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A History of the Behavior Program at the Jackson Laboratory: An Overview

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The behavior program at the Jackson laboratory in Bar Harbor, ME, flourished from 1945 through the late 1960s and was unique in the history of comparative psychology. The canine project was conducted on ~300 dogs of five purebred breeds reared under controlled conditions and tested on a predetermined schedule. This enabled a detailed study of genetic and environmental effects and their interaction as well as a variety of other problems in midsized mammals. I provide a comprehensive, though brief, overview of the origins, development, operation, and decline of the program. Although it was begun within a genetic framework, the role of both genetic and experiential influences came to be emphasized. An important additional part of the program entailed extensive studies of inbred strains of house mice (*Mus musculus*) and of deer mice (*Peromyscus maniculatus*). The work at the Jackson Laboratory had a significant impact on various aspects of comparative psychology.

Keywords: Jackson Laboratory, behavior genetics, dogs, early experience

Founded in 1945, the behavior program at the Jackson Laboratory was a truly unique project in the history of comparative psychology. It was focused on genetic and experiential influences on the development of behavior in dogs and mice. What made the program special was the availability of relatively uniform animals of known pedigrees, five breeds of dogs and numerous inbred strains of house mice, and controlled developmental environments. There may never have been another program favored with such animal subjects.

There has been a recent upsurge in research using dogs, particularly related to cognition (e.g., Miklósi, Topál, & Csáni, 2004; Morell, 2009; Udell, & Wynne, 2008). Such work has generally been conducted using pets or random source dogs from suppliers. The dogs have generally had varying, uncontrolled, and unknown developmental histories and both sexes are typically included. These characteristics stand in clear contrast to the work at the Jackson Laboratory. That current interest in canine behavior makes this an especially opportune time to revisit the unique program of the Jackson Laboratory and to compare its features to those of today's canine studies.

This is an example of institutional history. There were few "centers" of American comparative psychology at the time. Perhaps the American Museum of Natural History, the Yerkes Laboratory, and later the Institute of Animal Behavior were the most prominent. Surely, there were other important laboratories of the time but few had an organizational structure that transcended the work of a small number of comparative psychologists. These institutions can be an essential foundation for a discipline. My broad goal is to try to understand in a broad way how these facilities come into being, function, and decline.

Personnel of the behavior program conducted much research and published many papers and numerous books culminating in Scott and Fuller's, 1965 classic, *Genetics and the Social Behavior of the Dog*. I can only touch on a small part of this in the present brief overview.

The Jackson Laboratory

The Jackson Laboratory, originally the Roscoe B. Jackson Memorial Laboratory (or more affectionately "Jax Lab"), was founded by Clarence Cook Little in Bar Harbor, ME, in 1929. Little chose Bar Harbor for a number of reasons including the favorable summer climate in the days before air conditioning and the fact that the area offered a good workforce. Further, donors, such as George B. Dorr and Roscoe B. Jackson, were willing to provide funding for the laboratory (Holstein, 1979; Paigen, 1997). Little had known Jackson, an officer of the Hudson Motor Company, while Little was president of the University of Michigan. It was Little, along with John Paul Scott, who founded the behavior program.

Today, as in the past, the Jackson Laboratory has three primary missions. The first is research. The main emphasis is on cancer research; it is designated as a Cancer Center by the National Cancer Institute. The second is the provision of genetic material to scientists around the world. The facility is the primary source of strains of inbred house mice (*Mus musculus*). Many of the inbred strains of house mice used in behavioral and other research were developed and maintained in Bar Harbor. The third mission is education at many levels.

The Founding of the Behavior Program

The sequence of events leading up to the founding is interesting (see also Paul, 1991). These events occurred in the era of private

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foundations, before the availability of large federal grants. The behavior program was begun in an effort to both demonstrate the importance of genetics for behavior and to produce an ideal kind of dog. In 1945, John Paul Scott, who would become the founding director, was on the faculty of Wabash College, but felt limited in what research he could conduct in that environment. Meanwhile, Rockefeller Foundation (RF) administrator Alan Gregg decided to fund a program on dog behavior genetics as a way to increase the degree of attention paid by psychologists and psychiatrists to genetic influences on behavior. Dogs were chosen because of the availability of so many breeds and the probable similarity between the social organization of wolves, the presumed ancestors of dogs, and humans, a view that is still current (e.g., Tomasello & Kaminski, 2009). Gregg turned to his old Harvard classmate, C. C. Little, director of the Jackson Laboratory, to establish the program. The offer of $50,000 to set up the laboratory and $50,000 a year for 10 years to run it appealed to the financially strapped Little.

During the late 1920s, the RF priorities shifted to basic research and soon the focus became humans and the control of human behavior. The RF officials had grappled with problems of the controversial field of eugenics for some time but it, and programs associated with eugenics, fell largely out of favor. Then in the 1930s Gregg developed a program of "psychobiology," or "mental hygiene." Gregg viewed mental illness as a fundamental problem in society and believed that there was a strong genetic influence.

Foundation officials had a firm belief that the principles to be discovered in nonhuman animals would generalize to humans. Thus, fundamental problems of human behavior might be more conveniently and effectively studied in other species. The RF had already funded Charles Stockard's research on breed differences in the anatomy of dogs. Gregg had visited Ivan Pavlov's Russian laboratory and supported the work of W. Horsley Gantt, one of Pavlov's students, when he moved to the United States. He realized that the behavior of dogs is more complex than that of rats or fruit flies and clear breed differences were apparent.

Little (1941) wrote to Gregg suggesting that the Jackson Lab had the capability to produce uniform breed of dogs or other mammalian species, just as it was doing with mice. In reply, Gregg (1941) shifted the focus to his favorite topic, behavior, and proposed the breeding of a kind of "super dog" to serve as a household pet. He wrote that "if it were possible to devise means of testing what one might call rather vaguely intelligence in dogs, there would be eventually a steady and considerable demand for a small house dog of especially high degree of intelligence and amiability of disposition" (Gregg, 1941). He suggested that this would help the field because people would see the value of genetics in the production of intelligence and because people would see the importance of animal research. The idea sat dormant for a while. Late in 1943, Gregg tried the idea out on Edward B. Wilson at Harvard and he responded positively. Wilson (1943) recommended Little, with a background in working with dogs and whom he had seen judging a Boston dog show. Gregg (1943) replied that "I don't happen to have talked dogs with him," apparently forgetting his letter of 2 years earlier. He decided to follow up with Little.

Gregg (1944) again tried out his developing ideas on Little early in 1944. He reiterated his conviction that "there are some aspects of intelligence which are influenced by heredity or better, to say, transmitted hereditarily" and he noted the advantages of dogs over rats. As Gregg envisaged "15 or 20 years breeding out an extremely intelligent, relatively small dog just to show that genetically intelligence is capturable and reproducible." He noted the commercial potential for such dogs. In a 3-page letter, Little (1944a) responded positively. He cited the breed differences that were already apparent, ease of breeding, and possible social value of the project. He expressed regret that the Stockard project had been so dependent on one person that it collapsed after his death—a theme later appearing in Scott's documents. Little noted the presence at Bar Harbor of Emilia Vicari, who had worked with Stockard, and went on to suggest what breeds might be appropriate.

In March, Robert Yerkes (1944) also supported the project. He was particularly interested in the possibility of "breeding an animal to specification." Yerkes noted that he had proposed that earlier with chimpanzees and still hoped that Karl Lashley at the Yerkes Laboratories would conduct such primate research. Little (1944b) agreed with many of Yerkes' points but expressed skepticism as to the feasibility of the use of apes for such a breeding project. He also mentioned to Gregg the suitability of Paul Scott, whom he had mentioned to Gregg earlier, to run such a project. By May, Little (1944c) reported that a group was convened to consider various models for the project. The grant was made. When searching for someone to head the program, Little turned to Scott, who considered himself to be "at that time the only person in the country with formal training in genetics who was interested in the genetics of behavior" (Scott, 1985, p. 410). Scott accepted the job and the $5,000 salary.

