

DESCENDED FROM DARWIN
INSIGHTS INTO THE HISTORY OF
EVOLUTIONARY STUDIES, 1900–1970

Joe Cain and Michael Ruse, Editors

American Philosophical Society
Philadelphia • 2009

TRANSACTIONS
of the
AMERICAN PHILOSOPHICAL SOCIETY
Held at Philadelphia
For Promoting Useful Knowledge
Volume 99, Part 1

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ISBN: 978-1-60618-991-7

US ISSN: 0065-9746

Library of Congress Cataloging-in-Publication Data is available from the Library of Congress.

CHAPTER 8

“THE EXPERIMENTAL ANIMAL FROM THE NATURALIST’S POINT OF VIEW”

BEHAVIOR AND EVOLUTION AT THE AMERICAN MUSEUM
OF NATURAL HISTORY, 1928–1954

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The study of animal behavior in the United States expanded considerably between the two World Wars, in terms of the number of biologists interested in the subject and the scope of their research (Burkhardt, 2005; Dewsbury, 1989b; Mitman & Burkhardt, 1991). These biologists came from both naturalist and experimentalist traditions. For example, Warder Clyde Allee, at the University of Chicago, incorporated animal behavior into an ecological context. Allee stressed the importance of an organism’s interactions with the community in which it lived and the surrounding environmental conditions in producing its behavior (Mitman, 1992). Taking a very different approach, William C. Young, one of the founders of behavioral endocrinology, is remembered for his research on the role of sex hormones in producing mating behavior. These approaches within behavioral research of the interwar period built on strong disciplinary traditions in the study of behavior established at the turn of the twentieth century (Dewsbury, 1989b). By the mid-1930s, comparative psychology had also begun to attract more students. Comparative psychologists were interested primarily in the ability of animals to learn, although some also explored the role of behavior in the natural lives of organisms and the evolution of behavior more generally (Dewsbury, 1989b). Despite such methodological diversity, these communities of biologists were united in their belief that the study of animal behavior should be professionalized and rid of its amateurish, anthropomorphic roots.

Each group brought valuable contributions to the table: experimentalists found that the controlled environment of the laboratory provided an ideal location for modifying and observing behavior in developing organisms, while naturalists used

observation and modification of an organism's natural habitat to establish the normal behavior characteristic of the species. Without the behavioral data gathered in the natural environment of the organism, it was impossible to know whether behaviors observed in laboratory spaces were real or simply an artifact of the artificial conditions of the laboratory. During this period, as historian of science William Coleman suggested in 1974, "the activities of the experimentalist and of the naturalist are not really as sharply defined as they might seem to some of us [now]."¹

Gladwyn Kingsley Noble, curator of herpetology at the American Museum of Natural History (AMNH) from 1923–1940, was characteristic of biologists studying behavior in the 1930s. He embodied the fluid boundary between experimental and naturalist traditions and sought to put the study of behavior on a more professional footing. Noble founded the Laboratory of Experimental Biology (LEB) at the AMNH in 1928. In his laboratory spaces, he sought to map the evolution of social behavior "from fish to man," and to uncover the hormonal changes regulating behavioral differences between each taxonomic group he studied (Gregory, 1941a; Mitman & Burkhardt, 1991). To do so, Noble observed and gathered his research specimens in the field and used this data to construct naturalistic enclosures for his experimental subjects in the LEB. In 1939, Noble published an article entitled, "The experimental animal from the naturalist's point of view," in which he extolled the virtues of laboratory research for answering questions of concern to naturalists like himself (Noble, 1939).

Yet after Noble's untimely death in 1940, the LEB's experimental research program began to shift direction as subsequent curators strove to fit their experimental research on behavior into the overall mission of the AMNH. Frank Ambrose Beach, curator of the LEB from 1940–1946, continued Noble's comparative approach to behavioral research and changed the name of the research group to the "Laboratory of Animal Behavior." This change in name codified what had become the sole research agenda of the LEB under Noble's tenure. When Beach left the department, Lester Aronson took his place as curator of the Laboratory of Animal Behavior. Like Noble, Aronson initially worked to show that experimental animal behavior research was valuable to naturalists. Aronson's research into evolution and reproductive behavior, however, differed considerably from Noble's in its theoretical and methodological framework. Whereas Noble emphasized the *pattern* of behavioral development over evolutionary time, Aronson explored the role of mating behavior within the *process* of evolution. Additionally, Noble conducted his experiments at the Museum in the 1930s to describe the mating behavior of individuals from the same species. By the 1950s, Aronson designed his experiments to elucidate behavioral interactions between reproductively isolated groups of organisms.

This shift from pattern to process in the explanatory goals and experimental design of animal behavior research at the AMNH reflected the increasing influence of experimental population genetics in shaping the research practices characteristic of mid-twentieth century evolutionary biology. The most important theoretical development shaping biologists' ideas about evolution and sexual behavior was the new interest among these population geneticists in reproductive isolation.² During the late 1930s and early 1940s, works by geneticist Theodosius Dobzhansky, zoologist Ernst Mayr, and paleontologist George Gaylord Simpson brought natural selection to the fore as the most significant causal mechanism governing speciation and macroevolutionary change in nature (Dobzhansky, 1937; Mayr, 1942; Simpson, 1944; Stebbins, 1950).

As a result, biologists interested in behavior and evolution shifted their focus from the behavior of individuals to behavior as contributing factor in the process of genetic isolation and speciation (Provine, 1971).

In this chapter, I argue that although the modern synthesis was on the one hand an attempt to unify biology, on the other hand the effect of the synthesis in the 1940s was to restrict the ways in which it was acceptable to conduct evolutionary research and to occlude specific ways of conceptualizing behavior within an evolutionary framework. By the mid-1950s, experimental investigations of reproductive behavior in the U.S. no longer sought to demonstrate the evolution of species-specific reproductive behavior, but instead concentrated on the ways in which reproductive behavior, and specifically mate choice, might act as a mechanism of speciation. Thus, despite recent claims that the study of animal behavior was not synthesized with evolutionary theory until the 1970s, research on mate choice as an isolating mechanism formed one of the central questions in the study of animal behavior in the United States in the mid-twentieth century.³ This new research focus dramatically affected experimental investigations of behavioral evolution among many biologists in the U.S.

I begin by describing the institutional context of Gladwyn Kingsley Noble’s laboratory within a natural history museum. Subsequent sections explore in greater detail Noble’s and then Aronson’s research from the 1930s to the 1950s on the mating behavior of animals. Then, the narrative turns to describe the influence of experimental population genetics in the 1940s on the laboratory study of animal behavior in the following decade. As curators’ understanding of the evolutionary process changed, so too did their experimental designs, methodologies, and research questions. Finally, I conclude with some thoughts about the meaning of the new process-oriented evolutionary research program to the biological study of behavior for our historical understanding of evolutionary theory between 1925 and 1950.

