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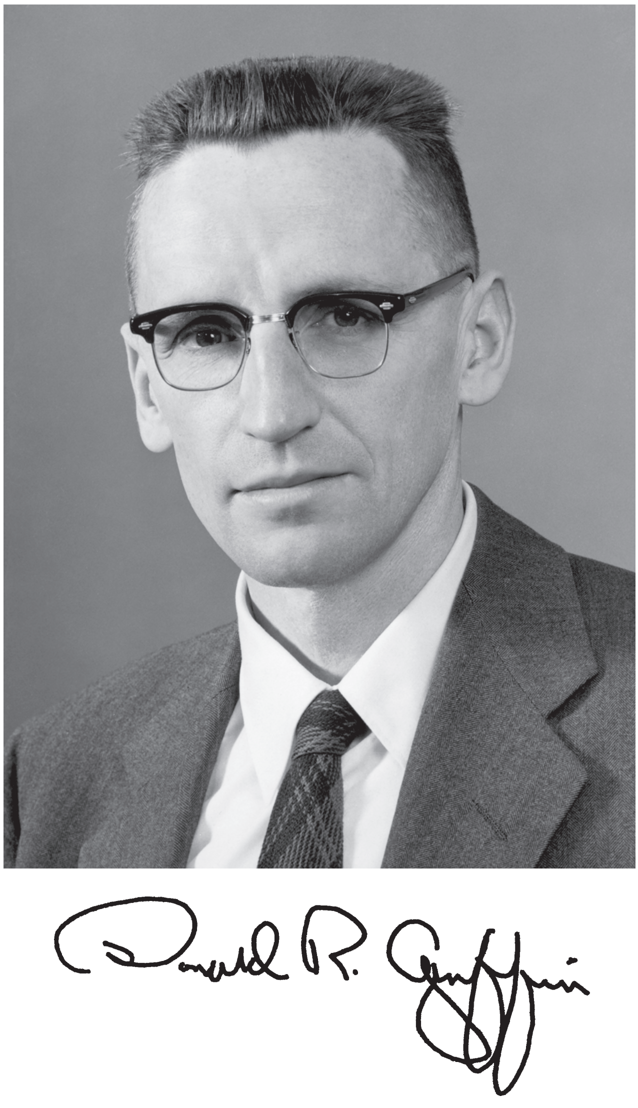

DONALD R. GRIFFIN

August 3, 1915–November 7, 2003

BY CHARLES G. GROSS

MOST SCIENTISTS SEEK—but never attain—two goals. The first is to discover something so new as to have been previously inconceivable. The second is to radically change the way the natural world is viewed. Don Griffin did both. He discovered (with Robert Galambos) a new and unique sensory world, echolocation, in which bats can perceive their surroundings by listening to echoes of ultrasonic sounds that they produce. In addition, he brought the study of animal consciousness back from the limbo of forbidden topics to make it a central subject in the contemporary study of brain and behavior.

EARLY YEARS

Donald R. (Redfield) Griffin was born in Southampton, New York, but spent his early childhood in an eighteenth-century farmhouse in a rural area near Scarsdale, New York. His father, Henry Farrand Griffin, was a serious amateur historian and novelist, who worked as a reporter and in advertising before retiring early to pursue his literary interests. His mother, Mary Whitney Redfield, read to him so much that his father feared for his ability to learn to read. His favorite books were Ernest Thompson Seton's animal stories and the *National Geographic Magazine's Mammals of North America*. An important scientific influence on the young Griffin was his uncle Alfred C. Redfield, a Harvard professor of biology, who was also a bird watcher, hunter, and one of the founders of the Woods Hole Oceanographic Institution.