Contrasting Views of Genetic Influences

Both the RF and Little had histories of support for the now discredited concepts of eugenics. Little, a former student of William E. Castle at Harvard, "set forth a research plan—breeding experiments with genetically homogeneous mice—and a social agenda—linking experimental genetics more closely with human eugenics" (Rader, 2004, p. 95). As noted, one of Gregg's goals related to the behavior program was to support a positive eugenic program for the breeding of dogs. That program, however, was never carried out. In the materials I have examined I found no evidence of efforts to breed some kind of super dog.

Scott had rather different views. In "A Challenge to the Eugenist," Scott (1936) had long ago registered his objections to the eugenic program. Indeed, Scott already appeared to have a more nuanced view of genetic effects than did Gregg (see also Mitman, 1992). Gregg (1945) passed along to Little a memorandum from Scott. He noted that Scott wrote of studying "heredity as producing differences in the physiological background of behavioral and emotional differences." Gregg viewed this as different language for essentially what he and Little had been discussing. It does differ, however, from what Gregg regarded as "research concerned with the hereditary transmission of what we call rather vaguely mental and emotional characteristics." Gregg was optimistic about the potential importance of the project noting "that I do hope that Scott understands and has some enthusiasm for not merely the accuracy of his procedures but for the potential importance to all the rest of living that progress in this field could bring." In fact, Scott did have his eye on the potential social importance of this research albeit not in the same manner as did Gregg.

True to his word, Little gave Scott a free hand to run the program. It will be seen that as the program developed both genetic and experiential factors received ample attention and eugenic research was largely ignored.

Key Personnel

Clarence Cook Little (1888–1971)

Little became attracted to the study of mammalian genetics while a graduate student at Harvard. He served as president of the University of Maine beginning in 1922 and, in 1924, established a summer program in Bar Harbor for biology students. Little moved on to the presidency at the University of Michigan in 1925 before returning to Maine in 1929 (Crow, 2002; Snell, 1975). He was controversial throughout his life. Little was encouraged to leave Michigan because of financial problems, support for birth control, euthanasia, and eugenics.

The general view is that Little was a great entrepreneur. He ran a laboratory using democratic principles and allowed his staff to function effectively. He had great charisma and put on lively parties.

John Paul Scott (1909–2000)

As noted, Scott was the primary builder of the behavior program. Little gave him relatively free reign as long as he remained director. Little's successor, Earl Green took a different approach.

The early years. Scott was born on December 17, 1909 in Kansas City, MO, the second of six children of Vivian and John W. Scott. His father, John W. Scott, was the chair of the Department of Zoology at the University of Wyoming. A summer at the Marine Biology Laboratory at Woods Hole, MA in 1929 implanted the possibility of a New England career and of a research station run on democratic principles (Scott, 1988). He graduated from the University of Wyoming and spent 2 years at Lincoln College of the University of Oxford, England in 1930 (Dewsbury, 2010; Dewsbury & Panksepp, 2001; Scott, 1985).

Scott then went to the University of Chicago, where he worked with famed geneticist Sewall Wright and was strongly influenced by animal ecologist W. C. Allee. It was in Allee's laboratory using *Drosophila* from Wright that Scott did his first study in behavior genetics. Scott was already more interested in behavior than in genetics and declined to follow up his early results in relation to genetic theory. Later in his career, Scott specialized further as he became more interested in social behavior, Allee's specialty. Thus, it might be argued that Allee's influence was more even lasting than was Wright's. Scott took with him the perspectives of the developmental biology program at Chicago (see Mitman, 1992). Rather than viewing genetic effects on behavior as relatively simple, one-way effects, he built in behavioral development in terms of the importance of early experience, especially critical periods and behavioral threshold models.

Graduating in 1935 during the depression, he took a job at Wabash College. Scott (1985) suggested that the idea of applying biological methods to the study of behavior came to him as a result of challenging historians and social scientists in an informal discussion group regarding the scientific status of biology versus their fields. In 1938–1939 he spent a year in Boston reading social science literature to try to get up to speed for his new effort. He already had the idea to call the field "sociobiology," well before E. O. Wilson used the term in quite a different sense. Scott simply meant that the social and biological sciences could cooperate. Later, he was critical of Wilson, whom he believed to be "trying to explain social behavior solely on the basis of evolutionary genetics, which you can't do" (Mehrtens, 1986a, p. 18). He added "I've spent most of my life saying 'No, no genetics can't do that" (p. 19).

Scott developed a lasting interest in the problems and prevention of aggression and war (e.g., Scott, 1958a). His general book, *Animal Behavior* (1958b) was published the same year.

He spent the summers of 1938 and 1939 at the Jackson Laboratory studying aggressive behavior in inbred strains of mice. Back at Chicago, Scott, Benson Ginsburg, and others followed up this research. Although strain differences were apparent, the effect of defeat on future behavior also were considerable and led Scott to work on these experiential effects. He began to interpret these results in terms of a systems theory of organized and disorganized behavior.

After Bar Harbor. Scott originally intended to stay just 10 years but stayed 20 years instead. He spent the 1963–1964 year at the Center for Advanced Study and decided to leave the Jackson Laboratory.

Scott was unhappy with Green's lack of support, unwillingness to support student programs, and exertion of pressures. He looked toward the future and declining years and decided that things might be better elsewhere. He moved to Bowling Green State University where he became a research professor with minimal teaching obligations and an increased salary. Scott founded a Center for the Study of Social Behavior. He retired in 1980. A year before his death, colleagues at Bowling Green had honored him by naming its most recent center The J. P. Scott Center for Neuroscience, Mind, and Behavior. He remained active until his death on March 26, 2000 in Toledo, OH.

Assessment. Scott did not impress one as a dynamic and charismatic leader. His speech was generally slow, quiet, and sometimes even somewhat soporific. This could lead colleagues to underestimate the value of his views. However, he had a great ability to organize people in effective ways. Scott had a knack in seeing trends that were developing or needed development. Frank Beach, possessed a similar skill and used it to write review articles and position papers as means to bring the approach to fruition; in Scott's case he organized conferences, societies, and programs. He "lacked the flashiness of many of his contemporaries. Rather, he was a quiet builder of organizations and structures that advanced the field of animal behavior and a solid researcher and sytematizer whose social conscience drove much of his work" (Dewsbury & Panksepp, 2001, p. 454).

John L. Fuller (1910–1992)

John Langworthy Fuller was born in Brandon, VT, July 22, 1910. He received his bachelor's degree in biology from Bates College in Lewiston, Maine in 1931 and went on to complete his PhD at the Massachusetts Institute of Technology 4 years later with a dissertation on "A Comparison of the Physiology, Ecology and Distribution of Some New England Wood Lice" (Fuller, 1985). Essentially, he was trained in physiological ecology. Fuller spent a summer at Woods Hole and then served on the faculties of

Sarah Lawrence College, Clark University, and the University of Maine (1937–1947). Fuller spent the summer of 1946 at the Jackson Laboratory measuring physiological responses in dogs on a fellowship. The next year he accepted a staff position at the laboratory. Like Little, Scott was concerned that the previous Rockefeller dog program run by C. R. Stockard at Cornell University had folded upon his death. He wanted a coinvestigator who could handle the program if something happened to himself. In Bar Harbor, Fuller was initially to study physiology and emotions in dogs but later conducted a large variety of projects primarily on the nature and nurture of behavior in dogs and mice.

In 1958 Fuller became the Assistant Director for Training of the entire Jackson Laboratory. By the mid-1960s, the situation had changed. Fuller was appointed Associate Director with half his responsibilities assigned to administration. Later the administrative responsibilities grew. In 1970, Fuller left the laboratory to accept a position at the State University of New York at Binghamton (now Binghamton University). Fuller (Mehrtens, 1986b) listed among his reasons for leaving Bar Harbor the lack of space in the main laboratory, competition between research and administrative activities, lack of equipment, and concern about future funding for his kind of work. He retired from the Binghamton position in 1978.