FOUNDING OF THE LABORATORY OF EXPERIMENTAL BIOLOGY

On the west side of Central Park in New York City, Gladwyn Kingsley Noble created what he hailed as a unique research environment. Construction of the Laboratory of Experimental Biology began at the American Museum of Natural History in 1928, and it was formally opened in May 1933. In a report for that year’s trustees meeting, Noble described the opening of his laboratory as “the most significant event of the year . . . this gives the American Museum the finest experimental laboratories in any museum in the world.”⁴ Although collecting and displaying live animals for the purposes of entertaining and educating the public had been relatively common in museums starting in the nineteenth century, the use of live animals as research organisms within a museum was far less common (Hanson, 2002; Jardine, Secord, & Spary, 1996; Mitman, 1996; Rothfels, 2002). Such experimental research was more likely to be conducted at a university or a zoo.

Modeled after Hans Przibram’s *Biologische Versuchsanstalt* in Vienna, the finished product included rooms for aquaria, greenhouses, animal breeding, balance apparatus, dark rooms, cold rooms, laboratories for histology and physiology, and facilities for sterilizing equipment.⁵ Six investigators could work in harmony. Construction of the laboratory was largely funded by money given to the Museum by the City of New York and private donors for the construction of the African Wing—the laboratory

occupied the uppermost floor of the new wing.⁶ The total bill came to approximately \$82,000, a substantial investment in 1933, but small when compared to Museum expenditure on field expeditions during the same period. From 1928 to 1933, the years of the laboratory's construction, the AMNH spent over \$263,000 on the Central Asiatic Exploration and Research Fund.⁷

Noble's research agenda provides a good idea of how he intended this laboratory to be integrated into the museum as a whole. As the laboratory opened its doors, he outlined 14 lines of research on the boundary between natural history and experimental zoology (Table 8.1).⁸ Noble hoped that in collaboration with the laboratory, other curators could solve questions they could not answer using data gathered solely in nature. For example, he believed that studying the hormonal basis of tooth formation would prove of great interest to vertebrate zoologists as dental morphology often formed the basis of classification in vertebrates. Noble also argued that species identification could be accurate only if tested with controlled breeding experiments that would establish the genetic constitution of new putative species or subspecies collected in nature. He further hoped that by injecting specimens of rare or cryptic species with pituitary extract, he could induce these individuals to breed out of season, thus allowing naturalists to study their life history for the first time. In this way, Noble thought the LEB would act as a central research space serving the needs of other departments in the museum. The AMNH trustees supported the construction of the laboratory with exactly this hope in mind—that it would engender cooperation among the traditionally fractious departments.⁹

However, the economic prospects of the country continued to decline following the opening of the laboratory's facilities, and it became clear to Noble that he would have to streamline his research to accommodate budgetary restrictions. In 1933, the AMNH trustees decided to halt all institutional expenditures on field expeditions and concentrate their resources on Museum-based research. (Privately financed field expeditions still occurred if the necessary funds had been donated to the Museum with the stipulation that they be used only for a specific expedition.) The ability of the Museum to continue functioning during the Great Depression was in large part due to the Works Progress Administration (WPA) and the Museum's status as a semipublic

Table 8.1. Noble's 14-point research agenda for his Laboratory of Experimental Biology at the American Museum of Natural History

1. Hormones of Reproduction	8. Blood Relationships as Determined by Serological Methods
2. Hormones and Tooth Form	9. The Species Problem
3. Morphogenic Factors of Development	10. Life History Studies
4. The Mechanism of Molt	11. Psycho-Biological Studies
5. Function of the Pineal Gland	12. Sexual Selection
6. Physiological Bonds Regulating Animal Societies	13. Genetics of Color Patterns
7. Physiological Controls to Animal Distribution	14. Physiology of Color Change

institution. For example, in 1936 the WPA granted the Museum sufficient funds to employ almost 250 WPA workers. Of these, about 60 were assigned to Noble for work in translating research papers, exhibit construction, and research. Although these funds were sufficient to keep the Museum’s exhibits open and the laboratory functioning, they were not sufficient for consumable laboratory supplies. So Noble also applied to the Josiah Macy Foundation and to the National Research Council’s Committee for Research on Problems of Sex for money to acquire research organisms, chemicals, cages, and food. Through a combination of outside grant money and WPA workers, research at the laboratory continued, and Noble’s team turned out papers.

Noble also chose to limit himself to what he considered the most “urgent” of his research plans—the evolutionary history of the psychological basis of behavior (Mitman & Burkhardt, 1991, p. 175). Noble’s work on sexual selection formed one of the central aspects of his research plan. Referring to his research on the significance of bright colors in fish, lizards, and birds, he wrote, “we have investigated this question both in the laboratory and the field with the result that we have been able to advance new views as to the significance of these adornments. Further observations are desirable on other species before these views will receive general acceptance.”¹⁰ He hoped that later, when financial conditions in the country had improved, he would be able to expand the scope of his research to include some of the other 14 questions he had originally intended to answer.¹¹ The laboratory, however, never stimulated the interdepartmental cooperative spirit for which Noble and the Trustees had hoped.

Although Noble was originally hired into the department of herpetology, in his laboratory he considered all vertebrates part of his scientific jurisdiction, and he published papers on fishes and birds in addition to the typical herpetological gamut of lizards, chameleons, turtles, snakes, and tadpoles. In 1937, he hired Frank A. Beach to be assistant curator of experimental biology, and further extended the reach of the department into mammalian physiology (Beach, 1978). Early in his career Noble argued, “it is evolution which makes zoology a unified science and the student of zoology at the outset of his career should be given the opportunity of glimpsing the whole edifice of animal life before being called upon . . . [to] analyze the functions of its various parts” (Noble, 1927, p. 501). This evolutionary zoological framework formed a central precept of his research on reproductive behavior.

Noble envisioned his interests in mating behavior and systematics as two aspects of the same enterprise. He wanted to know how mating behavior developed in evolutionary time. Using taxonomy as a proxy for time, he hoped to trace the development of sexual behavior from the lowest to the highest vertebrates, namely humans. Once Noble established what should count as “natural” behavior in a species from each major vertebrate group, he hoped to use laboratory techniques to elucidate the physiological mechanisms underlying the expression of those behaviors. He followed the same research plan with each species he investigated. The final product would have been a map of the evolution of hormonal and neural control of natural reproductive behavior in vertebrates (Noble, 1939).

However, when Noble died suddenly at the age of 46 (of Ludwig’s Quinsy), he had not yet completed his work. At Noble’s memorial, William King Gregory commended Noble for his broadly comparative approach:

The strange ways of courtship and mating among fishes, frogs, lizards, snakes, birds, to say nothing of rats, guinea-pigs and monkeys, used to be recorded separately by ichthyologists, herpetologists, all writing in as many different technical journals, which in turn were rarely seen by anyone outside their respective specialties. More than any other man Noble was rapidly integrating these fragments into a continuous and understandable picture . . . [to discover] the basic principles that have governed the evolution and behavior of vertebrate animals from fish to man.¹²

Noble had advanced only as far as the first or second step in his intended research program with a number of the species he planned on researching.¹³ Noble's hopes of integrating evolution and behavior represented his own attempt to arrive at a synthetic zoological knowledge.

After Noble's death, his widow Ruth Crosby Noble gathered up what she could find of his research notes and transformed them into a popular book—*The Nature of the Beast* (Noble, 1945)—so that his completed work could reach a general audience, at least.¹⁴ The book grew naturally out of her own work in the education department of the Museum, and was in keeping with Noble's commitment to his curatorial duties at the Museum: to maintain the collection, to conduct original research, and to ensure that the results of that research are communicated to the general public through the Museum's exhibitions, radio-shows, and public lectures (Myers, 2000).

