him. Next came the distinction of the John M. Prather Lectures at Harvard University, in 1953, where his subjects were again proto-cooperation among lower animals and social hierarchies among the higher.

As the age of 65 and retirement from his professorship approached, Dr. Allee had some hope of persuading the authorities that his case

should have individual consideration, with extension of his tenure as long as he might be able to carry his full load of teaching and research. When this proved impracticable, retirement was accepted as a kind of challenge. He had been offered the head professorship of the Department of Biology at the University of Florida at Gainesville, and he at once accepted. There were personnel problems in the Florida situation within the staff of twenty-one; and there was a considerable imbalance in the representation of the biological subsciences. These factors had made the choice of a chairman from outside the University of Florida desirable. The transfer from Chicago to Florida was negotiated successfully; and Clyde Allee took on challenging duties for a five-year term. His friends, who had hoped that he might turn to a quiet period of writing and research, were first dismayed and then astonished at his immediately successful coping with the new situation. When he sent in his first income-tax return in Florida he was rather sharply called to account for the amount of his deduction for medical expenses. He immediately paid a call to the District Collector; and he needed only to be wheeled into the room to be waved away again with instant understanding. As the years flowed past, little change in Clyde Allee's life was to be discerned; there were research papers still, though with new names as junior authors; there was Quaker meeting to attend on First Day; and the summers were still spent at the stimulating but far from peaceful Woods Hole Laboratory. Married students took over the management of the Allee household and cared for his transportation to and from house and office, as had been the arrangement in Chicago after the marriage of both daughters, and in fact before. The necessary transition from one couple to the next was always a hazard. The daughters were widely separated, Barbara Angell in Philadelphia, and Molly Barth in Norway.

In 1953 Clyde astonished his friends by plans for remarriage. It seemed to all to be a minor miracle that a woman of extraordinary charm, an old friend of the family, Ann Silver, should have

fallen in love with Clyde and evoked a downright youthful response from him. The marriage took place in the new home of the 57th Street Meeting in Chicago. In Quaker fashion, there were tributes from old friends, but advice and admonition, it was felt, could be omitted. All signed the marriage certificate, and the obviously happy couple was sped on its way to Woods Hole for the summer.

Ann Silver Allee brought a profoundly sincere and unselfish love into Clyde's life in Gainesville. She brought competence and continuity into the management of the household, and tact and charm into the University social circle. Next only to love, she brought deep understanding, and with these a deep-lying humor that effervesced in wit. There could be no change in the paralyzed limbs; but the long shadow of misfortune was lifted from Clyde Allee's mind as Ann evoked his reminiscences, and as he learned to laugh with her, with a spontaneity that had been wanting for thirty years. There was a happy visit from both daughters, with their small flock of brisk grandchildren. There should have been more happy years than the scant two that were allotted to this extraordinary idyll.

On Monday evening, the fourteenth of March, Clyde had a chill after the evening meal. There was a flare-up of a kidney infection that had made his life precarious for seventeen years. This time it did not yield at all to treatment in the hospital; for a day he was irrational, and then he sank into a coma from which he did not awake. Clyde Allee's breathing stopped on the morning of March 18, 1955. Only three months of his contract with the University of Florida remained unfulfilled, and only three months lacked of his reaching the biblical span of three score and ten.

Warder Clyde Allee was a man of strong and noble character, of extraordinary fortitude in the face of adversity, an American biologist of commanding stature. His contributions were great in the fields of ecology and ethology, as his two great merging interests have been named. They are by no means at an end, for his personality lives beyond him in his generations of students, and

the influence of his books expands in widening circles. The last major honor in his long career was his election to the National Academy of Sciences in 1951. His last conscious thoughts may well have been of the rising sap in the maples, of the pussy willows in the Wabash bottom lands, and of the farmers (to quote his words from another context) "without guarantee, but with the age-old wisdom born of long contact with the soil, preparing to put in another crop."

Toward the end of his career, a tract of some 200 acres of hardwood forest in the vicinity of the Allee farms was purchased with intent of establishing continuing ecological studies in this distinctive environment. It was his hope that a suitable guardian for this property might be found in Wabash College and that its scientific interest would be appreciated and its esthetic and historical significance to America understood. This, he thought, would be an appropriate memorial, expressing his love of the great forest and his love of his Indiana home. It would remind students in future generations of his own pioneer studies in ecology, and provide the stimulus for new ones.

KEY TO ABBREVIATIONS

Am. J. Path. = American Journal of Pathology
Am. J. Physiol. = American Journal of Physiology
Am. J. Soc. = American Journal of Sociology
Am. Nat. = American Naturalist
Anat. Rec. = Anatomical Record
Ann. Ent. Soc. Am. = Annals of the Entomological Society of America
Biol. Bull. = Biological Bulletin
Biol. Rev. = Biological Review
Biol. Symp. = Biological Symposium
Bull. Am. Assoc. Univ. Prof. = Bulletin, American Association of University Professors
Bull. Ecol. Soc. Am. = Bulletin, Ecological Society of America
Consumers Coop. = Consumers' Cooperative
Ecol. Mon. = Ecological Monographs
J. An. Ecol. = Journal of Animal Ecology
J. Anim. Beh. = Journal of Animal Behavior
J. Cell. Comp. Physiol. = Journal of Cellular and Comparative Physiology
J. Comp. Psychol. = Journal of Comparative Psychology
J. Ecol. = Journal of Ecology
J. Exp. Zool. = Journal of Experimental Zoology
Physiol. Zool. = Physiological Zoology
Proc. Am. Soc. Zool. = Proceedings, American Society of Zoologists
Proc. 11th. Ann. Ohio State Ed. Conf. Ohio State Univ. Bull. = Procceedings, Eleventh Annual Ohio State Educational Conference, Ohio State University Bulletin
Psychol. Rev. = Psychological Review
Quar. Rev. Biol. = Quarterly Review of Biology
Sci. Mo. = Scientific Monthly
Trans. Ill. Acad. Sci. = Transactions, Illinois Academy of Sciences
Univ. Chicago Alumni Mag. = University of Chicago Alumni Magazine

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