Other Key Personnel

Earl L. Green (1913–1995) (Taylor, 1995) assumed the directorship in 1956. In contrast to Little's permissive approach, Green tried to run a tight ship. Some of the staff resented his tight managerial style and his attention to detail and left. Green tried to focus the laboratory on cancer and genetics to the detriment of the behavior program.

John A. (Jack) King graduated with a PhD from the University of Michigan in 1951 and headed, with his pregnant wife, off to Bar Harbor on an National Institute of Mental Health (NIMH) fellowship (King, 1985). His dissertation had been a classic study of prairie dog towns but, with a developing family, he wanted to do laboratory work that would keep him closer to home. King also believed that the precision of laboratory work over field studies more than compensated for the reduced face validity. King's fellowship paid just $3,000 for the first year, increased by $500 for the second. He started on the staff at $3,000 and got only up to $5,000 by the time he left. In Bar Harbor King began working with dogs, then conducted much work on house mice before turning to deer mice, *Peromyscus maniculatus*. In 1960 King moved to Michigan State University in 1960 and retired in 1986.

Walter Czehura Stanley (1921-to present) received his three degrees, including the PhD from Yale University, the latter with a dissertation in animal learning. He was an Associate Staff Scientist at the Jackson Laboratory during 1958–1962, after which he moved to a position as research psychologist at the National Institute of Mental Health. His research with dogs focused on behavioral development, such as sucking, social behavior, and reinforcement.

There were many other significant members of the scientific staff who worked in the behavior program for various periods of time. These included Frank H. Bronson, Randy and Janey Chambers, Robert L. Collins, Anne Cornwall, Basil Eleftheriou, Orville Elliot, Emil Fredericson, Daniel Freedman, Sally Huff, Arlo K. Myers, Richard Sprott, W. Robert Thompson, Marcus and Patricia Waller, Jack Werboff, and Richard E. Wimer.

The scientific staff was augmented by a distinguished list of summer investigators and postdoctoral fellows. An abbreviated list includes W. Edward Bacon, David Blizard, Jan Bruell, Robert Cairns, John B. Calhoun, Joseph Church, Lincoln D. Clark, Victor Denenberg, Alan Fisher, Michael W. Fox, Benson Ginsburg, Calvin S. Hall, B. Elizabeth Horner, William James, Jerome Kagan, Seymour Levine, Gardner Lindzey, Howard Moltz, C. L. Pfaffenberger, Roberty Plutchik, Karl Pribram, Harriet Rheingold, C. Richard Terman, and Delbert D. Thiessen.

One can add to this impressive list some of those who worked in the program as undergraduate or graduate students. These included Lynwood Clemens, Donald Dewsbury, Carolyn Rovee-Collier, Z. Michael Nagy, and Evelyn Satinoff, among others. The Jackson Laboratory also had a summer program for high school students, some of whom participated in the research programs.

An unannotated list of this sort may seem to be of limited value. However, it provides some idea of the number and range of the scientists who contributed to the program's efforts. I have corresponded with as many of these scientists as I could locate and I hope to present further work on them.

Support Personnel

A laboratory needs support personnel for success as almost as much as it needs scientists. Obviously, the credentials and work are less demanding in some senses but that makes them no less important but they are often overlooked in studies of research institutions. It is much harder to locate information on this part of a facility than on the scientific staff.

Various research assistants were used, some of whom became coauthors on scientific papers. These included Frank Church, Edna DuBuis, and Emilia Vicari. Two, Mary 'Vesta Marston (later Scott's second wife) and Philip H. Gray, became motivated to go on and earn PhD degrees.

The foreman of buildings and grounds at Hamilton Station, the site of the behavior program, was Frank Clark. He and his family lived on the grounds. King (2006, pp. 3) described him as "a pleasant native of Mount Desert and a handy man, who cheerfully helped out when needed." Also living there was Leslie Bunker, who, with a crew, took care of the grounds. A Mrs. Cleaves served as Scott's secretary and helped organize the laboratory.

The Behavior Program

As noted above, Little gave Scott a free hand to run the program. Scott named himself the chairman of the Division of Behavior Studies and stayed for 20 years. In the early years, Scott and Little divided up the dog work with Scott handling the behavior and Little working on the genetics of coat color (e.g., Little, 1979). Like Little, Scott favored a democratic system in which all participants had a say and he tried to run the station according to such principles (Scott, 1988).

Overview of the Program

The behavior program was located at Hamilton Station, apart from the main station. It contained some 40 acres of land, most of

it covered with spruce trees and large boulders; only about three acres were cleared and developed (Scott, 1988). It was located about a mile north of Salisbury Cove and 8 miles from the village of Bar Harbor on Mount Dessert Island, ME. The facility was given to the laboratory by the estate of William Pierson Hamilton, a partner of J. P. Morgan. After he retired, Hamilton bought up various parcels of land in the area so that he could do diversified farming. When he died the family was unable to sell the property because the horse barns had no pastureland associated with them. Thus, they donated the barn that was to become Hamilton Station. Initially, it was modified so that the Jackson Laboratory staff could hold barn dances there. Scott first saw the facility in 1938–1939 (Mehrtens, 1986a).

When Scott moved to Bar Harbor in 1945, he converted the main barn into a behavior laboratory. When finally developed, the Hamilton Station dog facility was shared with a program in rabbit genetics run by Paul Sawin. They were in buildings near to each other but had relatively little contact between them.

Scott recalled that it turned out to be:

> "a very good animal behavior research laboratory. It was not only complete with inside facilities such as nursery rooms and testing laboratories but also with outside runs. We also had three big one-acre fields in which we could study the dogs in more or less natural field conditions. We therefore had almost unlimited space and opportunities" (Mehrtens, 1986a, pp. 3–4).

Because of his concern that a successor be in place should something happen to him, one of Scott's early acts was to seek a second scientist of roughly equal capacities. Calvin Hall, a former student of Robert Tryon, did not want to leave Western Reserve University and Benson Ginsburg, a student of Allee and Wright at Chicago, did not want to leave the windy city. In the end, Fuller was selected. Scott would move from genetics to a primary interest in social behavior while Fuller would be important in establishing the field of behavior genetics. Scott wrote that:

> "He was a fortunate choice. His research skills complemented mine; he was a dedicated and creative scholar, and we got along well personally. We were about the same age, and even looked somewhat alike, to the extent that we both favored mustaches in a beardless age" (Scott, 1978, p. 2).

Scott continued his earlier research on aggressive behavior in mice along with his assistant, and later second wife, Mary 'Vesta Marston while the Hamilton Station horse barn was being remodeled for dogs and the land was cleared so that thee large one-acre fields could be used for research. He also kept a flock of goats for research during the early years (Scott, 1988).

A major event in the history of Mount Desert Island was the fire of October, 1947, which destroyed many houses and forests as well as much of the main Jackson Laboratory. All of the mice there were killed; the strains were later reconstituted from animals that had been sent elsewhere. The center of Bar Harbor and the Hamilton Station facility were spared and the main laboratory was later rebuilt. For the year after the fire, until the main station could be rebuilt, Hamilton Station housed the entire Jackson Laboratory program. Consideration was then given to the possibility of moving the entire laboratory out to the Hamilton Station area. Scott advised against it but later regretted that advice (Scott, 1978).

At first, the staff consisted of just Scott, a veterinarian's assistant, Edna DuBuis to help care for the dogs, and Emilia Vicari, who had done research on dogs at Cornell with Stockard, Mary 'Vesta Marston, a recent graduate in psychology from the University of Maine, was added as a research assistant in 1946.