Noble cannot easily be categorized as either a naturalist or a laboratory-centered biologist; he represents what we might call an early organismal biologist.¹⁵ He used experiment and observation in nature and in his laboratory to understand the proximate and ultimate causes of reproductive behavior, and he hoped to determine the evolutionary pattern of behavior in vertebrates.

NOBLE'S RESEARCH ON NATURAL REPRODUCTIVE BEHAVIOR

The study of natural reproductive behavior was another crucial component of Noble's research agenda, and key to the position of his Laboratory of Experimental Biology in a museum of natural history. For Noble, his laboratories provided space in which he could investigate the normal process of evolution. Not only did he use wild-caught experimental subjects, he also created spaces for his experimental subjects, which mimicked their wild environments. He ensured that readers of his papers saw his laboratories as extensions of nature (see also Dobzhansky, 1937).¹⁶ Studying wild organisms in a naturalistic yet controlled environment allowed Noble to unite different ways of knowing biological phenomena into a single vision of the organism in question. Noble could then use this data to track the evolution of reproductive behavior "from fish to man" (Gregory, 1941a).

A natural research environment and wild organisms were important to Noble for several reasons. First, until he could breed organisms in the laboratory, the success of his experiments depended critically on expeditions to the field to gather subjects (such practices were common; Kohler, 2002).¹⁷ A certain portion of Noble's budget each year was devoted to procuring experimental organisms. He frequently took trips to Long Island and New Jersey to collect the fish, frogs, turtles, and birds he used in his experiments.¹⁸ Second, he worried that the rats and flies typically used in laboratory experiments were not representative of the diversity of behavioral mechanisms

that existed in nature. After countless generations in a laboratory environment, the animals themselves had probably become adapted to these artificial conditions, Noble reasoned. As a result, he never tried to standardize his laboratory animals for greater experimental control. Third, Noble believed that the environment of the laboratory could induce artificial behavior in animals. Behaviors never observed in nature might be produced in a laboratory environment due to a variety of unnatural factors, including a higher than usual density of organisms in a cage, or artificial lighting conditions. In his greenhouse, Noble constructed experimental environments that emulated the natural habitats of his research organisms (Greenberg & Noble, 1944).

Two of Noble’s investigations offer a flavor of his work to naturalize his laboratory spaces in practice: posthumously published experiments on the mating behavior of the American “chameleon” (*Anolis carolinensis* Voight), and his unpublished research on the mating behavior of box turtles (*Terrapene carolina*) at Jagger’s Swamp. In the first set of experiments, conducted with Bernard Greenberg on the role of male chameleons’ dewlap color in eliciting mating behavior in females, we can see the importance Noble ascribed to making his laboratory spaces appear natural to the organisms. At the beginning of the paper, Noble and Greenberg remarked,

Space restriction markedly influences social situations; for instance, homosexuality, never observed in the field, was frequently recorded in crowded laboratory cages. In order to obtain a truer picture of the behavior of a typical saurian, we have used larger cages and have released the lizards within a spacious greenhouse. This procedure offered the advantages of controlled experimental tests while avoiding artificiality as much as possible. (Greenberg & Noble, 1944, p. 392)

In the experimental cages, Noble and Greenberg established two territories of similar quality (Greenberg & Noble, 1944, p. 428). They placed a male in each territory and released a female into a box in the center of the cage (Figure 8.1). The female could then “choose” one of the males by walking along a branch to his territory. Females, in general, were attracted to both the physical vigor with which the male displayed and the red color of his dewlap (a brightly colored flap of skin hanging beneath his chin). In order to distinguish the effects of coloration on female choice, they would cover the dewlap of one of the males with green paint, or glue it in place with colloidon. They repeated this sequence a number of times, but never with very consistent results—sometimes a male would not display properly, or would hide in the greenery when they released the female. Thus, much of the evidence they present in the paper is anecdotal. Yet despite their difficulties with the experimental design, they never removed the branches. Noble and Greenberg’s use of greenery in the experimental cages and the greenhouse to create a natural environment for the lizards illustrates the importance they accorded to a natural background in which the experimental behaviors should be measured.

Noble’s consistent framing of his research problems in terms of natural behavior is also illustrated in his research on the reproduction of painted box turtles. Field research began in 1936 at Jagger’s Swamp on Long Island. He had already conducted research on box turtles in his laboratory, but wanted to ensure that the behaviors he had observed in the laboratory could also be observed in a natural setting. When the observed behaviors corresponded, Noble concluded that these were behaviors

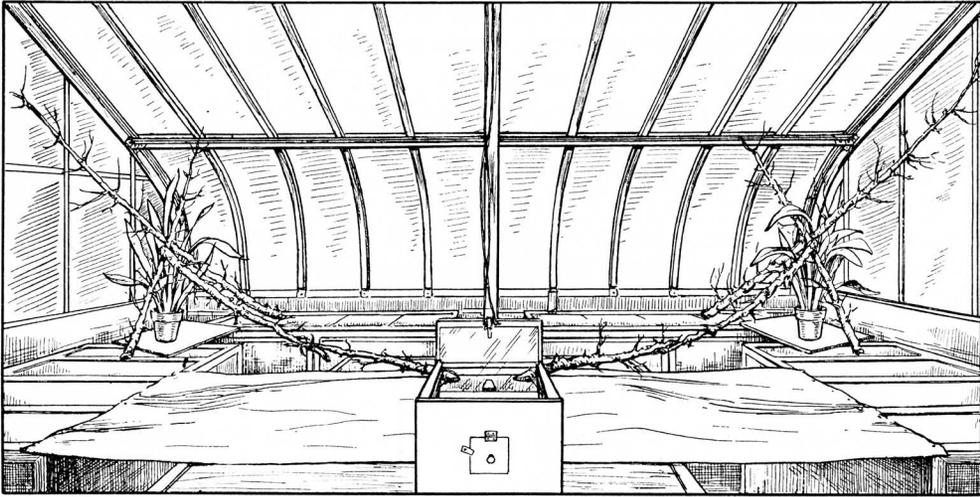


Figure 8.1. Experimental setup for mate-choice tests in *Anolis carolinensis* (Figure 16, Greenberg & Noble, 1944). Note the added greenery and branches that make the environment more natural from the organism's point of view. Figure from B. Greenberg & B. K. Noble, "Social Behavior of the American Chamelion (*Anolis carolinensis* voigt)," 1944, *Physiological Zoology*, 17, pp. 392–439, figure 16. Published by the University of Chicago Press. Reprinted with permission.

naturally exhibited by the turtles in both spaces. However, problems arose when the data from lab and field investigations conflicted. For example, in his laboratory Noble had recorded multiple observations of homosexual behavior (he used this term to describe the act of males "allowing" other males to mount and attempt to copulate with them). However, he did not observe a single ridden male at Jagger's Swamp: "our field work, however, rendered valueless these entire laboratory findings on the behavior of the ridden male, because there is no behavior of this kind among spotted turtles in their natural habitat."¹⁹ When his data gathered in the nature differed from his laboratory results, Noble made field observations trump what he saw in the laboratory. Only after data from the field was completed did Noble feel "thoroughly justified" in making conclusions about the normal breeding habits of the painted box turtles. In subsequent laboratory experiments, he further naturalized the laboratory surroundings by adding more leaves to act as ground cover, so that the females could bury themselves in it, and the males would have to find them in order to mate.