Young Griffin's hobbies were to become the core of his professional interests and achievements. By the age of 12, Griffin was trapping and skinning small local mammals. Because of his poor teeth, his parents regularly took him to a Boston dentist. These trips were rewarded with visits to the Boston Museum of Natural History, where its librarian introduced him to scientific journals, and its curators to turning his trapped animals into study skins. At 15, with his uncle's encouragement, he subscribed to the *Journal of Mammalogy*, where he was to publish five papers before graduating from college. In his autobiographical writings Griffin described his schooling as "extraordinarily irregular." After a few years at local private schools his "long-suffering" parents decided on home schooling. His father taught him English, history, Latin, and French. A former high school teacher handled the German and math. After a few years of trapping, skinning, sailing, and a couple of hours of daily lessons, his parents sent him to Phillips Andover, where he started but never finished the tenth and eleventh grades. The next year was spent at home again, collecting and sailing, and with tutoring adequate enough that he was admitted to Harvard College in the fall of 1934.

During his high school years Griffin seemed to be more of a nascent serious scientist than, say, Darwin, who had spent his undergraduate days hunting and collecting beetles rather than studying. For example, young Griffin thought he would be able to describe a new subspecies of California mice, but then he realized his hopes were based on errors in the literature, his first realization of the fragility of scientific fact. He tried to estimate the population of various hunted species by obtaining the number of animals killed from the state game authorities. He spent several weeks learning about bird banding at a major banding station and was then authorized to set up a banding substation of his own near his home.

Soon he combined his interests in trapping small mammals and banding birds by banding bats. Recruiting friends, he banded tens of thousands of little brown bats, *Myotis lucifugus*. (For the rest of his life he readily found research volunteers to help in such things as lugging heavy electronic equipment into the field, climbing into unexplored caverns, following birds in an airplane, building huts on remote sand spits, and navigating Amazon rivers in dugout canoes full of recording devices.) This bat-banding project resulted in finding that bats migrated between caves in Vermont and nurseries as far away as Cape Cod. Eventually it produced evidence of homing after displacement of more than 50 miles and of unsuspected longevity of these animals. It also yielded his first scientific publication, as a Harvard freshman, in 1934.

Griffin's sailing interests led to his second paper. While sailing in the summer before entering college, he had encountered several seal carcasses left by hunters who only wanted their noses for the bounty provided by the state. Little was known about what these animals ate, so he collected the contents of their stomachs and, with the help of several curators at Harvard's Museum of Comparative Zoology, identified their contents. In one of his characteristically dry and self-effacing memoirs Griffin tells of how, many years later when he was the chairman of the Harvard biology department, some young discontented molecular biologist in the department sent him reprint requests for this paper in the names of several well-known molecular biologists. Griffin actually sent out the faded reprints until he realized it was a hoax.

UNDERGRADUATE YEARS

As an undergraduate biology major, Griffin took his first science courses but reported mediocre grades in everything but the courses on mammals or birds. At this time John Welsh was studying circadian rhythms in invertebrates and encouraged Griffin to do so in bats. This was an interesting problem because the bats hibernated for long periods under constant conditions in dark caves. Griffin brought some of his bats into the lab and, using the standard physiological instrument of the time, the smoked drum kymograph, showed that indeed they had endogenous rhythms under constant conditions, yielding another paper in the *Journal of Mammalogy*.

Griffin knew Lazzaro Spallanzani's (1729-1799) work on bat orientation. In a brilliant series of experiments with all the requisite controls Spallanzani had demonstrated that bats do not require their eyes, but do need their ears, to navigate. He speculated that perhaps the sound of the bats' wings or body might be reflected from objects. Griffin also was familiar with the English physiologist Hartridge's suggestion that bats might use sounds of high frequency to orientate. At this time a Harvard physics professor, G. W. Pierce, had just developed devices (the first of their kind) that could detect and produce high-frequency sounds above the human hearing range. Two fellow students, James Fisk (later president of Bell Labs) and Talbot Waterman (later a Yale zoology professor), suggested to Griffin that he take his bats to Pierce to find out whether they produced high-frequency sounds.

Pierce was quite enthusiastic about the idea. In fact, he had been studying the ultrasonic sounds of insects (with the help of Vince Dethier, later the doyen of U.S. experimental entomologists). When they put the bat in front of Pierce's parabolic ultrasonic detector, they observed that the bats were producing sounds that the humans could not hear, but when the animals were flying around the room no such sounds were detected. Nor did the production of high-frequency sound seem to have any effect on the flying bats' ability to orient. When they published their observations, they suggested that the function of the supersonic sounds might be in social communication rather than orientation. (Later Griffin realized that the detector had not been sufficiently directional to pick up the bat signals in flight. Even later the social communication role for certain bat ultrasonic cries was confirmed.)