During much of the building's life, the central corridor on the ground floor contained Scott's office at the entrance. Across the hall was the office of executive secretary of the Behavior Division (King, 2006). Down the hall was a small office occupied by another secretary. At the end of the center hall had been a paneled rack room, where horse harnesses had previously been kept. This was converted into a library and seminar/meeting room. On rainy days it served as a lunch room. There were two wings. One held pens for raising the dogs; the other contained testing rooms, physiological equipment, and a small chemistry laboratory.

The basement held facilities for the mice. Caging, testing equipment, and plumbing were appropriate for the time. In addition to the house mice, King's deer mice were kept there.

King had a large office at the rear of the second floor; it featured a view of Frenchman's Bay. A large loft was reached through a door in that office. It was often used to store equipment but some testing of dogs was done there as well. The wooden floor was slick from use. I worked with a large T-maze that was built in the loft. Some excitable dogs, such as wire-haired terriers, would slide part of the way down the T-maze on the slick floor. Across the way from King's office were office occupied by Fuller, Fredericson, and Stanley at various times. Another office was used by the technical assistants.

The laboratory produced a large volume of published studies. In this short overview I can present only a few highlights.

As noted, the program was initially built with RF funds. However, eventually Foundation officials and their consultants (e.g., Carpenter, 1955) became disenchanted with it; they terminated funding in 1958. As this process unfolded, Scott's situation with the Foundation in 1955 was eerily similar to that experienced by Robert Yerkes at the Yerkes Laboratories of Primate Biology in the 1930s (see Dewsbury, 2006). Fortunately, by this time Federal funds and those from other private sources could fill the gap.

The Canine Program

Initially, Little had only springer spaniels and they turned out to be inappropriate for both cancer research and behavior. Little then obtained a variety of breeds from which Scott eventually chose five that were of medium size, reasonably fertile, and in good health. Beagles, Shetland sheep dogs (Shelties), wire-haired terriers, and cocker spaniels were representative of broader groups of dogs. The fifth, basenjis, from one of Little's friends in Wisconsin, was chosen because it had been isolated from other breeds for a long time and showed unusual behavior (Scott, 1978). The basenjis differ from other breeds of dogs in that, like many other mammals, they breed just once a year. Most will breed at various times when the female comes into heat.

The breeding program for dogs lasted about 5 years. All dogs were bred and raised in indoor kennels for about 2 or 3 months. The dogs then went outside and lived in unheated wooden houses during the winter (Mehtens, 1986b). They were generally healthy, with very little disease.

The cockers and basenjis were selected for a Mendelian cross study with parental, F1, and F2 generations. The data collecting phase of the dog program lasted 13 years. The average colony size was 225 dogs. That was a relatively large operation. With respect to personnel, Scott recalled

> "At one time, there were about 25 people who had doctoral preparation at work in the whole laboratory—fellows, and staff members and so on. Of these, eight were working at Hamilton Station on behavior, so we made up about a third of the whole laboratory" (Mehrtens, 1986a, p. 23).

One of the first tasks was to prepare standard testing procedures for use with puppies in their first year. Once in place, this was used for about 10 years (Fuller, 1985). That was accomplished during 1946–1947. The final "Manual of Dog Testing Techniques" ran 72 pages plus tables (Staff of the Division of Behavior, 1950); eight scientists participated in its development. This is an important document because it sets the procedural foundation for the whole project with a set of procedures that was adhered to studiously. Chapter I described the system of rearing and care. Here one can find details of the plant and laboratories, the social environment, both canine and human, nutrition, sanitation, veterinary care, and identification. Dogs were raised as litters for the first year, with the mothers for the first 10 weeks. There was no contact with other dogs for the first 16 weeks and minimal contact thereafter.

Chapter II includes a general description of the 26 tests used with the dogs. The tests were divided into four classes. The Performance tests included climbing tests, barrier tests, leash control, stair-climbing, obedience training, and retrieving. Emotional Reactivity Tests included a variety of short-term stress conditions in which the animal was exposed to mildly stressful situations, such as isolation, startling stimuli, and pain. Relationship Tests of social behavior included such tests as dominance tests, observations of maternal behavior, and play fighting. There was no explicit training involved. The Physical and Physiological Observations included measurements of growth, sensory function, and the like.

Chapter III includes the procedural descriptions of the various tests and is characterized by considerable detail. These tests were given to all dogs according to a stated schedule. Some tests were given daily and some weekly according to schedules for each test as described in the manual. For example, dogs received barrier tests in the 6th week, handling and dominance tests in the 11th week, and tests of trailing in the 27th week. The procedures for each test are described in detail and data sheets and scoring systems are included as appropriate.

Genetic and Environmental Factors

With 300 puppies from the 5 breeds in 30 odd behavioral tests the task of analyzing a large matrix was daunting in the days before high-speed computers (e.g., Anastasi, Fuller, Scott, & Schmitt, 1955; Royce, 1955). When analyzed the data revealed generally small correlations among tests and many breed differences, However, there was little pattern to the breed differences and none seemed "better" than another. There was no support of a general intelligence (*g*) factor. Similarly, with regard to temperament, there were no consistent differences as one breed may act fearful in one situation and another breed would do so under different conditions.

It was clear in these studies, as in others, that motivational and emotional factors affected performance. Physique had little to do with behavior in the test situations; Scott tried to relate results to William Sheldon's somatotype theory with categories of endomorph, ectomorph, and mesomorph.

There was evidence of some degree of heritability (understood as the proportion of variance in traits, not of the traits themselves, attributable to genetic effects) on virtually all of the tests. Overall, about 27% of the variability among breeds could be attributed to heredity. In general, physiological measures, such as heart rate, showed higher heritability coefficients than did most behavioral traits. As Scott (1985) noted, "it does not follow that behavior is genetically determined; only that some of the *variation* in behavior is genetically determined" (p. 416). Scott was a strong opponent of ideas of genetic determinism in behavior. He added "genetics does not put behavior in a straitjacket" (p. 416).

Part of the variance among breeds could be attributed to the developmental environment. Rearing puppies of two different breeds together decreased the differences between them. A program that started out in the context of genetics came to have a strong environmental flavor. The program culminated in the publication of the classic volume *Genetics and the Social Behavior of the Dog* (Scott & Fuller, 1965).

Early experience experiments in dogs. A substantial program of research on effects of early experience complemented the genetic analyses in the laboratory. Scott related this effort to problems of abnormal behavior in humans. Some of the abnormalities found in dogs, particularly the emotional reactions of the "kennel dog syndrome," bear some resemblance to emotional problems in humans.

Psychologists in the laboratory of D. O. Hebb, at McGill University, conducted early research on Scottish terriers that came from the Jackson Laboratory (Clarke, Heron, Fethersonhaugh, Forgays, & Hebb, 1951). They found major effects of early deprivation on problem solving, social behavior, and motivation before Harry Harlow's well-known studies of rhesus monkeys.

The work was continued in Bar Harbor by Alan Fisher and by Fuller and associates. Scott, Fredericson, and Fuller (1951) explored the effects of early experience in relation to the critical period hypothesis.

In the late 1950s, Fuller began a series of experiments on the effects of early experiential deprivation. The first experiment involved permissive versus disciplined rearing, with and without a tranquilizer (chlorpromazine). Effects of both rearing condition and the drug were transient (Fuller, Clark, & Waller, 1960).

The second experiment was the Kaspar Hauser study, named after the German boy who suffered early solitary confinement for 10 years. Dogs were raised in closed, individual cages and were removed for about 10 min one, two, or four times a week. The 0-group showed reduced social behavior. Those removed from isolation 2 or 4 times a week displayed normal behavior. Thus, only small bits of experience greatly mitigated deleterious effects.