Throughout his manuscript on turtles, Noble made references to the congruence or difference of observed breeding patterns in the field and in the laboratory. In particular, he noted behaviors he deemed important in inducing the turtles to breed successfully in the laboratory, such as diurnal patterns of copulation and feeding habits. Additionally, Noble's notes indicate that the turtles emerged from the water and sunned themselves at similar times of day in the field and in the laboratory. As this was not an experimental factor in his experiments, it appears to be an independent confirmation of the naturalness of the turtles' behavior patterns. These field investigations confirmed the importance of visual cues as mating signals.²⁰

When Noble returned to his laboratory, he obtained his experimental subjects from his field sites. These organisms gathered "in the wild" stayed wild in Noble's view of his

laboratory, because the conditions of his experimental cages recreated their natural environment. When describing his laboratory in a funding letter to the National Research Council—Committee for Research on Problems of Sex (NRC-CRPS) in 1935, Noble called it “unique in having been built for the purposes of studying the behavior of a variety of wild forms under ideally controlled conditions.”²¹ In his view, Noble’s experimental aquaria and cages were sufficiently natural to ensure that the behaviors of these wild organisms were not induced by their new artificial environment. The next year, in a similar letter requesting a continuation of funding from the NRC-CRPS, he wrote, “considerable time was spent in the field this spring in order to prove that the social systems worked out with the caged animals actually exist in nature.”²²

Noble worked to make his laboratory space at the AMNH an extension of his work in the bogs and lakes surrounding New York. The laboratory facilities allowed him greater ability to identify and understand the reproductive behavior characteristic of many animal species. He then used this understanding to begin reconstructing the evolution of social behavior in vertebrates (Noble, 1939). For Noble, his Laboratory of Experimental Biology was a tool for uncovering the mechanisms of hormonal control of natural behavior, and yet it needed careful regulation to ensure that behaviors he observed were not due to the artificial laboratory environment.

LABORATORY TRANSITIONS: FROM EXPERIMENTAL BIOLOGY TO ANIMAL BEHAVIOR

Following Noble’s death in December of 1940, the continued existence of the Laboratory of Experimental Biology was uncertain without the force of his personality and focus of vision. The Museum suffered financially in the aftermath of the Great Depression, and at least one trustee urged the Museum to abandon the Department of Experimental Biology and donate the facilities to a nearby university. In 1941 alone, the trustee argued, this would represent a \$10,000 savings in operating costs.²³ Yet the laboratory survived. One of the lasting effects of the ambiguity with which the Museum regarded the laboratory was the need for its curators to justify their research in terms of the Museum’s goals.

When Noble died, the end of his laboratory seemed imminent. Roy Chapman Andrews, the director of the Museum, threatened to close the laboratory. Frank Ambrose Beach was placed temporarily in charge of the department (Beach, 1948, 1950, 1965). The future of the laboratory was complicated by extenuating circumstances; in the summer after Beach assumed his position (and while he was doing field research in the Rockies), all of the WPA workers at the Museum were dismissed. This drastically reduced the available workforce and resulted in the deaths of many of the organisms kept in the laboratory, as no staff remained to care for them.²⁴ When Andrews asked Beach how long it would take to finish the ongoing research, Beach interpreted Andrews’ question as a threat to terminate the research program, and refused to “roll over and play dead.” He wrote to Karl Lashley (his graduate advisor) and Robert M. Yerkes (NRC-CRPS director and Yale professor), entreating them to talk to Andrews.²⁵ W. Douglas Burden, a major contributor to the Museum and old friend of Noble’s, also wrote convincingly to the trustees.²⁶ Through their efforts, the department survived and Beach was promoted to curator.

Beach followed in Noble's footsteps by focusing the laboratory's resources on the experimental investigation of comparative animal behavior. Like Noble, Beach argued for including a variety of experimental organisms in one's animal behavior studies, though he did so for very different reasons. Beach was far from interested in questions of the phylogeny of behavior. Trained as a psychologist by Lashley, Beach wished to infuse the community of experimental psychologists with the comparative approach he had acquired at the Museum. He criticized American psychologists for their reliance upon the rat as their sole model organism (Beach, 1950). In his 1949 address to the Division of Experimental Psychology of the American Psychological Association, Beach asked, "Are we building a general science of behavior or merely a science of rat learning?" (Figure 8.2). Although he agreed that rat mazes were useful for understanding trial and error learning in humans, they were useless, he argued, for understanding the role of reasoning or insight in learning, that is, the "upper limits of intelligent behavior in mammals or other highly developed animals" (Beach, 1947a, 1947b). Beach argued that different animals were suited to different kinds of research questions—for example, he came to believe that dogs were the best organisms with which to model the reproductive behavior of humans (Dewsbury, 1989a; Levens, 2005). Whereas Noble included multiple species in his research to determine the evolutionary development

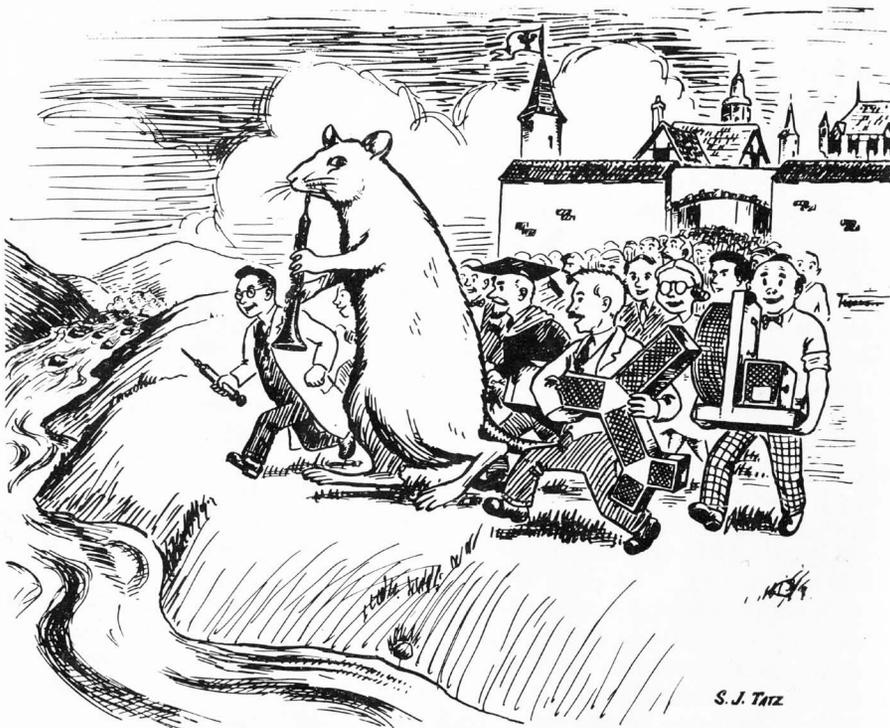


Figure 8.2. "Are we building a general science of behavior or merely a science of rat learning?" (Beach, 1950). Beach worried about the siren call of the Norway rat and its effect on American experimental psychologists. He advocated using a variety of animals to model different aspects of human behavior. Figure from F. A. Beach, "The Snark Was a Boojum," April 1950, *American Psychologist*, 5(4), pp. 115–124, figure 3. Published by the American Psychological Association. Reprinted with permission.

of social behavior, Beach included multiple species to model and understand different aspects of human behavior.