When Griffin was a senior, he was in a quandary about applying to Harvard's graduate school in biology because its faculty had little regard for Griffin's current interest in bird navigation. "Wiser heads emphasized that if I really wanted to be a serious scientist I should put aside such childish interest and turn to some important subject like physiology." The problem was solved with the announcement of the joint appointment of Karl Lashley to the Harvard psychology and biology departments. Lashley's appointment had been the result of the command of Harvard's president, James B. Conant, to hire "the best psychologist in the world." Karl Lashley was the leading "physiological psychologist" of his time and the teacher of many subsequently famous investigators of brain function and behavior. His particular interest to Griffin was that he had written a long and authoritative historical and experimental paper on bird homing (with J. B. Watson, later the founder of behaviorism) and had carried out his own experiments on orientation in terns. Lashley took him on as a graduate student but encouraged him to take several courses in experimental psychology, which he did.

GRADUATE SCHOOL

In graduate school Griffin met another student, Robert Galambos, who was recording cochlear microphonics from guinea pigs under Hallowell Davis, a leading auditory physiologist at Harvard Medical School and suggested Galambos look for bat cochlear microphonics in response to high-frequency sounds. They borrowed Pierce's instruments, and Galambos was soon able to demonstrate responses of the bat ear to ultrasonic sounds. In a series of experiments Griffin and Galambos then showed that bats do indeed avoid obstacles by hearing the echoes of their cries. Here is a recent reminiscence by Galambos of these experiments.

> Don divided a sound treated experimental room into equal parts by hanging a row of wires from the ceiling. We aimed the microphone of the Pierce device at this wire array, and began to count the number of times a bat flying through the wires will hit them when normal, or deaf or mute. . . . The impairments we produced [by plugging the ears or tying the mouth shut] were all reversible. . . . We also recorded the output of the Pierce device and correlated the bat's vocal output as it approached the barrier with whether it hit or missed the wires. . . . Everything we predicted did happen. Nothing ever went wrong. We never disagreed. . . . We suspected our claims might be controversial and decided a movie demonstration might help silence the skeptics. [In recent years this original silent and sound movie has been increasingly shown on nature and science television programs in many different countries around the world. Galambos at age 90 is a still a very active professor of neuroscience at the University of California, San Diego.]

Needless to say, the scientific community was very skeptical at first, but the film and visits to their laboratory were soon convincing. As Griffin put it later, "Radar and sonar were still highly classified developments in military technology, and the notion that bats might do anything even remotely analogous to the latest triumphs of electronic engineering struck most people as not only implausible but emotionally repugnant."

These experiments establishing bat echolocation were reported in Griffin and Galambos's two seminal papers and formed part of the latter's doctoral thesis. Griffin's thesis, by prior agreement, was on bird navigation, the problem he had originally planned to study in graduate school experiments. The central question was whether birds released in unfamiliar territory immediately determined the homeward direction and flew directly back to their nests. He captured petrels, gulls, and terns and transported them, often in rotating cages, in different directions from the site of their capture, then released them and timed their return home. However, their flight times home were consistent with both a search until they found familiar landmarks and a leisurely but direct route home.

Directly tracking them should disambiguate these possibilities he hoped, so he got Alexander Forbes (professor of physiology at Harvard Medical School and one of the founders of modern neurophysiology) to take him up in Forbes's single-engine plane to try to track some gulls. Later Griffin took flying lessons and bought his own two-seater with funds from the Harvard Society of Fellows. The results were again consistent with both a search pattern and true homing.