Perhaps the most remarkable result was found when dogs raised in isolation but given chlorpromazine before emergence showed greatly reduced symptoms compared to those that emerged without the drug. Fuller and Clark (1966) developed an Emergence Stress Hypothesis (see also Fuller, 1967). Although the early deprivation

may have been important, they stressed that the opportunity to repeatedly adjust to the sudden bombardment of stimuli encountered on emergence was critical. Thus, the effects of deprivation may have been as much an effect of events at the time of emergence as of the earlier deprivation itself. Fuller reflected that "this experiment is possibly the most significant I have performed, but it has not been widely cited or followed up by others" (Fuller, 1985, p. 102).

The critical period hypothesis. Borrowing from embryology, Scott gradually developed a critical period hypothesis for the development of socialization in puppies (Scott, 1962). He first reported the ideal age for socializing puppies to humans in 1951. He delineated three periods: neonatal (establishment of nutrition and nursing), transition (maturation of adult forms of nutrition, sensory processes, and locomotion), and socialization (formation of social relations and attachments). The critical period for socialization was set at 4–12 weeks. This was regarded as the optimal time to give puppies new homes and human owners. The developmental periods were studied and delineated in more systematic research by Freedman, King, and Elliot (1961). Scott placed the critical period for learning new things at 8–12 weeks. Scott's general critical period model was not published until much later (Scott, Stewart, & DeGhett, 1974).

Associated with this hypothesis and the concept of attachment in general was that of separation anxiety. This became another topic of investigation at the Laboratory (e.g., Cairns & Werboff, 1967).

It should be noted that the notion of critical periods has been controversial (e.g., Beach, 1951; Schneirla & Rosenblatt, 1963; Scott, 1963) and has often been out of favor in recent comparative developmental psychology. Most researchers today prefer the term "sensitive periods" because these appear to be stages of maximal sensitivity that are less rigid, less well defined, more flexible, and with more gradual onsets and offsets than implied by the word "critical." Nevertheless, some investigators still find the concept helpful (e.g., Coppinger & Coppinger, 2001).

The big shift. There was thus a major shift from the early goals of the project to develop the genetics of behavior to an emphasis on experience. Genetic effects were clearly present but the emphasis was tempered.

In her 1988 interview, Diane Paul summarized what Scott had been telling her succinctly:

> "When I read what you published in the 60s and compare it with various other correspondence from the early years it appears to me, though I may misconceive what I read, as though there was a substantial shift in thinking such that the interpretation of the results after the study is complete stress the plasticity and flexibility of behavior and away from the notion that highly specific chunks are under highly genetic control. the importance of learning. that's not what if I had read this that what I would have expected to come out of this" (Paul, 1988).

Scott agreed that this is a fair interpretation. He said that the general form of the behavior was actually very much the same in any breed of dogs. What were different concerned more how difficult it was to elicit this kind of behavior and the relative frequency. The basic patterns of behavior do not get shifted very much. The variation probably traces back mainly to differences in emotion and variation.

Other topics. The emphasis in this overview is on the study of genes and environment in behavioral development in dogs but many other topics were studied. A sample includes social facilitation, dominance, social behavior, breeding cycles, learning performance on various tasks, emotion, chromosome morphology, transfer of training, and behavioral pharmacology.

Mouse Research

Early experience. As the importance of private foundation funding was decreasing and that of federal funding increasing, in 1948 the laboratory was the recipient of an early grant from the National Institute of Mental Health (MH123) to study the effects of early experience on aggression. Along with clinical psychologist Emil Fredericson, Scott developed this program and developed new measures of aggression in mice (Scott & Fredericson, 1951). Fredericson was succeeded by Jack King, who had attended the early experience conference and later developed a program of his own (e.g., King, 1958).

Audiogenic seizures. Fuller conducted a long-term set of studies of the determinants of the audiogenic seizures in mice first observed by Calvin Hall (1947), publishing numerous articles and reviews. Although there was some suggestion of a single-locus effect, Fuller preferred a polygenic model with a threshold effect (Fuller, 1985; Fuller, Easler, & Smith, 1950).

Other behavioral patterns. During the 1960s, Fuller and his associates studied genetic influences on a variety of other behavioral patterns including food ingestion and saccharine preference. They also conducted a program on the determinants of alcohol preference. John B. Calhoun, who became well-known for studying rodent populations and crowding, began his research at the Jackson Laboratory (Scott, 1978).

Aggression. Scott had a long-term interest in the study of aggression (e.g., Scott, 1958a). Scott attributed his interest in social behavior to his concerns about WWII, which broke out during a critical period of his academic development. Issues of peace and aggression were very important to him. He believed that aggression was the product of complex interactions between genetic and environmental factors. Scott conducted pioneering research on aggression in house mice and many later researchers followed suit using mice for studies of aggression.

There are clear genetic difference among strains but situational and environmental factors are also important. Scott noted that "you can take the same mouse and either make a fierce fighter or make a peaceful animal out of it, by appropriate training methods, and the same is true of dogs" (Mehrtens, 1986a, p. 16).

In May of 1986, a group of scientists, including Scott, met in Seville, Spain and signed a "statement on violence" stating that genetics do affect aggression but that they do not determine whether or not an animal or human will fight. As Scott put it "the argument that war is an innate human quality, that people must go to war, is false" (Mehrtens, 1986a, p. 16). Scott adopted a program that was clearly progressivist, as was much of psychology during the early 20th century:

> "My whole idea, all the way along, has been that what we're trying to do is use research on animals to understand human behavior and so to modify it and improve it where possible" (Mehrtens, 1986a, p. 16).

This ties back to Gregg's original ideas about applicability but realized in a manner very different from Gregg's. Such statements can be self-serving fabrications of past events. We lack clear corroborating evidence that this was Scott's original motivation. However, it seems consistent with Scott's overall demeanor and career.

Deer mice. Unlike the other staff members, King got interested in nondomesticated mice. He began by trapping the local subspecies of deer mice. As they did not breed well in the laboratory, he obtained stock of two other subspecies, *P. m. gracilis* and *P. m. bairdi*, from Lee Dice, his old mentor at Michigan. The former were creatures of the forests; the latter of the prairies. King found many differences between them and was especially interested in the development of the differences. He conducted a number of studies of the interaction between the genotype of the two populations and a variety of experiences at different times in development. In one study early experience of early experience the mice were given early stimulation by being placed in an odd contraption that "gently compressed the infant mice between foam rubber pads several times each minute during the first weeks of life" (King, 1985, p. 214). Mice were later tested in a Sidman avoidance learning task. The same experience improved performance in the task in one race and decreased it in the other—a nice example of genotype x environment interaction.

Other Features of the Behavior Program

Conferences. As the program was just beginning, at the end of the summer of 1946 (September 10–13), Scott organized an important Conference on Genetics and Social Behavior (Scott, 1947a, 1946). A total of 37 conference members attended. This was a distinguished group that included most, if not all, of the scientists who might contribute to the emerging field of genetics and behavior. These included some who had published on genetics and behavior (such as Calvin Hall, Benson Ginsburg, and E. M. Vicari), some leading comparative psychologists (such as Frank Beach, C. R. Carpenter, T. C. Schneirla, and Robert Yerkes [the conference General Chairman]), some scientists with connections to the Jackson Laboratory (such as W. L. Russell), five science writers (such as G. Lal and A. Scheinfeld), several leading physiological psychologists (such as H. S. Liddell, Neal Miller, Clifford Morgan, and W. C. Young), two social psychologists (Gardner and Lois Barclay Murphy), some young animal behaviorists (Elizabeth Beeman, Nicholas Collias, and John Fuller), plus Alan Gregg and Robert Morrison of the RF and Fairfield Osborn of the New York Zoological Society. This was one of the first postwar scientific conferences.