Before Beach left the department in 1946 for a faculty position in Psychology at Yale University’s School of Medicine, he renamed the laboratory. Thus, when Lester Aronson took Beach’s place as curator, it was as head of the Laboratory of Animal Behavior (Aronson, 1967; Aronson & Noble, 1944; Aronson, Tobach, Lerhman, & Rosenblatt, 1970).

The question of the laboratory’s fate again returned, and the burden of proving that the experimental study of animal behavior fit within the larger goals of the AMNH fell on Aronson’s shoulders. On the one hand, Aronson’s research agenda directly echoed Noble’s (rather than Beach’s) commitment to comparative study: “Our main goal is not to apply the answers to human behavior directly, but rather to improve our understanding of the evolution of behavior.”²⁷ On the other hand, Aronson’s experiments differed significantly from Noble’s emphasis on the pattern of behavioral development; Aronson sought to demonstrate how behavior could affect the process of evolution. The difference between Noble and Aronson’s attempts to unite behavior and evolution into a single explanatory framework reflected the necessity of hitting the moving target of contemporary evolutionary theory.

Aronson’s experiments on the role of behavior in determining the reproductive isolation of natural species fit neatly with the research agendas of curators from other departments at the AMNH. For example, E. Thomas Gilliard, curator of the department of ornithology, investigated the possible role of display and song in maintaining species isolation among the birds of paradise and bower birds of New Guinea (Gilliard, 1969). Additionally, Charles Bogert, Noble’s successor as curator of herpetology, published on the role of mating calls as an isolating mechanism in toads (Bogert, 1962). Despite the contrary claims of recent biologists (Coyne & Orr, 2004, p. 3), research on reproductive choice as an isolating mechanism formed one of the central questions in the study of animal behavior in the United States starting in the 1950s.

Thus, the early 1940s substantially transformed the study of animal behavior within an evolutionary context at the American Museum of Natural History, in terms of both personnel and methodology. It is to Aronson’s efforts at fitting the laboratory’s research into the agenda of the museum that we now turn.

REPRODUCTIVE BEHAVIOR AND ISOLATING MECHANISMS IN GUPPIES

Lester Aronson’s interest in reproductive behavior as a mechanism for speciation was piqued through a unique confluence of biologists working at and associated with the AMNH. From 1942 to 1968, the experimental tanks of the New York Aquarium were housed at the AMNH—first in the Animal Behavior greenhouse (in space vacated when most of the animals died after the *en masse* departure of WPA), and then on the sixth floor of the Whitney Memorial Wing (the ornithological section) of the Museum.²⁸ The curator of the New York Aquarium, Myron Gordon, brought with him a research focus on the genetics of cancer and coloration in fishes (Gordon, 1926; Gordon & Rosen, 1951). Charles Breder became curator of ichthyology in 1944, and maintained a research interest in the evolution of reproductive modes in fishes throughout his career (Breder, 1934; Breder & Coates, 1935; Breder & Rosen,

1966). When Eugenie Clark, a graduate student at New York University, came to the AMNH in 1948 to conduct her doctoral dissertation research, her research focused the attention of these men on the question of how reproductive behavior could affect the genetics of speciation in fishes.²⁹

Caryl Haskins and Edna Haskins, at New York's Union College, provided an additional spark to Aronson's curiosity about the role of female preference in the isolation of different species of guppies (Haskins & Haskins, 1949).³⁰ Because male and female guppies differ strikingly in morphology and behavior, Haskins and Haskins hoped to demonstrate that female discrimination played an important role in the maintenance of reproductive isolation. They were dismayed to find that female choice in mating partners was not important in keeping the species isolated (Haskins & Haskins, 1949, p. 162).

Haskins and Haskins' experiments are also illustrative of the continuing effort biologists put forth to modify artificial laboratory environments to mimic nature. They arranged a 15-gallon aquarium "to simulate as closely as possible a section of the lagoon environment. This arrangement was made with considerable care since it was deemed important to maintain the ecological situation as nearly intact as possible" (Haskins & Haskins, 1949, p. 164). Even in an aquarium, a natural environment was seen as ideal. Wherever possible, they also used wild-caught individuals.

When Aronson began collaborating with Gordon and Clark, they chose to investigate the importance of psychological isolating mechanisms in two species of Mexican guppies: the platyfish (*Platypoecilus maculatus*), and the swordtail (*Xiphophorus helleri*) (Figure 8.3). They chose to investigate reproductive isolation in guppies because they noted that although closely related species maintain their reproductive isolation in nature, guppies readily interbreed in aquaria. Additionally, guppies were interesting fishes to study because all species are internally fertilized and had been popular subjects for both scientific researchers and home aquarists for almost a century (Gosse, 1854).³¹

By 1950, Clark, Aronson, and Gordon argued that their research threw considerable light on species isolating mechanisms. Early investigations had revealed that although males initiated many copulations ("jabs"), only a small percentage of them lasted long enough to result in transmission of seminal fluid.³² Additionally, Clark's experiments with artificial insemination in these species indicated that even if behavioral isolating factors broke down, species isolation was not necessarily lost. If a female was inseminated by a male of a different species, as long as she was also mated by a male of her own species, competition between the sperm of the two males would lead to the species-appropriate sperm fertilizing her eggs. Thus, the complete reproductive isolation observed in nature, they suggested, was due to the cumulative effect of several partial isolating factors—psychological, ecological, morphological, and physiological.³³

In spirit, Clark, Aronson, and Gordon had continued Noble's investigations of sexual selection in fishes, while in practice their research differed considerably. They included 48 tables of data, summarizing over 1,700 10-minute observations—a far cry from Noble and Greenberg's anecdotal observations of mate choice. Clark had started recording all their observations by hand, using a separate mark for each kind of behavior, but found it necessary to take her eyes off the fish in order to jot down comments or to look at the clock. To solve this problem, they devised a typewriter/polygraph