The Society of Fellows awarded three-year Junior Fellowships with generous research funds. The fellowship was originally supposed to be a super elite substitute for a Ph.D. with no required courses, teaching, exams, degrees, or requirements except for attending candlelit dinners along with the senior fellows. In practice, when the junior fellows went on the job market, say in distant Berkeley, they were told in effect "no degree, no job" and had to go back and get conventional doctorates. Today most junior fellows earn their doctorates first, and it is a kind of fancy postdoc club, imitated predictably at such places as Princeton and Columbia. Griffin was fortunate to get elected to a Junior Fellowship, since his undergraduate grades had been too poor for a conventional graduate fellowship.

WARTIME

With the onset of war in 1941 Griffin became involved in war research at Harvard. His first assignment was to S. S. Stevens's psychoacoustic laboratory. (Stevens was the founder of modern psychophysics.) There Griffin worked on auditory communication problems and acquired valuable familiarity with acoustic equipment. After a stint in the Harvard fatigue laboratory (working on such problems as the optimum gloves for handling fly buttons), he worked with George Wald (subsequently a Nobel laureate) on problems of night vision.

One rather weird wartime incident was the Bat Bomb project. One Lytle Adams came to Griffin with the idea of equipping bats with small incendiary bombs and releasing them by plane over Tokyo, where they would roost in Japanese "paper" houses and set fire to them. The government was supporting this idea, and Griffin agreed to help until he realized that there was no way bats could carry an adequate payload. In spite of Griffin's disavowal of its feasibility, the Bat Bomb project continued on, even involving at one point Louis Fieser, the distinguished organic chemist and inventor of napalm. In his account years later Adams continued to defend the project and claimed that it would have ended the war in a quicker and more humane way than Hiroshima and Nagasaki.

After the war Griffin moved to the Cornell zoology department for seven years before returning to Harvard for another twelve years. The next paragraphs summarize some of his research interest in those years.

FURTHER RESEARCH ON BAT NAVIGATION

Research on bat echolocation (Griffin's term) expanded in a number of different directions with an increasing number of collaborators. (Indeed by the time of his death most of the now numerous bat researchers everywhere in the world saw themselves directly or indirectly, implicitly or explicitly, as his collaborators.) One such direction was to determine the limits of the avoidance and object detection abilities afforded by echolocation. It was clear early that Myotis could discriminate wires down to a quarter of a millimeter, but could they actually echolocate moving-insect prey in the dark? Field experiments suggested that they could. This was confirmed by combining acoustic recording with ultra-high-speed strobe photography in an enclosure with released fruit flies and then weighing the bats before and after a short period of catching flies. Furthermore, the bats could quickly learn to discriminate pebbles and other inedible objects from flying insects. These experiments were carried out with Alan Grinnell, Fred Webster, and others.

Another direction initiated by Griffin with his collaborators Alan Grinnell and Nobuo Suga (and encouraged by Galambos) was the neurophysiology of bat echolocation. Today, largely due to the work of Suga and his students, more seems to be known about the organization of auditory cortex in the bat than in any other animal.

Whereas the North American bats initially studied by Griffin emitted brief frequency-modulated (FM) signals, in 1950 F. P. Mohres discovered that the European horseshoe bat used longer-duration constant-frequency signals for echolocation. This inspired Griffin, Alvin Novick, and other collaborators to survey the signals produced by different species of bats. As most bats species are tropical, this led Griffin, Novick, and their collaborators to a number of exciting Latin American expeditions and the discovery of many different modes of echolocation, including one specialized for fishing and others in cave-dwelling birds.

In the last weeks of his life Griffin was out "night after night" on Cape Cod "still trying to learn more about bats."

BIRDS AND OTHER CREATURES

Griffin continued to work on the mysteries of bird navigation. What made this a difficult problem was that although it became clear that birds (or some birds under some conditions) were using such cues as the elevation of the sun, the pattern of stars, their circadian rhythms, the earth's magnetism, and spatial memory, it was difficult to sort out the interaction and relative roles of these cues. Griffin pioneered in the use of airplanes, radar, and high-altitude balloons to study this problem. [My first publication, on bird navigation, arose out of a paper I wrote for an undergraduate seminar with Griffin. I then researched in his lab on the subject. My most vivid, if irrelevant, memory was the time he asked me to get the car battery from the next room for use as a power supply, and I answered, "What does it look like?" He gave this Brooklyn boy a brief strange look, and then went and picked it up himself].