The conference featured a series of talks and reports from various committees, on Genetic Background of Social Behavior, Social Behavior and Motivation, and the Physiological Background of Behavior, and the Committee on Social Organization and Leadership. One can see the stamp of Scott on the formation of these committees, as they reflect many of his interests. The focus was on generating new research ideas and the means to implement them, with an emphasis on the resources of the Jackson Laboratory. Fuller recalled that

> "the division [of Behavior Studies of the Jackson Laboratory] was advised to concentrate on laboratory rather than fieldwork in animal behavior, and on larger animals that could not be housed easily in most university facilities. Priority should be given to genetic influences on behavior, and the research programs of the staff should be augmented by encouraging visiting investigators and advanced students. This good advice was followed" (Fuller, 1985, p. 99).

Scott believed that because participants were not to prepare papers in advance and met and lived in one building, there was great cooperation and participation and the conference was a success (Scott, 1947a).

The origins of the Animal Behavior Society, the premier North American organization for the study of animal behavior, can be traced to this meeting. Carpenter, Beach, Schneirla, and Scott developed a Committee for the Study of Animal Societies under Natural Conditions (Scott, 1947b). Annual meetings were developed in association first with the American Association for the Advancement of Science and later with the Ecological Society of America and the American Society of Zoologists. In 1965, the Animal Behavior Society emerged from this structure as an independent group. Scott is regarded as the organization's founder (Guhl & Schein, 1976).

Morrison (1946) summarized his experiences at the conference from his RF perspective. He noted that the Hamilton Station buildings had been "very ably remodeled for experimental work with rabbits, goats, sheep and dogs." He was amazed at the progress that Little and Scott had made in so short a time at a time when materials and labor were in short supply. He added "it is a tribute to the thoughtful and careful planning of both J. P. Scott and C. C. Little." Morrison's opinions of others at the conference are equally candid and interesting as are his overall experiences at the conference.

Under the auspices of the New York Zoological Society in 1948, Scott organized a conference on "Methodology and Techniques for Studying Animal Societies Under Natural Conditions" (Scott, 1950).

A second major conference held in Bar Harbor was the Conference on Early Experience and Mental Health, held in 1951 (Scott, 1951). The emphasis in the conference, as in the laboratory, was shifting from genetics to experience. Scott brought together a group of scientists interested in animal behavior and clinical psychologists interested in research on mental health (Scott, 1951). King arrived in Bar Harbor just in time for the conference. He called it "a wonderful and influential experience" (King, 1985, p. 210). He added:

> "Since the Jackson Laboratory specializes in mammalian genetics, this conference on early experience was directed toward the interaction of genetic predisposition and their vulnerability to modification by developmental events. Epigenetics was resurrected, but with each participant adhering to his own concept of the interplay between genetics and early experience. My experience at this conference was stimulating and humbling. I wanted to become involved in this intellectual resurgence of the nature-nurture problem. Paul Scott and John Fuller warmly welcomed me" (King, 1985, p. 210).

The discipline of behavior genetics. The Jackson Laboratory played an important role in establishing the field of behavior genetics (Dewsbury, 2009). Although there was earlier research on the effects of genetics on behavior (see Hall, 1951), a case can be made that the field emerged as a discipline with the publication of Fuller and Thompson's textbook *Behavior Genetics* in 1960

(Fuller & Thompson, 1960). The book gave a name to the emerging discipline and brought diverse research results within a single pair of covers. Often such a volume has the effect of defining a subdiscipline, as with John B. Watson's *Behaviorism* and E. O. Wilson's *Sociobiology*. Fuller took a year off during the mid-1950s to write the book, working primarily at Yale University and the University of California, Berkeley. The duo produced an even more substantial book 18 years later (Fuller & Thompson, 1978).

Fuller helped to develop the field by organizing sessions at larger meetings. In 1954, Fuller organized what may have been the first symposium on genetics and behavior at the meetings of the American Psychological Association. Speakers were Raymond Cattell, Jerry Hirsch, and Thompson. He also organized the first behavioral session at the meetings of the International Congress of Genetics, with Gerald McClearn, Aubrey Manning, and Ernst Caspari as speakers. Fuller was one of the founders of the Behavior Genetics Association in 1970 and served as its president in 1973. He was also involved in the founding of the Animal Behavior Society and the International Society for Developmental Psychobiology.

Having worked with chlorpromazine with dogs and alcohol preference in mice, Fuller also developed an interest in pharmacogenetics. He conducted several studies with mice in this area (see Fuller, 1985).

Fuller and his associates also conducted a selection study for brain size in mice. They were able to select lines with different brain sizes but the correlations with behavior were disappointing (see Fuller, 1985).

Guide dogs for the blind. In 1946 Clarence J. Pfaffenberger, a trustee of Guide Dogs for the Blind in San Rafael, CA, contacted Scott and subsequently visited the laboratory with an interest in the breeding of guide dogs. He obtained a grant for that purpose and during 1961–1967 Scott, Fuller, and Benson Ginsburg made regular trips to California the help in the project. The effort was to breed, choose, and rear, and train guide dogs on a more scientific basis; data were collected from 1961–1967. The results are described by Pfaffenberger, Scott, Fuller, Ginsburg, and Bielfelt in their 1976 book *Guide Dogs for the Blind, Their Selection, Development, and Training* (Pfaffenberger, Scott, Fuller, Ginsburg, & Bielfelt, 1976). The themes of their findings will be familiar as they concern genetic differences, early experience, and training. They recommended that the dogs receive as wide a range of experience as possible. They speculated that F1 hybrids among the three most successful breeds, German shepherds, Labradors, and golden retrievers might produce the best guide dogs.

Atmosphere

The laboratory. Most laboratory alumni remember the atmosphere at the laboratory as being quite friendly. In general, they found it to be a stimulating and invigorating place to work. King (1985) called the intellectual climate at Hamilton Station "stimulating, exciting, and rewarding" (King, 1985, p. 211). He wrote that

> "Paul Scott and John Fuller. complemented each other precisely in personality, in scientific skills, and in administrative ability. Paul was serious, contemplative, detached, and as concerned about human social interactions as he was about the social behavior of the dogs and mice he studied. One of the basic premises was that science is noncompetitive and that severe competition could disastrously impede the flow of scientific progress. Cooperation was the name of the game at Hamilton Station and Paul Scott was an altruist."

"In contrast to Paul's idealism and detached seriousness, John Fuller was realistic, involved, and playfully competitive. It was always a pleasure to work, play, and talk with John." (King, 1985, p. 211).

Scott (Mehrtens, 1986a) recalled that many of the staff members were young and liked to give parties. He called it "a gay place" (p. 37). He noted that people were treated as equals regardless of their status. Surely, I think, some must have been more equal than others.

A highlight mentioned by many were the luncheons. Staff members, visiting scientists, and student would sit at a picnic table or outside on the grass and discuss the scientific issues of the day. The scientific staff at the Laboratory got together a seminars and meetings. Every summer the laboratory trustees and Scientific Advisors visited and the staff was expected to act as hosts to these distinguished visitors during the big party at the Laboratory and its grounds.

The town. Bar Harbor today is a small town of 2,680 full-time inhabitants. It swells to over 10,000 in the summer, as there is a big tourist trade. It is located on Mount Desert Island on the coast of Maine. The area has beautiful rugged, Maine coast and the beauties of Acadia National Park. In summer, there are many activities; in winter, the town is much quieter.

King (2006) noted that when he was there "Bar Harbor Village had a population of about 2,000 mostly centered about the town pier." Early on, Bar Harbor was known for its huge summer estates along the coasts and on the surrounding hilltops. They were basically summer homes. The 1947 forest fire destroyed many of these large homes and much of the industry of the town.

Life in and around Bar Harbor got mixed reviews. Most who worked there seemed to love the summers, with the good weather and opportunities for outdoor recreation. "Hiking the carriage trails built by the Rockefellers and the National Park trails provided wonderful opportunities to get out and enjoy nature and to view the drama of the rocky Maine coast" (King, 2006). Some bemoaned the winters with cold weather, isolation, and fewer activities. Some loved the isolation but others, particularly those from urban environments, felt isolated from scientific colleagues, certain intellectual pursuits, and major entertainment. Cultural activities were more substantial than one might expect in a town of this size.