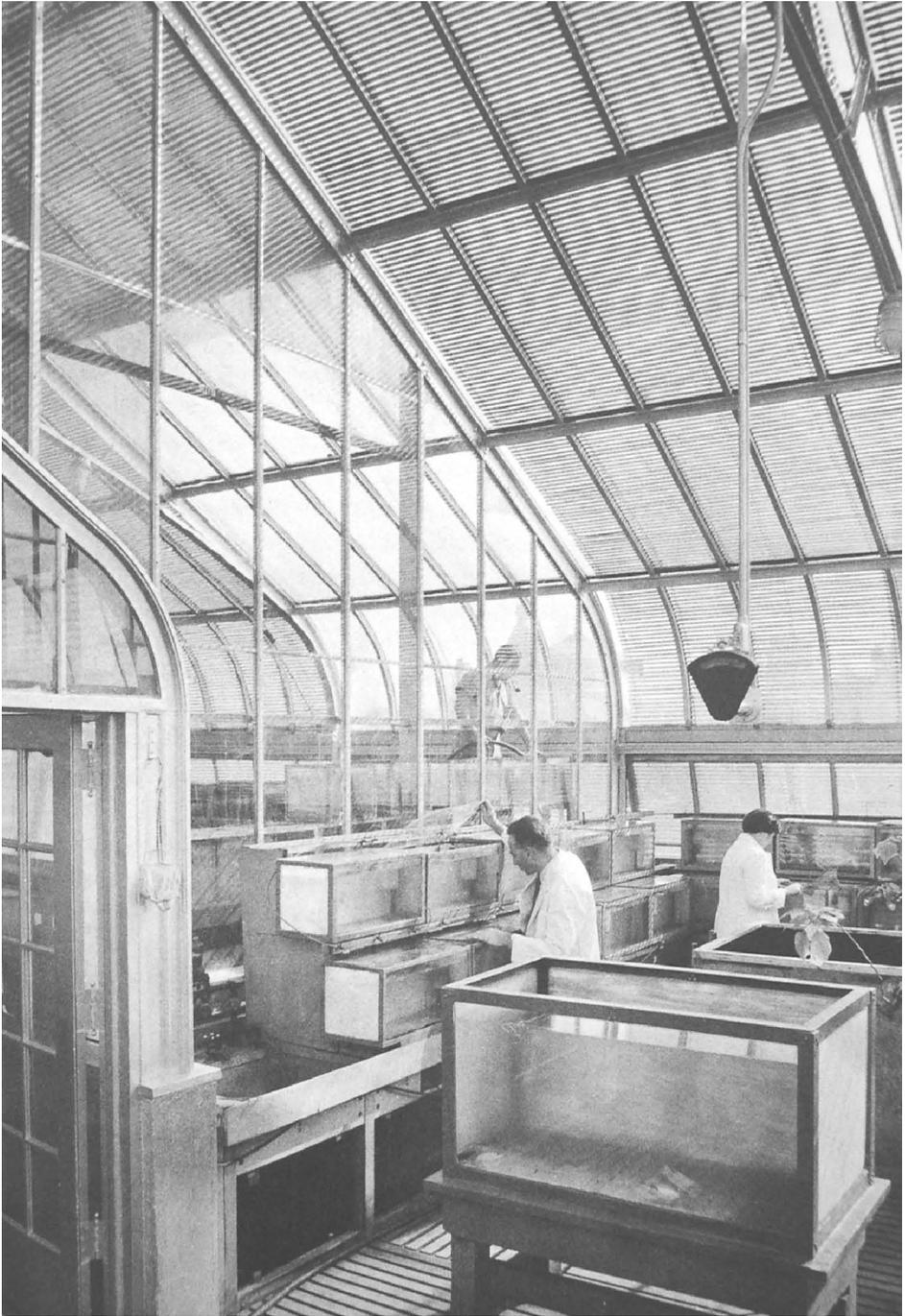


Figure 8.3. Aquaria on the roof of the AMNH. This greenhouse served as the research space in which Clark, Aronson, and Gordon carried out their experiments on reproductive isolation in guppies (Myers, 2002). AMNH Photographic Archives, Image #314414. © American Museum of Natural History.

machine that allowed them to hit particular keys for certain behaviors, increasing the efficiency of the observer markedly. Further, Clark, Aronson, and Gordon did not self-consciously attempt to emulate the natural environment in their experimental spaces in the same way as had Noble. They removed all plants from the observation tanks (although not from the fishes' normal tanks) because the plants sometimes obscured the courting fish from the view of the other fish delaying courtship activities, or prevented the researchers from observing what was happening in the tank.

Their experiments were designed to elucidate the processes of speciation by investigating the dynamics of reproductive isolation. To determine the role of mating behavior in maintaining reproductive isolation between these species of guppies, Clark, Aronson, and Gordon conducted "male-choice" tests. In a single aquarium, they placed one male and two females (one of the same species as the male, and one of a different species). They then recorded which female the male mated with. They probably chose to use "male-choice" tests, rather than "female-choice" tests because the latter experiments in guppies seemed technically infeasible. Males interrupt all attempts at courtship around them, with the result that it can be impossible to document a successful courtship attempt if more than one male is present in the tank (Tinbergen, 1974). As a result, working with guppies limited the range of possible experimental designs.

Clark, Aronson, and Gordon failed to find support for the importance of mate choice as an isolating mechanism in poeciliids; however, it was not from lack of interest in the topic. Why the sudden and dramatic shift in the relationship between behavior and evolution at the American Museum of Natural History? To address that question, we must turn our attention to the ongoing experiments of experimental population geneticists working with species of the fruit fly, *Drosophila*.

Drosophila BEHAVIOR AND EXPERIMENTAL POPULATION GENETICS

In an early grant application to the National Research Council's Committee for Research on Problems of Sex (the same institution that aided Noble's research during the Depression), Aronson couched their experiments on behavior as a mechanism for reproductive isolation in terms of recent research with experimental population genetics:

In cases where distinctly separate animal populations represented by related species have overlapping ranges and yet are physiologically capable of hybridization, students of population genetics have hypothesized psychological or behavioral factors as the isolating mechanism. Drs. Th. Dobzhansky, E. Mayr, and H. Spieth have been actively investigating the existence of psychological isolating mechanisms in overlapping populations of *Drosophila* . . . we have undertaken the investigation of this fundamental problem of evolution in two species of Mexican fishes, which have overlapping natural ranges, interbreed readily in captivity, but never hybridize under natural conditions.³⁴

When they published their results, Clark, Aronson, and Gordon comprehensively reviewed the literature concerning the role of the male and female in sexual isolation in both fishes and *Drosophila*, grounding their study of sexual selection in recent experimental population genetics (Clarke, Aronson, & Gordon, 1954).

Historians of science generally accord the greatest credit for changing the study of the evolution of natural populations of animals in the United States of the 1940s to two men—Theodosius Dobzhansky and Ernst Mayr (Ayala & Fitch, 1997; Mayr & Provine, 1980). In 1927, Dobzhansky left the Soviet Union to work in Thomas Hunt Morgan’s *Drosophila* laboratory. Exactly one decade later, Dobzhansky published *Genetics and the Origin of Species* (Dobzhansky, 1937). In his book, Dobzhansky made available in readily accessible prose the conclusions of the mathematical population geneticists of the 1920s and early 1930s—small genetic changes in a population could, over time, account for large physical differences between populations. In 1940, Dobzhansky returned to Columbia University, less than three miles from the AMNH in New York City. Mayr, a Bavarian by birth, emigrated to the United States in 1931, when he accepted a post as curator of the Rothschild ornithological collection at the American Museum of Natural History. Mayr subsequently published *Systematics and the Origin of Species* (1942), in which he extended Dobzhansky’s conclusions to suggest that such processes operating within a single species (microevolution) were functionally equivalent to the processes governing speciation, when one population split into two populations (macroevolution). Together, these two books provided Americans with a new research focus on understanding the processes regulating animal evolution in natural populations, and new ways of defining animal species.³⁵

Dobzhansky and Mayr thought of species in very similar ways, as self-defining groups in which members of the population mated only with other members of the same population. In *Genetics and the Origin of Species*, Dobzhansky defined “species as that stage of evolutionary process, ‘at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding’” (Dobzhansky, 1937, p. 312; Dobzhansky, 1935). Mayr modified this definition only slightly. “Species are groups of actually (or potentially) interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr, 1942, p. 120). Their definitions of species as interbreeding populations generated two new questions. First, how did species become reproductively isolated? Second, was it possible to use the degree of sexual isolation between populations as a way of diagnosing species? Searching for answers to these questions formed important components of the research program of experimental population genetics in the 1950s.