Griffin's discovery of a "new sense" in bats probably influenced, at least in part, the discovery of other "new animal senses" such as infrared vision in snakes, infrasonic signals in elephants, and orientation and discrimination in electric fish. He played a more direct role in the story of the dancing language of bees. During the war the Austrian zoologist Karl von Frisch had discovered that honeybees could communicate the distance, direction, and desirability of food sources by a dance-like behavior. This work was hardly known in America in 1949 when Griffin arranged for him to give a series of lectures at Cornell, and then across the country, and shepherded their publication through Cornell University Press. Griffin had initially been skeptical until he replicated some of the critical experiments himself. (At the age of 72, Griffin published his last experimental paper; it was on bees.)

Griffin was interested in how beavers communicate. The last weeks of his life found him introducing microphones into beavers' nests near the Harvard Field Station in Concord. Indeed, the number of anecdotes about the field studies he carried out in his last, and eighty-eighth, year that I collected while preparing this memoir is a measure of the man.

THE ROCKEFELLER INSTITUTE AND BACK TO HARVARD

In 1965 Griffin left Harvard to organize a new Institute for Research in Animal Behavior jointly sponsored by the Rockefeller University and the New York Zoological Society. It eventually included a field station in Millbrook, New York. Joined by the leading ethologist, Peter Marler, and Ferdinando Nottebohm, the well-known investigator of bird song and adult neurogenesis, the institute became one of the leading U.S. centers for the study of animal behavior. Among Griffin's collaborators and students at the institute were Roger Payne, discoverer of acoustic hunting by owls and of whale songs and now the leading advocate of whale conservation; Jim Gould, who extended von Frisch's bee studies; and Carol Ristau, pioneer in the study of intentionality in the piping plover. From 1979 to 1983 Griffin was president of the Henry Frank Guggenheim Foundation, and he used this position to encourage research on animal behavior.

When Griffin retired from Rockefeller in 1986 he spent a year at Princeton University and then returned to Harvard, where he worked at the Concord Field Station and occasionally taught undergraduates. In this final period of his life he continued his experimental work on bats, birds, and beavers, as well as his cognitive ethology advocacy described below.

COGNITIVE ETHOLOGY

For about the first 40 years Griffin's career had been that of the very hard-nosed empiricist and skeptic, typified by the following oft told tale (attributed to Griffin's students Donald Kennedy, former president of Stanford and FDA commissioner, and Roger Payne, among others). "When passing a flock of sheep while traveling in a car, his companion noted that among the flock of sheep there were two that were black. Griffin replied, 'They're black on the side facing us anyway.'" Then in 1976 Griffin began to publish a series of books and papers that contained no new data, no figures, but a host of citations and arguments from philosophers as well as scientists that challenged the contemporary worldview of animals. He claimed that animals (and not just chimpanzees or even mammals) were aware and conscious and these properties of their mind should be the subject of scientific study, a field he named "cognitive ethology."

At least at the beginning, these claims and exhortations were usually greeted by harsh and angry criticism (one critic called them the satanic verses of animal cognition) or the sadness of seeing a great experimenter supposedly slipping into premature senility. (He himself even called this interest an example of "philosopause.") To better understand why imputing awareness, or even minds, to animals was considered outrageous, or at least, extra-scientific, by most of those who studied animal behavior, we need to go back to Charles Darwin and the beginning of modern biology.

One of Darwin's central points was the continuity of humans and other animals. As evidence of mental continuity Darwin cited examples from animals of humanlike emotions of joy, affection, anger, and terror, as well as of what we now call cognitive functions, such as attention, memory, imagination, and reason. George Romanes continued this tradition in what became know as the anecdotal school. C. Lloyd Morgan reacted against this approach and formulated what became known as Lloyd Morgan's canon, essentially the application of the law of parsimony to animal behavior: "In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale." This quickly came to imply the rejection of animal consciousness and awareness, and a wariness to impute any complex cognitive function to animals. This tendency was reinforced by Jacques Loeb's theory of tropisms and the Russian school of reflexology, which also downplayed or denied consciousness in animals as well as humans. All these "objectivist" tendencies came together in the behaviorist movement, founded by J. B. Watson. The dominant figure in behaviorism, indeed in all of U.S. psychology until the rise of cognitive psychology, was B. F. Skinner. Skinner and the other "radical behaviorists" flatly denied the validity of the scientific study of consciousness, attention, awareness, thought, and other mental phenomena in humans as well as other animals.