In general, "town-gown" relations seemed to be good, as the local natives appreciated the financial impact of the laboratory. Several members of the laboratory staff served in political offices for the community. However, King (2006) did note that "like any community, the natives were special citizens, who had grown up and gone to school with each other. There were town-gown differences, but they were rarely mean or antagonistic."

The End of the Program

As noted earlier, with the change in higher administration and administrative style many staff members in the behavior program felt less welcome and less appreciated than in the early years of the program. Green's organizational style contrasted with Little's and staff members drifted away. In 1986, Scott noted

> "the behavioral research has almost gone. When I left the Hamilton Station, it was in good running condition, with strong grant support for dog research. I had tried to get people in here who would carry it on, but actually, after I left, they were not able to keep it going more than a couple of years, so the dog research got all phased out, a couple of years after I left. Fuller stayed on, for several years after I left– I think about five—but he was working at the main lab with behavioral genetics research on mice. Then, he decided to do the same thing that I had done, namely to leave and go into an academic institution" (Mehrtens, 1986a, pp. 28–29).

The only person left doing behavioral research in 1986 was Robert Collins and that was with mice. The Hamilton Station property was sold in 1982.

Hamilton Station After the Behavior Program

Scott summarized part of the subsequent history of the property:

> "Hamilton, the Station that started out as a rich man's toy, then became a very serious laboratory for many, many years, then was abandoned and sold by the Jackson Laboratory. For a year of two, it was owned by someone who wanted to develop it into an amusement park. Fortunately, the town Planning Board was able to stop this. Apparently, it has now been bought by another wealthy person, so the thing has come a full circle. He has bought it, we are told, for his children" (Scott in Mehrtens, 1986a, pp. 30–40).

The only subsequent information I have been able to obtain was from a July 13, 2007 issue of the *Mount Desert Islander* (65 units eyed, 2007). At that point developers had proposed a development with mixed residential and commercial functions. They suggested single-family lots, multifamily units, and some commercial uses. Permits had not yet been obtained and I have been unable to determine whether the facilities were built.

Perspectives of Scott and His Contemporaries

Asked about the ultimate impact of the Jackson Laboratory for the history of science, Scott began with new fundamental research in the field of cancer. These included the demonstration of a viral cause of breast cancer and the genetics of immunity reactions in mice and other mammals. With regard to the behavior program, he replied that there were discoveries of equal importance to the science of behavior and behavior genetics but did not mention specific research findings. Instead, he emphasized the research environment for students and colleagues:

> "one of the most important things that I and my associates were able to accomplish was, by making this an attractive place to work, an interesting place, and a stimulating place, we attracted during those 20 years of my residence, almost all of the people who were then working in the fields of comparative psychology and animal behavior in this country" (Mehrtens, 1986a, p. 31).

Among the success stories that Scott cited were Philip H. Gray of the University of Montana, and Mary 'Vesta Marston Scott, Scott's second wife. Orville Elliot was a former research assistant who later went to Harvard and has a career in physical anthropology. All started out as research assistants and went on to graduate schools and careers.

Fuller (in Mehrtens, 1986b) noted:

> I'm quite proud of the work done by the group at Hamilton Station. As to the quality of our research, I now think that our genetic work on the dogs could have been better done in a center closely associated with a university with strong psychological and genetic departments" (p. 10).

The program took various kinds of criticism throughout its lifetime. Schneirla and Rosenblatt (1963), among others, believe that the laboratory's would have been better spent if used to study dog-dog interactions rather than dog-human ones or if more experimental, rather than observational, methods would have been used. It is notable, however, that dog-human orientation has returned to comparative psychology. Carpenter (1955) criticized the quality of the research, the isolation from a university environment, and a lack of objectivity, among more minor concerns. Some felt that the research did not reflect growing perspectives in behavioral ecology sufficiently. Surely, the program reflected Scott's personality and priorities.

Current Perspectives

Although a complete survey would be beyond the scope of this article, it is interesting to view the canine research conducted in Bar Harbor from current perspectives. Much recent interest has been focused on dogs' responsiveness to human cues from gestures or gaze.

Critical Periods

The critical period hypothesis has been largely ignored in some applied contexts. Coppinger and Coppinger (2001) expressed concern that 50 years Scott and Marston's critical period hypothesis was promulgated "the dog industry still doesn't seem to understand its significance for traits such as temperament and learning" (p. 223). However, there is some indication of influence. Agencies providing guide dogs for the blind often assign the puppy to a human "walker" at about 40 days; they later interact with a trainer and their blind owner (e.g., Valsecchi, Previde, Accorsi, & Fallani, 2010). The latter authors found that treated this way the dogs could develop attachments to particular individual humans that was apparent at the age of 1 year.

The hypothesis has generated some, albeit limited, interest in recent research literature as well. Thus, for example, Ward, Bauer, and Smuts (2008) studied the ontogeny of social play analyzing their data in relation to three of the critical periods defined by Scott and Marston.

Nature, Nurture, and the Selection of Research Subjects

If there is one lesson from the Scott and Fuller research it is that genes and environment interact in affecting canine behavior. These differences can be subtle. Coppinger and Coppinger (2001) got the message writing that "when I buy a dog, my work in shaping that animal has just begun. I want a great set of genes, but the behavior I want is not totally determined by those genes" (p. 223).

Unfortunately, because of the difficulty of maintaining a Jackson-Laboratory-type facility, the variability of subjects used in laboratory research with dogs is greater than that which would be acceptable for other subjects. Often, but not always, dogs of varying breeds, different rearing histories, and the two sexes are

combined in research reports. This probably inflates the error term in studies where group comparisons are made and surely makes replication across different studies from different laboratories difficult. The current situation makes that at the Jackson Laboratory stand out by contrast.

Miklósi, Topáli, and Csáni (2004) emphasized the need to study breed differences and they noted, quite reasonably, that the social environment may be equally important. There have been a few studies of breed differences. However, in most studies breeds are grouped according to the uses for which they have been selectively bred. Coppinger and Coppinger (2001), for example discriminated among various groups including sled dogs, herding dogs, and livestock-guarding dogs. Udell and Wynne (2008) differentiated herding, hunting, and sled dogs. Reidel, Schumann, Kaminski, Call, and Tomasello (2008) used a French system that differentiates 10 breed types and included breeds of herding dogs, hunting dogs, mongrels, terriers, and working dogs in their study. Gagnon and Doré (1992) used an American Kennel Club taxonomy of breeds. Scott and Fuller did not support the idea that there might be several behavioral "types."

There have been some interesting results nevertheless. Breeds or groups of breeds have been found to differ in at least some respects. Jakovcevic, Elgier, Mustaca, and Bentosela (2010) found retrievers to gaze at human faces more than German shepherds or poodles without explicit training and in extinction of a task in which they had to learn to attend to gaze. However, Reidel et al. (2008) found no difference between puppies of herding versus hunting species with respect to responsiveness to pointing gestures. Gagnon and Doré (1992) found no group differences among terriers, sporting, and working dogs in an object permanence task. In an interesting approach, Svartberg, Tapper, Temrin, Radesäter, and Thorman (2005) studied the consistency of personality traits assessed with standardized measures; they found individual differences but no consistent differences among breed groups. From the data of the Jackson Laboratory project, one would expect only very subtle and complex breed differences that might be missed with the groupings that are common in these studies. The problem is that it is rarely possible to obtain dogs of pure breeds in sufficient numbers for an adequate analysis. The fact that few breed differences have been reported need not imply that they are unimportant but it is likely that they would be complex and subtle at best.

In a few studies no breed comparisons were made but at least the subject population was limited to a single breed. Fiset (2007) studied five purebred Labrador retrievers in a study of landmark-based search memory; Macpherson and Roberts (2010) studied five rough collies in a radial maze.