Dobzhansky identified two broad categories of mechanisms that could potentially act to isolate populations genetically—geographical and physiological (Dobzhansky, 1937, pp. 231–232). Physiological isolating mechanisms were broadly defined, and included everything from ecological specializations, to morphological and behavioral differences between species, to physical incompatibility of the gametes. The relative importance of these physiological isolating mechanisms was a subject of debate among biologists in subsequent decades (Baker, 2005), and was a question Clark, Aronson, and Gordon sought to answer with their experiments in the Laboratory of Animal Behavior at the AMNH.

In 1944, Dobzhansky and Mayr had also proposed an experimental method for quantifying the degree of reproductive isolation between two species of *Drosophila* (Dobzhansky, 1944).³⁶ In a laboratory, they presented males of one species with females of the same species and females from a different species. They defined the degree of reproductive isolation as the proportion of males that chose mates of the

correct species—the fewer “mistakes” made by the male, the greater the proportion of intraspecific matings, and the more isolated the two populations. Although the male-choice model later met with criticism, it became the first standard methodology for determining if two populations were sexually isolated from each other (for example, Merrell, 1950). It was also the same male-choice experimental design cited and used by Clark, Aronson, and Gordon in their experiments.

In a 1954 retrospective about the utility of *Drosophila* for biological research, geneticist Curt Stern waxed poetic: “When with foresight and luck, Morgan selected this species for studies on heredity . . . the significance of the results was not due to *Drosophila* as a unique organism, but as a representative of all organisms” (Stern, 1954, p. 214). Yet at the AMNH, it was curatorial interest in animals that could not be relied upon to behave similarly in laboratory and field environments that drove their interest in measuring mechanisms of reproductive isolation in a variety of other species. Additionally, the issue of reproductive isolating mechanisms provided an opportunity for curators interested in animal behavior to contribute to the new research focus on the process of evolution.

CONCLUSION

In the United States from the 1930s to the 1950s, the study of animal behavior within an evolutionary context underwent drastic methodological and theoretical changes. In the 1930s, Gladwyn Kingsley Noble designed experiments to help him reconstruct an evolutionary history of behavior, mapping the increasing complexity of social and sexual behavior in animals. He hoped his descriptive analyses of individual courtship would uncover the zoological antecedents of human behavior. In the 1950s, Lester Aronson designed experiments that emphasized massive quantities of experimental data, and examined the outcome of hundreds of mating pairs of fishes. His collaborators hoped to prove that males of one species could differentiate between females of their own species and females of other species.

These changes can best be described as simultaneous shifts in experimental design, theoretical framework, and underlying assumptions about the relationship of animal behavior and evolution. In terms of experimental design, Noble employed narrative explanations of mating behavior in a few individuals, whereas Aronson, Eugenie Clark, and Myron Gordon collected quantified statistical data of the outcomes of matings. In terms of theoretical framework, the contrast of Noble and Aronson’s research reveals a trend away from uncovering the evolution of behavior, toward understanding the process of evolutionary change. To Noble in the 1930s, behavior was a biological trait shaped by evolution; Aronson’s research group, on the other hand, investigated behavior as a mechanism of evolution. Underlying these two research programs were different theoretical approaches to synthesizing research on animal behavior and evolutionary theory. Whereas Noble incorporated evolution into an animal behavior framework, Aronson incorporated animal behavior into an evolutionary framework. These shifts reflected biologists’ changing convictions on how to best study evolution.

During this same period, however, “the experimental organism from the naturalist’s point of view,” changed very little. Curators of the Laboratory of Experimental Biology (Laboratory of Animal Behavior) fully recognized the potential influence of

a laboratory environment on the expression of normal reproductive behavior in their experimental subjects. Noble sought to minimize these effects by creating laboratory conditions that reproduced the most critical natural conditions of his experimental organisms. Aronson and his collaborators took advantage of the discrepancy between natural and laboratory reproductive behaviors of guppies to investigate the relative importance of barriers to hybridization in maintaining reproductive isolation. Aronson's work of the 1950s should be seen as a combination of an interest in laboratory investigations of social behavior and a desire to study the behavior of natural organisms within an evolutionary context.³⁷ From the 1930s to the 1950s, zoologists at the AMNH with an interest in animal behavior sought to understand and control for the ways in which the laboratory might induce artificial behaviors.

The history of the Laboratory of Animal Behavior at the AMNH also provides us with a microcosm in which to understand the history of research on behavior and evolution in the United States more generally. Even after the mathematization of evolutionary theory in the 1920s and early 1930s, biologists interested in the evolution of behavior continued to conceive of evolution as a primarily linear process by which they could map the increasing complexity of behavior in animals. Noble certainly envisioned evolution as the history of what had happened to behavior over millions of years, and used extant species as placeholders for the behavior of animal antecedents of human behavior. Yet as the study of evolution in the United States shifted from mapping the evolution of particular traits or behaviors to studying mechanisms of the evolutionary process, it became increasingly unacceptable for experimentalists to study the progressive evolution of behavior, as Noble had envisioned. Instead, Clark, Aronson, and Gordon's investigations of the role of behavior as an isolating mechanism in fish were modeled explicitly on similar experiments in *Drosophila* designed to elucidate mechanisms of speciation. The populational approach to research on the genetics of *Drosophila* was remarkable for its pervasive tendency to establish what should qualify as an appropriate evolutionary question, even in the realm of behavior. In the 1950s, citing the direct influence of Dobzhansky and Mayr's research on their experimental questions, Aronson instead began to investigate evolution as a process, and behavior as a possible mechanism for evolutionary change in contemporaneous nature.

The effect of the research program promoted by Theodosius Dobzhansky and Ernst Mayr on the study of mating behavior was profound. Experimental design, methodologies, questions, and theoretical underpinnings all changed in a very short period of time. The research program of the evolutionary synthesis thus served to define and restrict how biologists investigated behavior as a function of evolutionary theory, even in the 1950s.

NOTES

1. Transcript of the Evolutionary Synthesis Conference, May 23, 1974, Evening Session, p. 4. Ernst Mayr, *Evolutionary Synthesis Papers*, B/M451t, Folder 1.7. American Philosophical Society, Manuscript Collections, Philadelphia, PA.
2. The rise of ethology in continental Europe and the U.K. provides an interesting counterpoint to the history of animal behavior in the U.S.A. (Burkhardt, 2005).
3. Note the lack of behavior as a topic within Mayr and Provine (1980), and Coyne and Orr (2005).