The other principal group studying animal behavior was the ethologists deriving from a European zoological tradition. They tended to stress the role of innate wiring in animal behavior, in contrast to the behaviorists who stressed the role of experience, however they too obeyed Morgan's canon and were generally uninterested in the role of consciousness, intention, and mental experience in animal behavior. The cognitive revolution against behaviorism starting in the 1960s brought consciousness, attention, and awareness back into human psychology but left other animals still essentially mindless and unaware.

Thus Griffin's plea for studying the question of animal awareness (1976) was fiercely counter to the prevailing ideology in both psychology and zoology. Griffin used a variety of arguments, coming from different directions and different fields, to attack this view. One central argument was that it was simply anti-intellectual and antiscientific to deny any subject an objective and experimental inquiry. A second argument was Darwin's original one: the continuity of humans and other animals. Another argument was that animal communication, albeit admittedly fundamentally different from human language, might provide "a window on the animal mind."

In his next two books, *Animal Thinking* (1984) and *Animal Minds* (1992), these arguments were amplified and supported by a Romanes-like compendium of experiments and observations that greatly enhanced the case for animal consciousness and awareness. They included studies of tool construction and use, communication, planning, deception, blindsight, cooperative hunting, and intentionality. Two new lines of evidence came into prominence. The first was a host of neurophysiological experiments seeking mechanisms of consciousness. Since most of these were invasive, such as single neuron recording, they could only be done in animals and thus, with all due respects to Morgan, they assumed animals were conscious, reflecting the change in the intellectual air that Griffin had helped bring about.

The second line of new evidence, increasingly prominent in Griffin's last book and papers on cognitive ethnology, was of studies done by Griffin's students, such as Gould, Payne, or Ristau, and by the increasing number of quasi students, investigators who were never formally his graduate students but readily acknowledge him as their mentors, such as Dorothy Cheney and Robert Seyfarth (communicative alarm calls and deception in vervet monkeys) and Irene Pepperberg (who trained a grey parrot to answer cognitive questions in English). (Even his formal students are not readily identified, as he rarely attached his name to their work.)

Although many biologists and psychologists are still skeptical or uneasy about Griffin's attribution of consciousness to nonhumans, particularly invertebrates, there is no question that he has radically opened up the field of animal behavior to new questions, ideas, and experiments about animal cognition. Because of his own towering achievements as a meticulous and skeptical experimental naturalist, his cogent and repeated arguments about studying the animal mind and his support and encouragement of others, coupled with his unusual modesty and soft-spoken nature, Donald Griffin was able to affect a major revolution in what scientists do and think about the cognition of nonhuman animals.

Griffin was elected to the American Philosophical Society, the National Academy of Sciences, and the American Academy of Arts and Sciences. He received the Eliot Medal of the National Academy of Sciences for *Listening in the Dark* (1959) and the Phi Beta Kappa science prize for *Bird Migration* (1964), and was awarded honorary degrees by Ripon College and Eberhard-Karls Universität.

Griffin leaves two daughters, Janet Abbott and Margaret Griffin, and a son, John, from his first marriage to the late Ruth Castle. His second wife was Jocelyn Crane, an expert on crab behavior and biology, who died in 1998.

THE ACCOUNT OF Griffin's early life comes from his own memoirs (e.g., 1998). Previous drafts of this essay received valuable comments from Robert Galambos, Alan Grinnell, Marc Hauser, Byron Campbell, and Elizabeth Gould. In addition, the following provided helpful comments on Griffin's life and contributions: Robert Galambos, Alan Grinnell, James Simmons, Roger Payne, Marc Hauser, Greg Auger, Jim Gould, Janet Abbott, and Herb Terrace.

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