In addition to breed differences, developmental histories are often uncontrolled in recent research. Frans de Waal was quoted as noting that "the investigator has no control over the nurture side; how owners feed, train, or treat their dogs."[that] introduces unknown variables we would normally not accept in animal behavior research" (Morrell, 2009, p. 1063).

An example of the impact of early treatment is the study of Gazzano, Mariti, Notari, Sighieri, and McBride (2008) with dogs reared in homes or kennels and either gentled or not. These dogs they showed differences in responses that might be labeled emotional as a function of these early rearing manipulations. Hare, Brown, Williamson, and Tomasello (2002) found no difference in responsiveness to human cues between home-raised and kennel-raised puppies tested between 9 and 26 weeks.

Some research suggests that sensitivity to human gestures is not greatly affected by age and presumed ontogenetic influences (e.g., Gácsi, Kara, Belényi, Topál, & Miklósi, 2009; Reidel et al., 2008). These developmental studies have been criticized on methodological grounds (e.g., Wynne, Udell, & Lord, 2008). Dorey, Udell, and Wynne (2010) found no evidence that puppies respond to human pointing before the age of 21 weeks.

In some literature, interpretations of reports assigning prominence to ontogeny are contrasted with those of selective breeding (e.g., Hare, Rosati, Kaminski, Bräuer, Call, & Tomasello, 2010; Udell & Wynne, 2010). As part of this, the question of whether wolves and dogs are differentially sensitive to human gestures is controversial. If wolves are unresponsive, the difference is attributed primarily to selective breeding during the domestication in dogs (e.g., Hare et al., 2002). There are also indications, however, that, under some conditions, wolves may respond to human gestures (e.g., Udell, Dorey, & Wynne, 2008). This, together with the developmental data in dogs, suggests to some authors that wolf-dog differences may be primarily ontogenetic rather than phylogenetic, although both must play a role (e.g., Udell & Wynne, 2010).

If the responsiveness is not a product of domestication, it is possible that it may reflect part of the use of pointing in wolves as part of their cooperative hunting patterns (van Rooijen, 2009). If the responsiveness is a product, at least in part, of domestication there are several theories as to its origin. According to one, human-guided selection might have been for tameness and the responsiveness to human cues may be a byproduct of such selection (Hare & Tomasello, 2005). This possibility is given credence by the results of a 40-year selection study conducted by Dmitry K. Belyaev and his colleagues on silver foxes (Trut, 1999). Selection for tameability produced a variety of changes not only in behavior but morphology and endocrine function as well. If similar changes occurred in the domestication of dogs, this could provide the basis for increased sensitivity to human gestures. We come full circle to the views of Scott and Fuller (1965) who wrote that "the general trait of tameability is a basic one, because it must have been involved in the original domestication of the dog (p. 267). We also see the importance of their interactionist view.

The Proper Context for Canine Behavioral Research

Earlier, the Bar Harbor studies were criticized for their use of dog-human interactions rather than intraspecific social behavior. In recent literature it has been argued that dogs have become adapted more toward interaction with humans than with other dogs and thus it is more appropriate to study their interactions with humans. Miklósi et al. (2004) wrote that "earlier studies of social learning in dogs were concerned mainly with within-species learning. the ethological question is whether dogs are able to learn from their heterospecific companions" (p. 1001). According to Tomasello (in Morrell, 2009, p. 1065) "dogs are collaborating with us; they aren't doing this with other dogs." Thus, more recent interpretations have been more favorable toward the approach of Scott and Fuller.

Another important context for studying dog behavior is with so-called "town dogs." (Coppinger and Coppinger (2001). These studies resemble, in some respects, the kinds of research envisaged

by the critics of the Bar Harbor approach. Examples are the study of social bonds and dominance interactions by Cafazzo, Valsecchi, Bonanni, and Natoli (2010) and of social behavior in Bengalese free-ringing dogs by Pal (2008).

Industrializing Organisms

Some of the insights of recent work in the history of science can be applied to the current project. Schrepfer and Scranton (2004) provide an interesting perspective in a volume dealing with "industrializing organisms." There, for example, Russell (2004) noted that it is a mistake to claim that machines have replaced animals in the process of industrialization. Rather, animals and their uses have been altered but they remain an important aspect if industrialization. Thus, humans have shaped the evolution of other species, and. such intervention has significantly changed both humans and other species" (p. 2). He used the term "anthropogenic evolution" (p. 3). The authors in the Schrepfer and Scranton volume analyzed such phenomena as the production of improved cows, hemophiliac dogs for research, and the chickens of tomorrow. An even more elaborate analysis is that of Rader (2004) on the development of inbred strains of mice for research. Much of this development was conducted at the Jackson Laboratory.

In this spirit, Todes (2002) summarized the development and organization of the laboratory of probably the most famous student of dog behavior, Ivan Pavlov, as "Pavlov's Physiology Factory." Pavlov's was a true factory for the production of knowledge in several senses. Pavlov oversaw a tightly organized ship under hierarchical control and integrated to form an organized whole. The primary aspect of the production of the dogs was surgical as each needed to be prepared to serve in his physiological experiments; they were thus viewed as intermediate byproducts in the physiology factory. As summarized by Todes (1997), "the relations of production featured an authoritarian structure and cooperative ethos that allowed Pavlov to use coworkers as extensions of his sensory reach, while enabling him constantly to monitor the work process, to control the "interpretive moments" in experiments, to incorporate results into his developing ideas, and to convert them efficiently into marketable products" (p. 205).

One can apply these principles to the Jackson Laboratory. Scott and Gregg both wanted to utilize dogs in a technological instruments but they did so in very different ways. Like many, Gregg envisaged altering the course of the evolution of dogs in Russell's sense. His goal was to modify dogs so that they might rather directly be better adapted for their interactions with humans primarily as pets. This is in the same spirit as the projects discussed in the Schrepfer and Scranton (2004) volume with regard to the production of improved cows, hemophiliac dogs for research, and the more user-friendly chickens.

Contrasting with Gregg's approach, Scott utilized dogs in the production of knowledge that he believed would indirectly lead to the betterment of humanity. There is no indication that he was ever interested in improving canine-kind. This is closer to Pavlov's goals. Both approaches can be treated as a technological application of canine life but in very different ways.

Although both Scott and Pavlov maintained substantial research groups, Scott's was never as tightly organized as was Pavlov's. In contrast to Pavlov's top-down approach, Scott favored a democratic organizational structure with peers influencing the decision-making process. In addition, Scott generally worked with dogs as they were and studied their development and behavior without any overt physiological manipulation. Like Pavlov, Scott's immediate goal was the production of knowledge and in that sense both can be regarded as organized technologies.

It is difficult, and perhaps unfair, to try to provide an evaluation of the research itself from today's perspective. Were this unique resource available today, the research conducted and the impact it would have certainly would have been quite different from the program that was realized in Scott's time. Like most research 40 or more years old, it is only occasionally cited today. Nevertheless, 45 years after its publication, *Genetics and the Social Behavior of the Dog* is still in print. How many of our books will still be available after such a period?

Conclusion

Scott's goal was to improve the human condition. One can wonder to what degree any such program can truly do that. In fact, much was learned about aggression in animals and the extent to which it is affected by environmental factors. The program improved our understanding of behavioral development; we now know much more about the interactions of organism, genes, and environment in ontogeny. Following Scott and others, few today would posit an innate aggressive drive. Although it may difficult to see any observable effect on peace and tranquility in humans, Scott aimed high. He and the others in the Jackson Laboratory behavior program produced significant scientific knowledge.

The field of behavior genetics is thriving, albeit in a different manner from that initially conceived in Bar Harbor. The same is true for notions of gene-environment interaction and epigenesis. There is much interest in the psychology of aggression. We are still building on such foundations.

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