4. "Notes for the Trustees' Meeting," n.d., but attached to April 28, 1933, letter. Departmental folder, Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, American Museum of Natural History (hereafter AMNH).
5. Przibram's Institute for Experimental Biology was also known as "the Sorcerers' Institute" and burned in the Russian bombardment of Vienna in 1945. Arthur Zitrin, 1988. Arthur Zitrin folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
6. AMNH Annual Reports to the Trustees, 1928–1933. Departmental folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
7. For a detailed account of the construction costs of the laboratory, see the "Departmental" section of Noble's archived papers at the Herpetology Department of the AMNH. The financial records for institutional expenditures were also published as the *Annual Report of the Trustees for the Year* until 1938, when they stopped including annual departmental expenditures.
8. "The Laboratory of Experimental Biology of the American Museum of Natural History," sent to Mr. Burden and the other trustees, May 19, 1933. W. Douglas Burden folder. Gladwyn Kingsley Noble Papers. Department of Herpetology AMNH.
9. Arthur Zitrin folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
10. "The Laboratory of Experimental Biology of the American Museum of Natural History," sent to Mr. Burden, May 19, 1933, p. 7. W. Douglas Burden folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
11. Noble, "History of the Laboratory of Experimental Biology, American Museum of Natural History," Departmental folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH; and Mitman and Burkhardt (1991, p. 175) have interpreted this stance as a change from his original intention, yet Noble's subsequent research was based both in the field and in the laboratory. I believe he was disappointed merely because he had to scale back the number of questions he was investigating, not because he had to shift his focus away from the intersection of naturalist studies and experimentation.
12. W. K. Gregory, Address to the AMNH at Noble's memorial. December 19, 1940. Noble biographical file, AMNH Central Archives. Gregory expressed similar sentiments in his formal obituaries of Noble (Gregory, 1941a, 1941b).
13. It is worth noting that Noble had difficulty obtaining funding for field research for his behavioral work. At the time of his death, he had completed the laboratory, but not the fieldwork for this species.
14. #IA-1 Biographical folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH. See also Myers (2002); historian Gregg Mitman has written extensively on Noble's commitment to reaching a popular audience through film and radio (Mitman, 1993, 1999).
15. Although the term "organismal biologist" does not come into widespread use until the 1960s, the intent with which it was used then—to specify a holistic approach to the biology of an organism—works equally well for Noble (Mitman & Burkhardt, 1991, p. 175).
16. Noble's work, in particular, mirrors similar work by Dobzhansky to demonstrate to naturalists that genetic studies of populations could inform their studies of nature (Dobzhansky, 1937).
17. "Much of the material utilized in the research work of the Department is secured in the local field. This has necessitated numerous trips to Long Island and New Jersey for fish, frogs, turtles and birds." Noble to Dr. Roy Chapman Andrews on the Department of Experimental Biology's Annual Report 1938, dated January 14, 1939. Experimental Biology Papers, Departmental Files, Special Collections, AMNH.
18. Noble to Dr. Roy Chapman Andrews on the Department of Experimental Biology's Annual Report 1938, dated January 14, 1939. Experimental Biology Papers, Departmental Files, Special Collections, AMNH.

19. “Turtle Research,” unpublished manuscript. This research was interrupted by Noble’s death, and was never finished nor published. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
20. “Turtle Research,” unpublished manuscript. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
21. Noble to Professor Robert M. Yerkes, Chairman, NRC—CRPS, dated April 8, 1935. NRC Folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
22. Noble to Professor Robert M. Yerkes, July 17, 1936. NRC Folder. Gladwyn Kingsley Noble Papers. Department of Herpetology Archives, AMNH.
23. Burden to Trubee Davison (fellow trustee of the AMNH), January 13, 1941. Beach folder 1196.1. Departmental Files, Animal Behavior Department, Research Library, Special Collections, AMNH.
24. Charles Bogert to Beach, August 7, 1941. Frank A. Beach folder. Charles M. Bogert Papers. Department of Herpetology Archives, AMNH.
25. Beach to Andrews, February 1, 1941. 1196.1. Departmental Files, Animal Behavior Department, Research Library, Special Collections, AMNH.
26. Burden was a long-time friend and advocate of Noble’s work. He collaborated with him on several film projects and greatly admired Noble’s research at the Museum. As a trustee with an excellent fund-raising record, he wielded considerable influence at the Museum until he retired from the Board in 1962. W. Douglas Burden Folders, Gladwyn Kingsley Noble Papers and Charles M. Bogert Papers. Department of Herpetology Archives, AMNH. See also Mitman (1993, 1999).
27. Memorandum from Aronson to Mr. Wayne M. Faunce June 29, 1949. 1196.1. Departmental Files, Animal Behavior Department, Research Library, Special Collections, AMNH.
28. Charles M. Breder to Robert Cushman Murphy, April 25, 1946; Murphy’s reply May 23, 1946; Charles M. Breder folder, Charles Cushman Murphy Papers, B M957, Manuscript Collection, American Philosophical Society.
29. After leaving the AMNH, Eugenie Clark quickly entered the public limelight as a beautiful woman ichthyologist and authority on sharks, popularly known as “Shark Lady.” According to Clark’s Web site, her *Lady and a Spear* (1953) was a Book-of-the-Month Club selection, was translated into seven languages, and was encoded into Braille.
30. Haskins and Haskins thank Dr. Dobzhansky “for suggesting the approach to the problem outlined herewith and for much critical help and encouragement, and to Dr. Myron Gordon, Dr. Lester Aronson, and Miss Eugenie Clark for reading the manuscript and offering most helpful suggestions and criticism” (Haskins & Haskins, 1949, p. 168).
31. For more information, see historian Lynn Nyhart’s work in progress on the early history of the aquarium trade in Europe and the United States.
32. Letter to George W. Corner, Chairman, NRC—CRPS. March 12, 1949. Grantees: Aronson LR, NRC-CRPS Papers, 1946–1952. National Research Council, Division of Medical Sciences, Committee for Research in Problems of Sex, 1920–1965 (NRC: DIV: MED: CRPS).
33. Letter to George W. Corner, Chairman, NRC—CRPS. March 13, 1950. NRC-CRPS Papers, 1946–1952. Grantees: Aronson LR, NRC-CRPS Papers, 1946–1952. National Research Council, Division of Medical Sciences, Committee for Research in Problems of Sex, 1920–1965 (NRC: DIV: MED: CRPS).
34. Letter to George W. Corner, Chairman, NRC—CRPS. March 12, 1949. Grantees: Aronson LR, NRC-CRPS Papers, 1946–1952. National Research Council, Division of Medical Sciences, Committee for Research in Problems of Sex, 1920–1965 (NRC: DIV: MED: CRPS).
35. The training Dobzhansky and Mayr received while in Russia and Germany, respectively, proved crucial to the methods and theoretical framework they transported to the U.S. (Adams, 1968, 1970; Haffer, 1994, 2001).
36. Dobzhansky and Mayr’s experimental method was a quantified version of the method developed by Alfred Sturtevant over a decade earlier (Sturtevant, 1915).

37. Which J. P. Scott, Theodore Schneirla (of the Department of Animal Behavior at the AMNH), and the entire Committee for the Study of Animal Societies Under Natural Conditions (founded in 1946), agreed was best understood through field studies of behavior (Scott, 1950).

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